Range Expansion of the Rainbow Lorikeet (Trichoglossus moluccanus) under Environmental Change

by

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Candidate's Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author's knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Rosie Bella Stockton Date: 29/05/2025

Rainbow Lorikeet Pair Image: Wikimedia Commons

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Abstract

The expansion of species' ranges in response to environmental change is a growing topic of interest. While most studies on species' responses to global change have focused on range contractions, this thesis examines the underexplored phenomenon of native species expanding into new environments. Numerous anecdotal reports have noted range expansion in some native parrot species in eastern Australia. This aligns with observational evidence of several species' ability to exploit novel environmental conditions found in highly modified landscapes. However, range expansion in native parrots has not been robustly quantified. My thesis examines the Rainbow Lorikeet (*Trichoglossus moluccanus*), as a case study of this broader ecological phenomenon. Originally found in north-eastern Queensland, the Rainbow Lorikeet is a large-brained, competitive nectivore, characterised by its mobility and adaptability. This study provides a detailed quantification of the Rainbow Lorikeet's rapid natural range expansion across eastern Australia. It then examines bioclimatic and anthropogenic factors associated with this expansion. Key results included positive associations between colonisation and urban and agricultural land use. Further, my results support anecdotal reports that the Rainbow Lorikeet has expanded into environmental conditions that it rarely occupied in its historical distribution, suggestive of ecological niche expansion. These findings support my hypothesis that land use changes, rather than climatic drivers alone under environmental change, are a primary driver of expansion. My results underscored the need for systematic efforts to track distributional changes across a wider range of species to understand emerging patterns of species responses to climate change and land use practises. The major expansion of the Rainbow Lorikeet is likely to have a broad range of implications for other native bird species, including competition for food resources and limited tree hollows. Overall, my thesis provides a robust case study of a species thriving under anthropogenic pressures, providing insights into range and niche shifts under environmental change.

Table Of Contents

List of Figures

List of Tables

Table 3. Model table showing contributions of predictor variables to the top-ranked Rainbow Lorikeet multinomial model. The 'never occupied' classification was used as a reference baseline. Coefficient estimates indicate the magnitude of effect on the top 'colonised' model, with higher values indicative of a stronger effect/contribution to the model. P values shown, with $p < 0.05$ indicating significance in bold. Standard Error (SE) indicates the statistical accuracy of an estimate.

List of Acronyms/Abbreviations

AIC: Akaike Information Criterion

ΔAIC: Delta AIC

AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c) package in R

BAM: Conditions that determine species' distribution - Biotic, Abiotic, Movement

CAR: Conditional Auto-regressive

DOM: Dynamic Occupancy Modelling

MCMC: Markov Chain Monte–Carlo

SF: Simple Features package in R

Glossary

Anthropogenic: caused by human activity

Bioclimatic: relating to climate

Colonisation: sustained expansion in areas that species previously did not occupy

Endemic: native to and found only within a specific geographic area

Environmental Space: the multidimensional set of conditions that impacts species ecology

Environmental Change: human-driven ongoing changes in environmental conditions

Ecological niche: the multidimensional set of conditions that define a species' distribution. The fundamental niche being the set of conditions in which persistence is possible, limited by genetics and physiological barriers. The realised niche being the set of conditions that are occupied after abiotic limitations on the fundamental niche

Invasive: species that have experienced human-assisted dispersal into previously inaccessible areas

Invasion: range expansion facilitated by human-mediated means

Nectarivore: a species which feeds on sugar-rich nectar produced by flowering flora

Niche shift: a change (any direction) in fundamental or realised niche of a species

Parsimonious: a parsimonious model explains the data well with the fewest parameters possible

Passerine: birds of the Passeriformes order, or perching birds

Phylogenetic: relating to a species evolutionary traits

Range: geographic distribution of a species

Range shift: change (any direction) in a species range

Range Expansion: growth in a species range

Niche Breadth: the diversity of resources and conditions used or tolerated by a species

Macroecology: an area of ecology which focusses on broad-scale ecological patterns

Raster: spatially explicit dataset in which each cell represents a geographic location

Taxa: taxonomic grouping

Chapter 1: Introduction

1.1 Context

Globally, the distribution of numerous species is rapidly shifting (Rubenstein et al. 2023, Lawlor et al. 2024). Changes in species distributions are driven by a broad range of factors associated with environmental change (Lawlor et al. 2024). Understanding changes in species distributions and their associated environmental conditions is essential for informing species conservation in the face of rapid, anthropogenic global change (Britnell et al. 2023). As species' geographical distribution patterns change, the conditions they live within, or their ecological niche, also changes (Liu et al. 2025). Species ecological niches can change over time and across environmental space, in response to changes in their environment (Pearman et al. 2008). My thesis will explore range and niche change in an expanding eastern Australian parrot species.

Patterns of range shifts globally are predominantly negative, with distribution and niche contractions common (Scheele et al. 2023). Due to intensifying environmental threats across landscapes like climate change and invasive species, which interact with pre-existing pressures like vegetation clearing, agriculture and altered disturbance regimes, many Australian native species are declining in response to environmental change (Lindenmayer et al. 2010, Lustenhouwer and Parker 2022). In Australia, research on the effects of environmental change on species distributions has largely focussed on this negative influence, and the contractions of declining species under these pressures has been widely studied (Legge et al. 2023, Lawlor et al. 2024).

Some species are also expanding their ranges and ecological niches under environmental change (Essl et al. 2019, Sjödin et al. 2018). Invasive species are perhaps the most significant example of this (Dukes and Mooney 1999). Introduced species often find success due to possessing strong generalist and competitive traits, especially in areas that lack their natural predators (Dukes and Mooney 1999, Romanuk et al. 2009). On a smaller scale, human-facilitated range expansion has also occurred in some species, where individuals have been moved successfully to areas outside their historical distribution (Vitousek et al. 1997). Another group of species are those that are experiencing gradual range expansion along their range boundaries (Angert et al. 2011, Rubenstein et al. 2023). However, there is a gap in understanding of how environmental change may contribute to species expansion occurring naturally (Essl et al. 2019). Understanding environmental and anthropogenic factors associated with range expansions can help inform our understanding of when and where they are most likely to occur (Liu et al. 2025).

My thesis will examine the phenomenon of native species expansion under environmental change, focussing on Australian native bird species, with the Rainbow Lorikeet (T*richoglossus moluccanus),*

an adaptable native parrot, as a representative case study. This highly mobile species has abundant occurrence records, enabling occupancy modelling and analysis of associated covariates to explore environmental characteristics of recently colonised areas. More broadly, bird species are extremely responsive to changes in the environment and can act as bioindicators for ecological change (Bino et al. 2021). Birds are among the most easily observed and widely studied taxa globally, and analysing this wealth of occurrence information provides an opportunity for understanding how species respond to change (Mekonen 2017).

1.2 Case Study: Rainbow Lorikeet Expansion

Since the 1960s, the Rainbow Lorikeet's distribution has been reported to be expanding, including in Western Australia, Tasmania, and across eastern Australia (Chapman 2005, Robinson et al. 2020, Cobden et al. 2021). Observational research has centred on the lorikeet's ability to exploit modified urban park landscapes and anthropogenic food resources like artificial feeding stations and the availability of fruiting and flowering plants (Smith and Lill 2008, Davis et al. 2012).

The species' arrival into Tasmania and Western Australia may have been largely a result of human-assisted dispersal through aviary releases (Cobden et al. 2021, Chapman 2005). Further research is needed to determine whether these expansions represent natural colonisations or are primarily the result of human-facilitated introductions, which may not be reflective of dynamics driven by environmental change. In contrast, whilst human introductions may have played some part in local expansion into some areas throughout eastern Australia, it is likely that the expansion of Rainbow Lorikeets in these regions occurred via natural dispersal and colonisation (Shukuroglou and Mccarthy 2006, Smith and Lill 2008). As such, my thesis will focus on range expansion in eastern mainland Australian populations under environmental change through a macroecological lens.

1.3 Thesis aims and hypothesis

My thesis examines how environmental change may contribute to Rainbow Lorikeet expansion. To do this, I focus on:

- Quantifying the range expansion of the Rainbow Lorikeet.
- The key drivers/predictors that facilitate Rainbow Lorikeet expansion over time.

I hypothesise that native Australian parrot species like Rainbow Lorikeets are rapidly expanding in geographic distribution throughout eastern Australia under environmental change and that this is largely driven by land use change, rather than climatic influences.

1.4 Thesis structure

Chapter 1 – Overview of project research, including aims and hypothesis.

Chapter 2 – Review and synthesis of relevant literature.

Chapter 3 – Methods.

Chapter 4 – Results.

Chapter 5 – Discussion of key findings, implications, and limitations of results.

Chapter 6 – Concluding remarks.

Chapter 2: Literature Review

This chapter provides background and synthesises key literature surrounding ecological niche theory, range quantification methods, and eastern Australian native bird expansion, with a focus on the Rainbow Lorikeet.

2.1 Environmental Change in the Anthropocene

Environmental change is driving a significant restructuring of life on Earth (Boivin et al. 2016). The Anthropocene refers to the current period of Earth's history as one where humans have, and continue to have, a marked impact on ecosystems and natural processes (Seddon et al. 2016). The global population is forecasted to exceed nine billion by 2050 (IPBES 2020) and anthropogenic influences are a critical driver of the current sixth mass extinction event (Barnosky et al. 2011). As climate change intensifies, global average temperatures are increasing, extreme weather events are becoming more frequent, and human influence on the environment continues to escalate (IPCC 2023). These impacts amplify one another and are reshaping ecological communities globally (Malhi et al. 2020 Wang et al. 2023).

In this thesis, 'environmental change' refers to human-driven, significant, ongoing changes in environmental conditions. Synonyms in the literature include 'global change' and 'global environmental change'. Environmental change impacts are prevalent at regional, ecosystem and species scales and include climate change, habitat loss, and introduced species invasions (Lindenmayer et al. 2024). One of the most significant challenges met by ecologists today is interrogating the effects of, and species responses to, rapid environmental change (Angert et al. 2011). Investigating changes in species occurrences at different scales provides an opportunity to develop an understanding of the key mechanisms that determine how species respond to global change (Scheele et al. 2023). However, interrogating driving forces of broad-scale ecological change is complex, as cascading evolutionary and ecological processes can shape observed patterns (Brown and Maurer 1989).

2.2 Species Distribution Shifts under Environmental change

2.2.1 Defining Distribution

Shifts in species distribution are a common response to environmental change (Lawlor et al. 2024). A species distribution encompasses its geographic range and distribution patterns are shaped by interactions within ecological communities and environmental conditions (Wisz et al. 2013). These interacting factors can be separated into three categories: those that meet its biotic needs ("B"), abiotic

needs (“A”), and its capacity for movement (“M”) (Soberon and Peterson 2005). Abiotic conditions are non-living environmental factors like temperature, precipitation, light or humidity (Wingfield 2013). Biotic conditions are the living components like predation, competition, intraspecific interaction, and resource availability (Fraser et al. 2021). Lastly, movement is the physical ability of species to disperse into areas where they may occupy optimal conditions (Peterson and Soberon 2012). This categorisation of factors determining species distributions has been termed the “BAM” 3-factor conceptual framework (Peterson and Soberon 2012, Soberon and Peterson 2005, Figure 1). BAM describes species distribution as the intersection of these three factors, which together may determine if the species can be found at a certain locality (Feng et al. 2024, Figure 1).

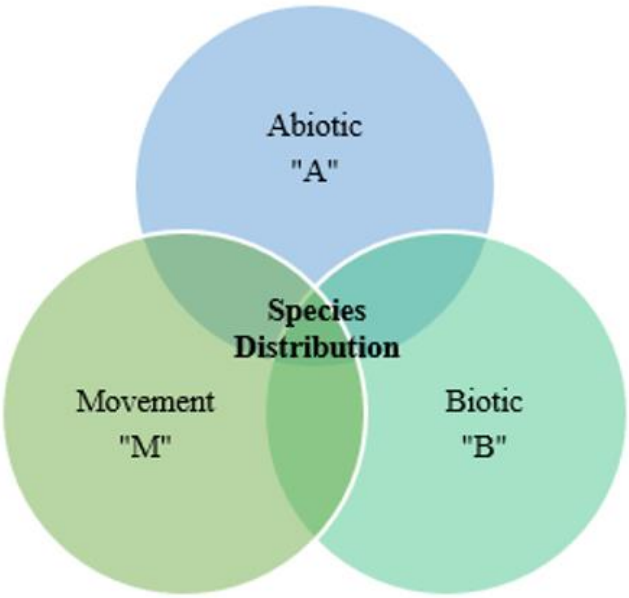

Figure 1. 3-factor conceptual framework of conditions that determine species distribution or “BAM”. B for Biotically suitable area, A for Abiotically suitable area and M for Movement ability (reproduced from Peterson and Soberon 2012).

2.2.2 Environmental Change Driven Distribution Shifts

Environmental change is driving unprecedented and rapid distribution shifts in species globally (Lawlor et al. 2024). In response to changing climates and environmental variables, species may shift, contract, or expand their occupied ranges (Wingfield et al. 2015). Range expansion involves species dispersal into and occupation of areas, which were not historically occupied; range contraction refers to a decline in areas of occupation (Lawlor et al. 2024). Interrogating mechanisms behind these distribution shifts provides insight into species’ preferred conditions and if these have changed in response to environmental changes (Scheele et al. 2017).

Lawlor et al. (2024) explored how distribution shifts are influenced by climatic and non-climatic drivers. This intersects with the "BAM" conceptual model (Figure 1), where climatic drivers align with abiotic factors, and non-climatic drivers with biotic factors. Climatic or abiotic driven shifts involve climatic variables like precipitation or temperature changes. As the climate changes, many species distribution patterns are moving in poleward and upslope directions, occupying areas that may have been too cold or wet for them to persist previously, and no longer occupying areas where they were historically present as these areas warm (Pecl et al. 2017, Rubenstein et al. 2023).

Non-climatic or biotic mechanisms also contribute to species distributions under environmental change. One of the most significant of these is habitat modification, including loss and fragmentation (Lawlor et al. 2024). This is especially pertinent under rapid urbanisation and land clearing, which creates dispersal barriers, and contributes to the presence of other threats like human disturbance and invasive species prevalence (Legge et al. 2023). Another example is changes in food resource availability, which can have a strong influence on species distribution patterns (Lawlor et al. 2024). Changes in biotic interactions between species also contributes to species redistributions, which manifests in processes like predation, competition and mutualism (Lawlor et al. 2024). Finally, phenological changes, like the modified timing of biological factors including vegetation flowering time frames, the breeding rate of species, or the mortality rate of offspring, impact how species interact with their environment and help shape range dynamics (Lawlor et al. 2024). Climatic and non-climatic mechanisms can result in species altering their range to track conditions that will allow them to persist (Tingley et al. 2009).

2.2.3 Contraction as the Norm under Environmental Change

The last century of human-dominated ecosystems has witnessed species range shifts that often reflect common response patterns. Although directions of distribution shifts are highly variable across species, ecological changes throughout history have largely followed shifts in climate (Lawlor et al. 2024). Overwhelmingly, mechanisms behind these shifts noted previously mean that contemporary range shifts occurring under current environmental change are predominantly negative (Legge et al. 2023).

Marked by a high proportion of endemic species, Australia has experienced extinction rates that exceed those of most other countries (Legge et al. 2023, Woinarski et al. 2015). Due to key environmental threats likes invasive species and climate change impacts, and pre-existing pressures like vegetation clearing, agriculture and altered fire and disturbance regimes, range contraction is occurring across numerous taxa in response to environmental changes (Lindenmayer et al. 2010, Lustenhouwer and Parker 2022). Range contraction patterns are projected to continue in Australia and globally (Bradshaw et al. 2021). Therefore, research on the effect of environmental change on species distribution has largely focussed on this negative influence, and the contractions of declining species under these pressures has been widely studied (Kannan and James 2009, Rubenstein et al. 2023).

2.2.4 Expansion under Environmental Change

Responses to environmental change are not always representative of the trajectory of specific species and there are exceptions to the overwhelming pattern of range and niche contraction. A significant anomaly to these patterns is where species ranges are expanding in response to environmental changes (Lawlor et al. 2024). Expanding species include cases of human-facilitated range expansion, the intentional or unintentional movement of species to new areas where they occupy geographic areas outside their historical range, which may encompass environmental conditions analogous or different to in their native range (Weiss-Lehman and Shaw 2022).

Globally, invasive species encompass many expanding species and are widely recognised as a key driver of biodiversity loss (Didham et al. 2005, Duke and Mooney 1999). Vernacular like 'introduced', 'non-native', and 'exotic' terms are used to describe species that occur outside of their native range, mostly due to human activities (Liu et al. 2025). Invasive species often find success due to possessing strong generalist and competitive traits, especially in areas that lack their natural predators (Romanuk et al. 2009, Doherty et al. 2016). Once established, their rapid expansion is facilitated through outcompeting native species, as they can generally tolerate a wide range of conditions (Romanuk et al. 2009). A key example of invasive species in Australia are introduced mesopredators (Moseby et al. 2012). The European Red Fox (*Vulpes vulpes*) and Domestic Cat (*Felis cattus*) now persist across the majority of Australia and are strongly associated with the rapid declines and extinction in native mammals (Mahon 2009, Moseby et al. 2012).

The terms and concepts of 'expansion', 'invasion', and 'colonisation' are often used interchangeably and overlap in meaning (Soto et al. 2024). Within the context of my thesis, expansion refers to growth in species' range or niche, colonisation refers to sustained expansion in areas that species previously did not occupy, and invasion refers to expansion facilitated by human-mediated means. In other words, expanding species refers to native species that are increasing in range, and invasive species refers to species that have experienced human-assisted dispersal into previously inaccessible areas.

Colonisation processes usually start with introduction as the catalyst and are associated with non-native species (Han et al. 2024, Soto et al. 2024). However, native species already present can naturally expand and colonise new areas (Han et al. 2024). In cases where natives are causing ecological harm to other native communities, native species can exhibit invasive behaviour and be considered a form of 'biological invasion' (Carey et al. 2012) and can be classed as pests (Beggs 2020, Chapman 2005).

The difference between human-assisted invasions and natural colonisation or expansion is important. Indeed, it is often unclear to what extent urbanisation and human influence impact colonisation processes at species range edges (Hoffman and Courchamp 2016). Emphasis should be placed on the understanding of the processes and mechanisms involved and any associated impacts, rather than how these phenomena are defined (Hoffman and Courchamp 2016). Although invasive species colonisation is well researched, understanding of how environmental change may contribute to native species expansions is not (Han et al. 2024). Understanding species' capacity to shift their ranges holds significant implications for insights into niche dynamics, future community structures, and extinction and biological invasion risk assessments (Angert et al. 2011).

2.3 Range and Niche Shift Analyses

"Given the central role of the environment in many ecological and evolutionary hypotheses, why is biodiversity studied predominantly using geographical locations as units of analyses?"
(Graham et al. 2025:1)

2.3.1 What is a Species' Ecological Niche?

An ecological niche can be defined as the multidimensional set of environmental conditions that characterise a species' geographic distribution (Scheele et al. 2017). The species' niche concept is used to identify the ecological and biotic factors that determine species distributions and explains why a species' actual geographic range is often smaller than its potential range (Holt 2009, McInerny and Etienne 2012, Peterson et al. 2015). The ecological niche concept explores how conditions impact distribution at a species level.

There are two key terms that are central to research on species niche dynamics; the fundamental niche and the realised niche. The fundamental niche is the set of abiotic conditions a species could potentially occupy in the absence of biotic limitations or dispersal barriers, determined by its genetic and physiological traits (Pearman et al. 2008, Soberon 2007). The realised niche is a subset of the fundamental niche that encompasses the set of conditions the species occupies once biotic interactions and dispersal barriers are accounted for (Pearman et al. 2008). Examining conditions of expanded areas may build understanding of species niche change, and how species respond to environmental mechanisms (Scheele et al. 2023). As species ranges and geographical distribution patterns change, the conditions they live within, or their ecological niche, also typically changes (Guisan et al. 2014).

2.3.2 Distinction between Range Shifts and Niche Shifts

Species distribution change, seen in range contractions or expansions, is usually associated with a concurrent change in a species realised ecological niche (Scheele et al. 2017). Quantifying range expansion can promote understanding of whether the environmental conditions in newly occupied areas differ from those in the historical range. Distribution shifts, growth or contraction can happen without ecological niche change, if there is movement into areas where conditions are analogous to historically occupied areas, as the characteristics of the distribution remains unchanged. However, if the conditions in areas of recent expansion are not analogous to those in the species' historical range, this may indicate a shift or expansion in the species' ecological niche (Broennimann et al. 2007, Guisan et al. 2014).

Generally, species responses to environmental change have been studied spatially, predominantly by measuring geographic distribution (Graham et al. 2025). Quantifying changes in niche conditions associated with range expansions can help identify key drivers of distribution shifts and the specific conditions contributing to expansion or contraction. This thesis will examine range expansion from a distributional lens, investigating environmental variables associated with expansion to gain understanding of potential niche change.

2.3.3 Investigating Range Shifts using Dynamic Occupancy Models

Dynamic occupancy modelling (DOM) is an emerging method to quantify species range shifts (Kelleher et al. 2024). This method analyses how species occupancy of sites changes over time, focussing on colonisation or extirpation dynamics, and can account for sampling efforts and detection errors to infer range niche shifts (Kelleher et al. 2024). DOM works by estimating the probability that a species occupies a site in each time period, while accounting for the possibility that it may not be detected even if present (Kelleher et al. 2024, Tingley and Beissinger 2009). It does this by modelling two processes separately: the true occupancy state (presence or absence) and the detection process, using repeated observations and covariates like survey effort to improve accuracy (Bled et al. 2013, Mackenzie et al. 2003). Hence, DOMs are highly effective at partitioning detection error from true occupancy changes, allowing for the estimation of colonisation over time and large geographic space (Bled et al. 2013, Mackenzie et al. 2003). Moreover, by incorporating temporal autocorrelation, these models provide critical insights into species' dynamic responses to environmental pressures (Kelleher et al. 2024).

Quantifying range expansion and isolating colonisation processes is difficult, especially when considering flawed occurrence detection and ongoing distributional shifts (Kelleher et al. 2024). Traditionally, the underlying data that DOMs require is relatively limited (Tingley and Beissinger 2009). A limitation of these methods is that they do not distinguish between areas of high and low suitability associated with species occurrence records (Graham et al. 2025). This means that while offering strong

range quantification abilities, DOM alone can sometimes fail to predict the full extent of niche expansion or invasion (Kelleher et a. 2024). Ongoing assessment of species range change through space and time is becoming increasingly relevant as environmental change escalates (Guisan et al. 2014). DOMs may enable robust inferences about range dynamics, modelling distribution change and covariate parameters that drive distributional change (Kery et al. 2013, Tingley and Beissinger 2009).

2.4 Birds as Focal Species for Investigating Range Expansion

2.4.1 Birds as a Case Study of Range Dynamics

Birds provide a robust case study of range dynamics. Some taxa are more likely than others to see range and niche expansion (Sjödin et al. 2018). This is generally the case for those that possess strong dispersal abilities, and the capacity for adaptation to new environmental conditions within short time scales (Duckworth 2008, Wingfield et al. 2015). These traits allow birds to access resources in different areas, shifting their ranges to follow emerging opportunities (Wingfield et al. 2015). Birds are highly mobile, and their distribution is largely resource driven, meaning that understanding how species respond to varied resource availability across landscapes is essential for predicting their distribution (Webb et al. 2019). Birds provide an excellent case study for understanding niche and range changes, as they are diverse in their responses to disturbance, with some species experiencing significant colonisation success like select parrot species, while others are being pushed to the brink of extinction like many songbird species (Wingfield et al. 2015). Furthermore, many bird species are readily observed, with numerous occurrence records, enabling analyses to investigate changes in distribution and niche characteristics through time (Zurrell 2017).

2.4.2 Expanding Birds in Australia

Australia is home to more native bird species than most other countries (Garnett 2023). Whilst many of these birds are experiencing ongoing population decline driven by environmental change (Bennett et al. 2024), there is significant anecdotal evidence that multiple eastern Australian native bird species are undergoing range expansion (Campbell et al. 2022, Davis et al. 2012). Evidence suggests that birds are capable of persisting, and sometimes effectively colonizing areas in cities and towns globally (Campbell et al. 2022). Several bird species have found success in exploiting novel environments in areas that they may not have historically occupied prior to environmental change (Wingfield et al. 2015). Recently, significant expansion has been observed in key Australian songbird *(Passeriformes*) species like the Noisy Miner (*Manorina melanocephala)* and the Australian Magpie (*Gymnorhina tibicen)* (Beggs 2020, Toon et al. 2007). Notable expansion has also been anecdotally reported in the migratory cuckoo species, like the Eastern Koel in eastern Australia (*Eudynamys orientalis*) (Holland 2021). However, my thesis will place emphasis on the substantial expansion patterns seen in the parrot order (*Psittaciformes*) across

eastern Australia (Figure 2). This includes cockatoo species (*Cacatuidae*) like the Galah (*Eolophus roseicapilla*), the Little Corella (*Cacatua sanguinea*), and the Sulphur Crested Cockatoo *(Cacatua galerita)* (Polley and Lill 2020, Engelhard et al. 2015, Spenneman 2023). This phenomenon also includes examples from the true parrot family (*Psittaculidae*), like the Musk Lorikeet (*Glossopsitta concinna*) and my focal species, the Rainbow Lorikeet (*Trichoglossus moluccanus*) (Davis et al. 2012).

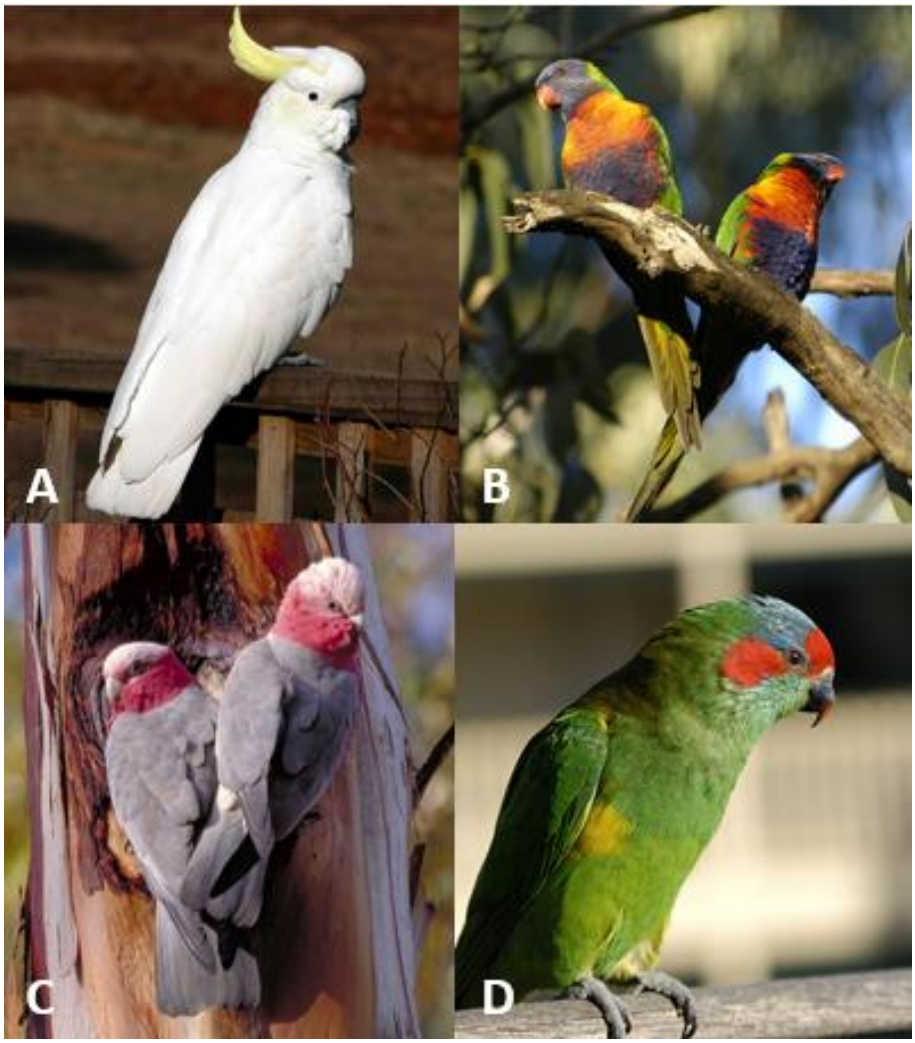

Figure 2. Examples of observed expanding native Australian parrots; A - Sulphur-crested Cockatoo (*Cacatua galerita)*, B - Rainbow Lorikeet (*Trichoglossus moluccanus)*, C - Galahs (*Eolophus roseicapill*a), and D - Musk Lorikeet (*Glossopsitta concinna*). *Photos from Canberra Birds (2025), taken by Peter Fullagar, James Rolevink, and Geoffrey Dabb.*

2.4.3 Native Parrot Case Studies

Use of novel environments is particularly prominent in parrots (Figure 2) (Davis et al. 2012, Rogers and Kark 2021). Australian parrots in some cases are extremely effective adapters, with many

establishing wild populations outside of their historical ranges, particularly across urban landscapes (Davis et al. 2012). Lorikeet and cockatoo species may have found success within increasingly urbanised landscapes through harnessing artificial water sources, non-native trees, and exotic food resources (Bennett et al. 2024). For some of these expanding species, escaped or deliberately-released cage birds are also thought to have contributed to their establishment in areas outside their native range (Vall-Llosera and Cassey 2017).

Expanding parrot species include those that historically occurred in urban locations but have increased in abundance in recent decades with developing landscape modification (Burgin and Saunders 2007, Campbell et al. 2022). Sulphur-Crested Cockatoos (*Cacatua galerita*), are now widely distributed across northern and eastern mainland Australia and Tasmania (Birdlife Australia 2024a). There is evidence that their adaptability to urban environments has driven expansion in niche space use, particularly in urban foraging behaviour, with observed changes in range use among populations in response to human activity (Fehlmann et al. 2024). Fehlmann and colleagues (2024) found that green urban areas like parklands were used for roosting, while more densely built-up areas were utilized when food availability was higher. The Musk Lorikeet (*Glossopsitta concinna*) is another species that has expanded its range significantly within urban areas of eastern Australia. Smith and Lill (2008) contend that increases in these environments' spatial heterogeneity have allowed these species to adapt to diverse conditions. For example, at the time of their study, 74% of the Musk Lorikeet feeding records in Melbourne were associated with non-native plant species (Smith and Lill 2008).

There are also parrot species that once predominantly occurred in inland regions but have expanded coastward into urbanised areas. Historically restricted to remote areas of far-north South Australia, the Little Corella (*Cacatua sanguinea*) has expanded into cities since the 1960s and are now common in coastal and urban areas (Australian Museum 2022). This successful expansion is largely attributed to the species' adaptability, and facilitated by land clearing, increased water availability, and access to agricultural food sources (Davis et al. 2012). Another example is the Galah (*Eolophus roseicapill*a). Once confined to inland plains beyond the Great Divide in eastern Australia, north of the Flinders Ranges in South Australia, and north of the Mulga–Eucalypt line in Western Australia, the Galah has expanded significantly across the broader Australian landscape (Birdlife Australia 2024b). Galahs have colonised much of Australia, and can persist in all types of open country, from arid agricultural plains to coastal urban areas including those on islands (Menkhorst et al. 2017). This is thought to be largely driven by habitat changes such as coastal woodland clearing for agriculture (Birdlife Australia 2024b). This growth has been further supported by increased food and water availability in human-modified environments, with escaped aviary birds also contributing to population increases (Engelhard et al. 2015). These examples of parrots use of fragmented and fluctuating urban resources illustrate how a range of species have expanded and shifted their ranges in response to urbanisation, expanding from

seeded and unseeded urban distributions. I seek to build on this foundation of anecdotal reports and local scale studies to quantify range wide changes in the distribution of Rainbow Lorikeets in eastern Australia.

2.5 Common Traits of Expanding Native Parrot Species

Understanding similarities amongst range expanding species may shed light on the traits and ecological variables that contribute to their colonisation success (Liu et al. 2025). Advantageous species traits can be linked to increases in the prevalence of key birds in Australian communities (Campbell et al. 2022). The relationship between native Australian parrot species evolved traits and colonisation is complicated, but the possession of select phylogenetic and behavioural traits may contribute significantly to expansion success (Campbell et al. 2022, Royle and Donner 2021, Roger and Kark 2021).

2.5.1 Generalism

Species with generalist traits are expected to perform best under rapid environmental change (Callaghan et al. 2019). Across landscapes, there is usually the presence of both specialist and generalist species (Buchi and Vuilleumier 2014). Specialist species typically show restricted environmental tolerances, meaning their traits are well adapted to certain habitats, whilst generalist species show wider environmental tolerances, and often persist in multiple and more variable habitat types (Buchi and Vuilleumier 2014, Romanuk et al. 2009). In comparison to generalist species, specialist species persist within a narrower set of environmental conditions, so often show less adaptable responses to environmental changes (Avidad et al. 2025). Generalist traits that make species more adaptable to change often are associated with larger niche breadth, and broad niche breadth has been linked to "urban tolerance" in bird species (Campbell et al. 2022, Callaghan et al. 2019).

Generalist traits include both phenotypical and life history traits. Phenotypical advantages of expanding eastern Australian species include that they are typically larger-brained (Campbell et al. 2022). There is evidence that larger brain size may be connected to persistence in novel environments, as it may be associated with advanced behaviour, learning and stress response especially under modified conditions, compared to their smaller brained counterparts (Patankar et al. 2021, Sayol et al. 2018). Many birds with observed range expansions also show similarities in body mass, wing shape and plumage, which may bolster important mechanisms like dispersal and camouflage (Zurrel 2017). However, more research is needed to disentangle how important different phenotypical traits are to species persistence and expansion success (Campbell et al. 2022). Life history traits include rapid dispersal and reproduction rates, which are important determinants of colonisation success (Angert et al. 2011). There is also evidence that changes in food resources and interspecies interactions in urban areas have seen

changes in bird life history traits, with some species showing extended breeding duration, and increased clutch and brood sizes under environmental change (Pantaker et al. 2021). These advantageous life history traits help species compensate for predation or mortality that is particularly pertinent in urban areas due to factors like invasive carnivore species and collisions with infrastructure and vehicles (Patankar et al. 2021). As urbanisation continues globally, generalist species, characterised by their broader ecological niches and high capacity to tolerate diverse environments, are increasingly likely to inhabit areas in closer proximity to humans (Liu et al. 2025).

2.5.2 Competition

Many successful eastern Australian parrot species also share common behavioural traits that contribute to their success. All examples of expanding native parrots live in large, social and predominantly territorial groups (Menkhorst et al. 2017, Figure 2). This enables them to build and establish strong, adaptable populations, protected by numbers (Campbell et al. 2022). Many of these species also show gregarious behaviour, feeding and flocking with other similar species, bolstering these strong social colonies (Menkhorst et al. 2017). These species also present aggressive and vocal behaviour, especially towards other birds, making them strong competitors and in some cases pushing other birds out of areas they have colonised (Crates et al. 2018, Campbell et al. 2022). Patankar and colleagues (2021) contend that within the same species of birds, those found in urban areas compared to those in rural locations exhibit increased call frequency and volume, and increased competitive behaviour. However, the role of human activity outweighs that of any phylogenetic characteristic in determining species establishment (Royle and Donner 2021).

2.5.3 Exploitation of Urban, Parkland and Agricultural Areas

Australia has a population of over 27 million people, and this is projected to reach around 40 million by 2070 (ABS 2024). Nearly 90% of this population reside within 50 kilometres of the coastline, and 73% live in major cities (DCCEEW 2021). This places Australia among the most highly urbanised nations globally (Rogers and Kark 2021). As populations grow in Australia, so too do urban areas, fringes, and recreational parklands (DCCEEW 2021). Urbanisation is the process of land clearing and modification for the purpose of residential infrastructure (Campbell et al. 2022). Urbanisation is a leading cause of biodiversity declines and contributes significantly to species decline through processes like habitat loss, degradation, and fragmentation, creating ideal conditions for invasive species (Kirkpatrick et al. 2023). It gives rise to light and noise pollution, as well as landscape composition and nutrient changes (Kirkpatrick et al. 2023). However, there is evidence that several eastern Australian avian species are persisting and thriving in increasingly urban areas (Campbell et al. 2022, Burgin and Saunders 2007). Understanding the traits that enable species to thrive in urban areas can demonstrate

biodiversity patterns within rapidly urbanising landscapes (Callaghan et al. 2019). Most areas of eastern Australian suburbia contain small patches of natural habitats, parks, sporting fields and residential gardens, which provide environmental conditions that a range of species can utilise as habitat (Kirkpatrick et al. 2023). Thus, as urban areas expand, some species manage to persist in these areas by utilising both natural and anthropogenic resources (Johnson and Munshi-South 2017).

There is evidence that land clearing, access agricultural crop food sources, increased water sources, and increased ornamental flowering vegetation in urban parks and gardens, have contributed to native parrot species' expansion and colonisation of areas not analogous to their historical ranges (Shukuroglou and Mccarthy 2006, Chapman 2005). The aesthetic appeal of their colourful plumage and their confident nature also means that many of these birds are regularly fed by humans in some areas, reinforcing their occurrence in many cases (Rogers and Kark 2021, Gailbraith et al. 2015). Galbraith and colleagues (2015) argue that bird feeding is a critical factor that influences bird community structure in urban areas and can contribute to shaping patterns of species dominance.

Urban areas provide a unique opportunity to study species' ability to expand and exploit resources that were perhaps not naturally occurring in their natural ranges (Fehlmann et al. 2024). Literature suggests that ecological generalisation like dispersal ability and reproductive rate, strong competitive behavioural traits, as well as the presence of advantageous conditions in urban areas, often mean that these species are more likely to persist in new regions under environmental change. Analyses of species traits that contribute to native parrot success is important to understanding their colonisation success, and these traits are observationally well-known. However, knowledge surrounding quantified conditions of their range expansions remains limited.

2.6 Absence of Systematic Quantification

Research efforts across urban dwelling bird species in Australia are largely inadequate and not representative (Campbell et al. 2022, Burgin and Saunders 2007). There is evidence that despite their expansion and colonisation of new areas being anecdotally well-known, there is poor research understanding of these species' persistence and success in urban and other areas (Campbell et al. 2022, Burgin and Saunders 2007). While there is documentation surrounding these expansions, this literature is largely observational and tends to focus on species' behaviour and local scale habitat use in novel environments. Despite extensive research, I could not locate any research articles that systematically quantify range and niche expansion in native Australian parrot species.

Using the search term of the species common or scientific name and “expansion” or “niche shift” in Google Scholar and Web of Science illustrates the lack of systematic research in many cases of parrot expansion (Table 1).

Table 1. Number of results found in Web of Science, for observed expanding eastern Australian Parrot Species.

Species	***Anecdotal/Observational***	***Empirical/Quantification***
Rainbow Lorikeet *(Trichoglossus moluccanus)*	3	0
Musk Lorikeet *(Glossopsitta concinna)*	1	0
Sulphur Crested Cockatoo *(Cacatua galerita)*	1	0
Little Corella ***(****Cacatua sanguinea)*	0	0
Galah *(Eolophus roseicapilla)*	0	1

2.7 Rainbow Lorikeets: as a Model Example

“Birds are responding to the way we have changed our environment. The most numerous birds reported in the Aussie Bird Count are the ones that adapt better to these changes.”
Sean Dooley 2025 (Birdlife Australia 2024c, para 4)

The 2024 Australian Bird Count had Rainbow Lorikeets (*Trichoglossus moluccanus)* as the most frequently recorded species, topping the list for the eleventh year in a row (Birdlife Australia 2024c). It was the most recorded bird in New South Wales, South Australia, Victoria, Western Australia and Queensland. This citizen science count provides a window into how Australian birds are responding to modified habitats, especially in urban areas, as they are the most surveyed (Birdlife Australia 2024c).

The Rainbow Lorikeet is one of the most significant examples of native bird expansion in Australia. It occupies most types of forest, plain, and woodland ecosystems across coastal and subcoastal eastern Australia (Menkhorst et al. 2017). Its vibrant colours and adaptability make it a common sight in urban areas, feeding on nectar and fruits in city parks and gardens (Birdlife Australia 2017). The Rainbow Lorikeet boasts loud rolling calls in noisy aggressive flocks, with sizable communal roosts sometimes numbering in the thousands (Menkhorst et al. 2017). In eastern Australia, these gregarious flocks can

sometimes include other parrot species like the Musk (*Glossopsitta concinna)* or Little *(Glossopsitta pusilla)* Lorikeets (Chapman 2005).

Robinson et al. (2020) have described the species as invasive in Western Australia and Tasmania, where it has adapted well to urban conditions, becoming dominant to the detriment of other species. It is believed that the species' introduction into Tasmania and Western Australia was largely a result of aviary releases, so the characteristics of its expansion into these likely represent a human-facilitated introduction and expansion, more analogous to an invasive species, rather than expanding native species (Cobden et al. 2021). Therefore, my thesis will focus on Rainbow Lorikeets expansion in eastern mainland Australia, to explore range expansion in the absence of human-assisted dispersal. There are increasing observations of Rainbow Lorikeets across major urban centres in mainland Australia, including Melbourne, Sydney, Adelaide, and Brisbane (Chapman 2005, Davis et al. 2015, Sazima and Sazima 2024). Smith and Lill (2008) studied its distributional expansion across Melbourne and argue that it is largely attributed to the lorikeets' ability to exploit modified park landscapes, especially for anthropogenic food resources like artificial feeding stations, and the availability of prolific fruiting and flowering plants. In urban areas like Sydney, Rainbow Lorikeets dominate feeding stations, excluding other nectarivores (Stanford and Lill 2008). The species' ability to follow flowering and fruiting events over large areas is a key trait linked to its success in novel environments, that co-existing species do not always possess (Stanford and Lill 2008). Rainbow Lorikeets were described by the Canberra Ornithology Group in 2000 as "not common in Canberra" and that records from Canberra were either "wild birds moving through or aviary escapees" (COG 2000:8). Ecological definitions of what constitutes 'wild' have changed vastly and have continued to do so since then (Delancey 2012). However, what is certain is that Rainbow Lorikeets are now a common sight in Canberra (Canberra Birds 2017, Figure 3).

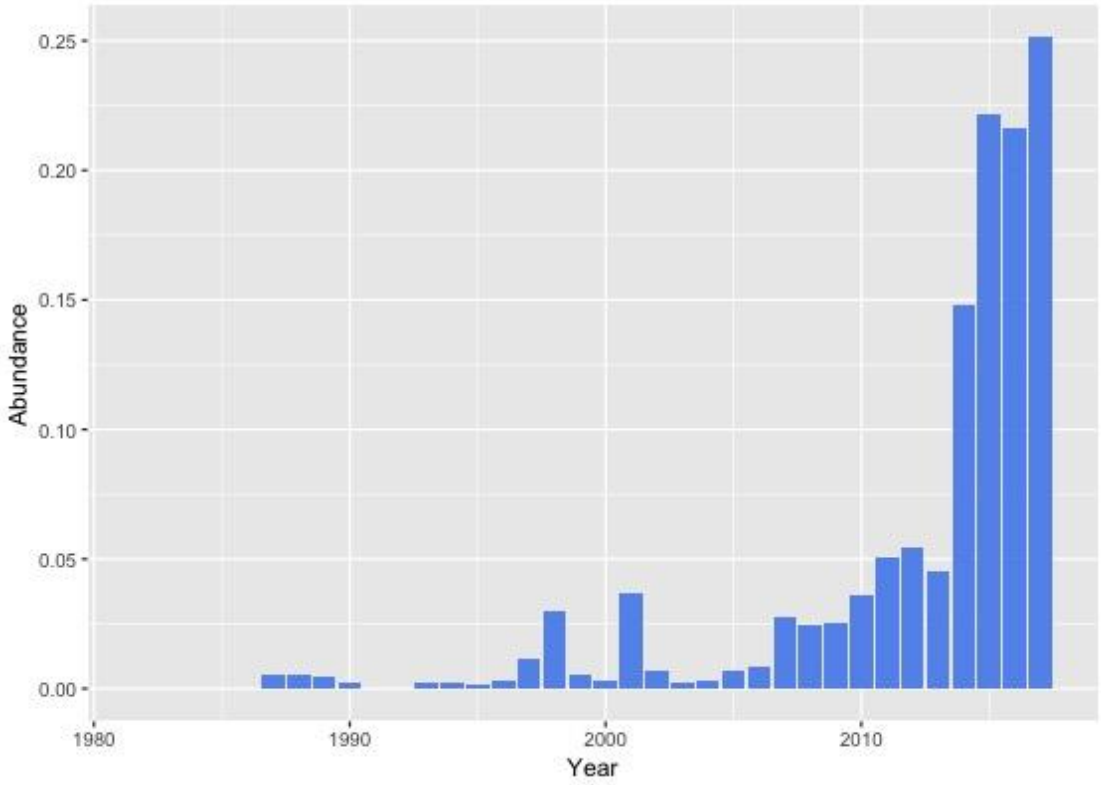

Figure 3. Canberra Birds (2017) graph showing the relative abundance of Rainbow Lorikeets in Canberra between 1982 and 2017. Abundance represents the average number of Rainbow Lorikeets per survey.

Due to key traits such as high mobility, generalised feeding and breeding requirements, and the capacity to rapidly adapt to and exploit new resources, Rainbow Lorikeets have been particularly successful in expanding their range under environmental change (Chapman 2005). As one of Australia's most widely recognised parrot species, the Rainbow Lorikeet provides a representative case through which the broader phenomenon of native parrots expanding their ecological niche in response to environmental change can be examined. This case offers valuable insights into the ecological and behavioural mechanisms driving range shifts in urbanising landscapes.

2.8 Conclusion

As ecological redistributions occur across landscapes globally, research focussed on understanding range shifts is timely (Graham et al. 2025, Lawlor et al. 2024). This chapter aimed to provide an overview of species range shifts and the expansion of select eastern Australian native birds. The findings from recent literature emphasise that key native bird species, particularly from the parrot family, are expanding their ranges under environmental change. There is evidence that these expansions are predominantly related to advantageous behavioural and life history traits compared to competitor co-existing species, facilitated by their use of anthropogenically modified environments. However, there

is a lack of current research that systematically quantifies range and niche expansions for these species. For effective conservation, we must seek to understand how environmental change is shaping species distributions, and what this may mean for species future ranges and landscape compositions (Scheele et al. 2023).

Chapter 3: Methodology

3.1 Software and Data Sources

All data collation and analyses were conducted using the statistical programming language *R* version 4.4.3 (2024), employing various packages to facilitate analysis and modelling (described below). Rainbow Lorikeet occurrence records were sourced from the Atlas of Living Australia's *galah* package (2025), along with all records for both passerine and non-passerine birds. Range shapefiles for the Rainbow and Red-collared Lorikeets (*Trichoglossus rubritorquis*) — a sister-species in northern Australia that has only recently been split from Rainbow Lorikeets — were sourced from Birdlife Australia. Bioclimatic variable data were sourced from WorldClim, downloaded at a 2.5 minute resolution (Fick and Hijmans 2017). The key bioclimatic variables from Worldclim used were Annual Mean Temperature in degrees Celsius (BIO1), Annual Precipitation in millimetres (BIO12), and Elevation in metres (Fick and Hijmans 2017). A national land use data set was sourced from the Australian Government's Department of Agriculture, Fisheries and Forestry (DAFF), giving a land use categorisation at a 250 m grid cell resolution for the entire Australian mainland (DAFF 2024).

3.2 Occurrence Records

I obtained 250,251 records of Rainbow Lorikeets from the Atlas of Living Australia, after removing those for which geographic coordinates and the year of recording were not available. These records were further limited to those intersecting with the Australian mainland and within a 300 km buffer of the species' range, as defined by BirdLife Australia. This excludes recently established populations in the Perth region of Western Australia and in Tasmania, for which the source of colonists are deliberate releases or escaped caged birds. Records likely to be those of the Red-collared Lorikeet, west of Cape York Peninsula in northern Australia, were removed by cutting all records north of -21.5 degrees latitude and east of 140.5 degrees longitude, guided by BirdLife Australia's range polygon for Red-collared Lorikeets. A total of 227,962 records of Rainbow Lorikeets were retained for assessing the species' range expansion in eastern Australia (Figure 4).

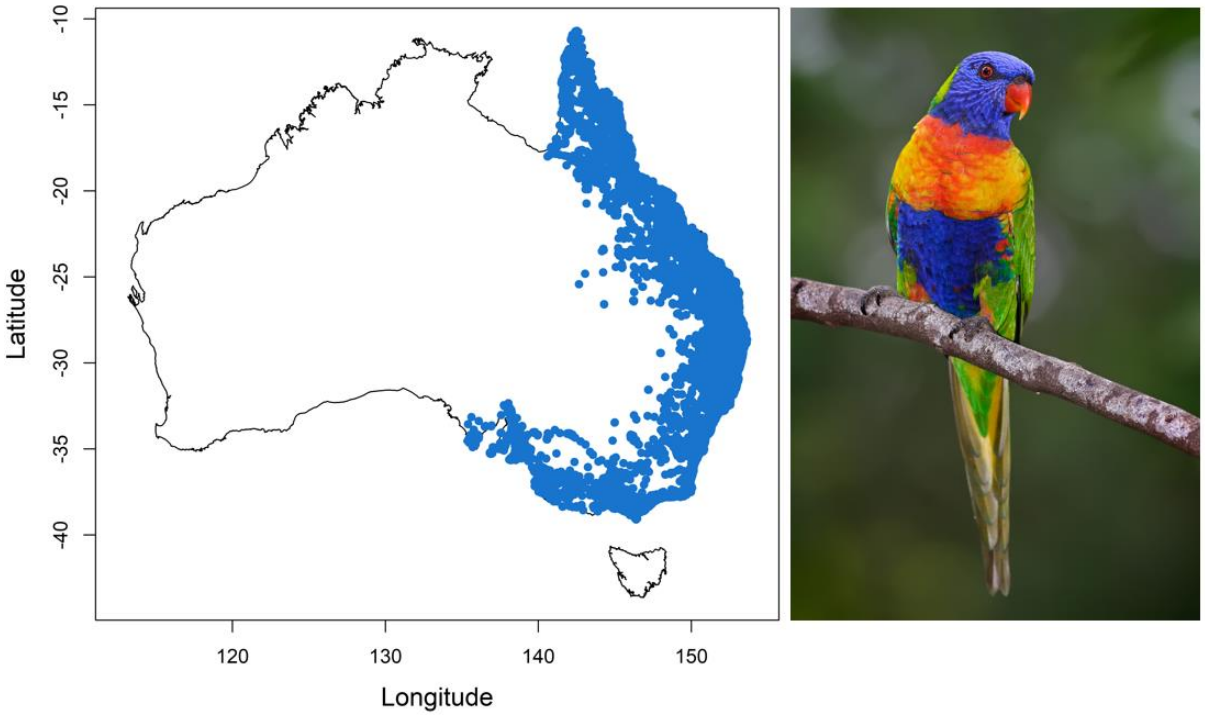

Figure 4. Distribution records for the Rainbow Lorikeet used to explore the species' range expansion in eastern Australia. All records derive from the Atlas of Living Australia. Lorikeet image: Flagstaffotos / Wikimedia

3.3 Study Area

To define the study area for analysis, I first generated a raster covering mainland Australia with a resolution of 0.36° (approximately 40 km), with the aid of the *terra* package (Hijmans 2025). This resolution aimed to represent areas capable of supporting populations of Rainbow Lorikeet populations, in which case colonisation could reasonably be assumed to produce self-supporting populations with relatively low chances of extirpation following initial immigration.

To limit the study area to only those areas either known to be occupied by Rainbow Lorikeets in eastern Australia, or areas within dispersal distance, I used the *sf* package (Pebesma et al. 2018), to create a polygon spanning a 100-kilometre buffer around all records of Rainbow Lorikeets collated from the Atlas of Living Australia, as above (see Figure 4). All grid cells not intersecting with this polygon were masked, as were those that did not intersect with the Australian mainland. Likewise, to account for the fact that the Red-collared Lorikeet constrains the distribution of Rainbow Lorikeets in northern Australia, west of Cape York, all grid cells intersecting with the distribution of this species were masked. The study area within which the range dynamics of Rainbow Lorikeets were investigated subsequently covered an area of ~2.5M square kilometres across eastern Australia (Figure 5).

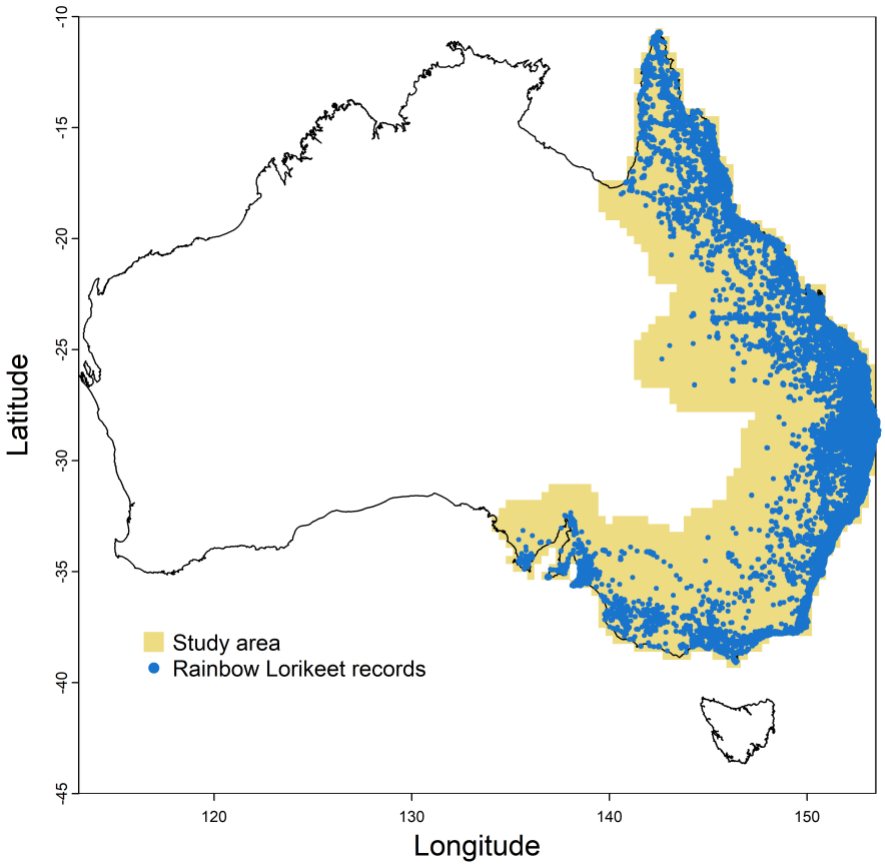

Figure 5. Study area for assessing the range expansion of Rainbow Lorikeets in eastern Australia. All occurrence records derive from the Atlas of Living Australia.

3.4 Range Expansion Modelling

To quantify the spatial and temporal pattern of Rainbow Lorikeets' range expansion, I employed a novel Dynamic Occupancy Modelling (DOM) approach currently being developed for modelling the range dynamics of Australian fauna (Duncan *et al.* in prep). The key advantage of this approach is its ability to estimate changes in occupancy probabilities across the range through time from atlas records, which represent spatially and temporally patchy set of detections. The DOM has two key parameters, both of which are binary quantities (0 or 1): species true occupancy for each grid cell i in each time-period t, denoted $z_{i,t}$, and; species detection for each cell i and time-period t, denoted $y_{i,t}$. For Rainbow Lorikeets, I used decadal time-periods, binning each record into decades from 1890 until 2020. The atlas records provide a partially observed matrix of z, being 1 for each cell and decade whenever $y = 1$. For expanding species such as Rainbow Lorikeets, it is reasonable to assume that $z = 1$ for each cell in each decade subsequent to the first detection in that cell ($y = 1$), further filling the matrix of z. In this

case, z is only unknown when $y = 0$ prior to the first detection for each cell, as non-detection could arise from observers visiting the cell in a given decade and not detecting the species, or few or no observers visiting that cell in that decade. A model can be fitted to these data if it is assumed that the probability of detection for each cell in each decade ($p_{i,t}$) is a function of some independent measure of observer effort. For Rainbow Lorikeets, I used the total number of records of both passerine and non-passerines for each cell in each decade from the Atlas of Living Australia as a measure of effort (with a log(x+1) transformation), fitted with a sigmoidal function. The model had the following form:

$$z_{i,t} \sim Bernoulli(\varphi_{i,t})$$

$$y_{i,t} \sim Bernoulli\left(z_{i,t} \times p_{i,t}\right)$$

$$p_{i,t} = \frac{\theta_1 - \theta_2}{1 + exp(\theta_3 - \theta_4 \times effort_{i,t}) + \theta_2}$$

where $\varphi_{i,t}$ is the probability of occupancy in cell i in decade t, $effort_{i,t}$ is the log(x+1) transformed sum of records of passerine and non-passerine birds for cell i in decade t and θ_1 - θ_4 are parameters to be estimated.

The probability of occupancy for each cell in each decade ($\varphi_{i,t}$) was in turn modelled using spatiotemporal functions commonly used in disease spread modelling (Duncan et al. 2024). Specifically, φ was modelled using a Conditional Autoregressive (CAR) approach that allows for correlation in this parameter with neighbouring cells in both space and time, where neighbouring cells are those directly adjacent to them (Duncan et al. 2024). This is relevant for mapping species distributional spread, as in real-world ecological data, species occurrence in one locality means that nearby localities are more likely to be occupied (Dormann et al. 2007). CAR models account for this by employing an adjacency matrix, which defines cells as neighbours (Dormann et al. 2007). In this study, a "queen" neighbourhood adjacency matrix was employed, such that estimated occupancy of the 8 surrounding cells were considered for the focal cell (Earnest et al. 2007). This modelling allowed for the 'borrowing of strength' from neighbours, improving estimates of occupancy probabilities in sparsely sampled areas (Earnest et al. 2007).

The model was fitted to the data using Markov Chain Monte–Carlo (MCMC) with the aid of the *nimble* package (De Valpine 2024). MCMC is a widely used tool in distribution modelling that estimates the posterior distribution via Bayesian inference (Ravenzwaaij et al. 2018). Spatiotemporal autocorrelation of occupancy probabilities was implemented using the Intrinsic Gaussian CAR approach (ICAR) with the *nimble* function 'dcar_normal'. Vague (uninformative) prior distributions were employed for all parameters. Posterior distributions were drawn from 7000 samples of three independent MCMC chains, with a burn-in of 2000 samples.

The DOM provided estimates of the probability of occupancy of Rainbow Lorikeets for each grid cell in each decade. For simplicity, I took the mean posterior estimate for each cell in each decade. This output was used to identify areas Rainbow Lorikeets have colonised, focussing on the comparison of two key decades; 1930-1939 and 2010-2019. Occupancy in 1930-1939 was used to represent the historical distribution, prior to major agricultural expansion and landscape modification that occurred after the Second World War. For each time-period, I converted the probability of occupancy for each cell into presence or absence of Rainbow Lorikeets, using a cut-off of 0.5. Hence, cells were considered occupied if φ was ≥0.5 or unoccupied if φ was <0.5.

Each cell within the study region was further classified into one of three categories:

1. **Never occupied (1)**: Sites that were not occupied by the species in either time-period.
2. **Always occupied (2)**: Sites that were occupied by the species in both time-periods.
3. **Colonised (3)**: Sites that were not occupied in the initial time period but were occupied in the second.

3.5 Relationships between Range Expansion and Environmental Variables

Outputs of the DOM were used to explore the ecological and land use factors associated with the species' range expansion with the aid of multinomial logistic regression modelling. Multinomial logistic regression is used to predict outcomes with multiple, non-ordered categories. It estimates the probability of each category by modelling the log odds of each outcome (relative to a reference category) as a linear function of the predictor variables (UCLA 2024).

Multinomial regression models were fitted to the data using the *nnet* package (Ripley 2022), and considered both bioclimatic predictors (e.g., temperature) and non-climatic factors (e.g., land use) as potential drivers of occupancy changes. Five key variables were selected given their hypothesised role in the expansion of Rainbow Lorikeets. Bioclimatic variables from WorldClim —mean annual temperature, annual precipitation (mm), and elevation (m) — were resampled to match the raster used for Rainbow Lorikeets (see Figure 5 above). These key bioclimatic variables were selected to capture ecologically meaningful aspects of climate, facilitating exploration of climatic constraints of Rainbow Lorikeets, as well as any new climatic conditions they may tolerate based on their occurrence records. Climatic factors have been shown to contribute to the species' expansion (Robinson et al. 2020), and the use of high-resolution, standardised bioclimatic datasets from WorldClim enables effective modelling of this phenomenon (Fick and Hijmans 2017). The proportional cover of urban and agricultural land for each cell in this raster were derived from the 250 m resolution land use layer. Urban

and agricultural land proportions were chosen as predictor variables because they represent human-driven landscape transformation over time. These land use types hold important mechanisms behind the expansion of native parrot species (Campbell et al. 2022). Urban and agricultural land use type categorisations were mapped using the DAFF 2021 data set as this was the most recent national scale data available at the time my thesis was undertaken. Multinomial modelling proceeded with the aim of evaluating relationships between these variables and the probability of a cell being classified into ‘never occupied’, 'always occupied' and 'colonised' categories. Prior to model fitting, all predictors were standardised (mean = 0, SD = 0.5) to facilitate model convergence and aid interpretability and comparability of coefficients.

Using the ‘never occupied’ category data as the baseline or null model, I fitted models with all combinations of the predictors and completed model selection using Akaike Information Criterion (AIC) with the *AICcmodavg* package (Mazerolle 2025). Akaike Information Criteria (AIC) was chosen as it estimates the effect strength of covariate combinations relative to other models (Cavanaugh and Neath 2019). Models with lower AIC variables are more parsimonious, maximising model fit relative to the number of parameters (Anderson and Burnham 2002).

Chapter 4: Results

4.1 Range Expansion Modelling

The dynamic occupancy modelling over decadal time increments from 1890 to 2020 reveals a distinct pattern of range expansion in Rainbow Lorikeets. While it is important to note that this species' expansion is ongoing, static distributional snapshots for each decade illustrate progressive colonisation across eastern Australia (Figure 6). Range expansion became particularly pronounced from the 1960s onwards (Figure 6). Areas that initially exhibited sparse or isolated occupancy, transitioned into fully occupied regions over subsequent decades. In addition to infill within areas with initially patchy occupancy, the species also expanded into regions where no prior presence was recorded, highlighting a possibility for both local colonisation and long-distance dispersal (Figure 6, 7). In contrast to the substantial changes observed in southern and south-eastern Australia, the distribution of Rainbow Lorikeets in Queensland has remained largely stable. This indicates limited range contraction or expansion within their original range (Figure 6, 7).

Results indicate spatially distinct patterns between 'never occupied' (absent in both 1930-1939 and 2010-2019), 'always occupied' (present in both decades), and 'colonised' (absent in 1930-1939 but present in 2010-2019) cells (Figure 7). The 'always occupied' category was primarily concentrated within the species' historical native range in Queensland, where occupancy remained consistent over time. This is seen in the limited range edge expansion above the Tropic of Capricorn, particularly in north-west Queensland (Figure 7). In contrast, 'colonised' cells were primarily located along the eastern and south-eastern coastal corridors, including many urban and peri-urban regions (Figure 7). Colonisation also occurred in some areas that were unexpected. For example, in more arid and semi-arid regions like the Murray River corridor and parts of the Murray-Darling Basin, and a thin corridor of inland Queensland. Areas like these showed clear signs of colonisation despite generally drier conditions and less urban influence. There are also areas that remain uncolonised by Rainbow Lorikeets. For example, alpine environments throughout the Australian Alps and cooler, temperate zones like the Otway Ranges in southwest Victoria (Figure 7).

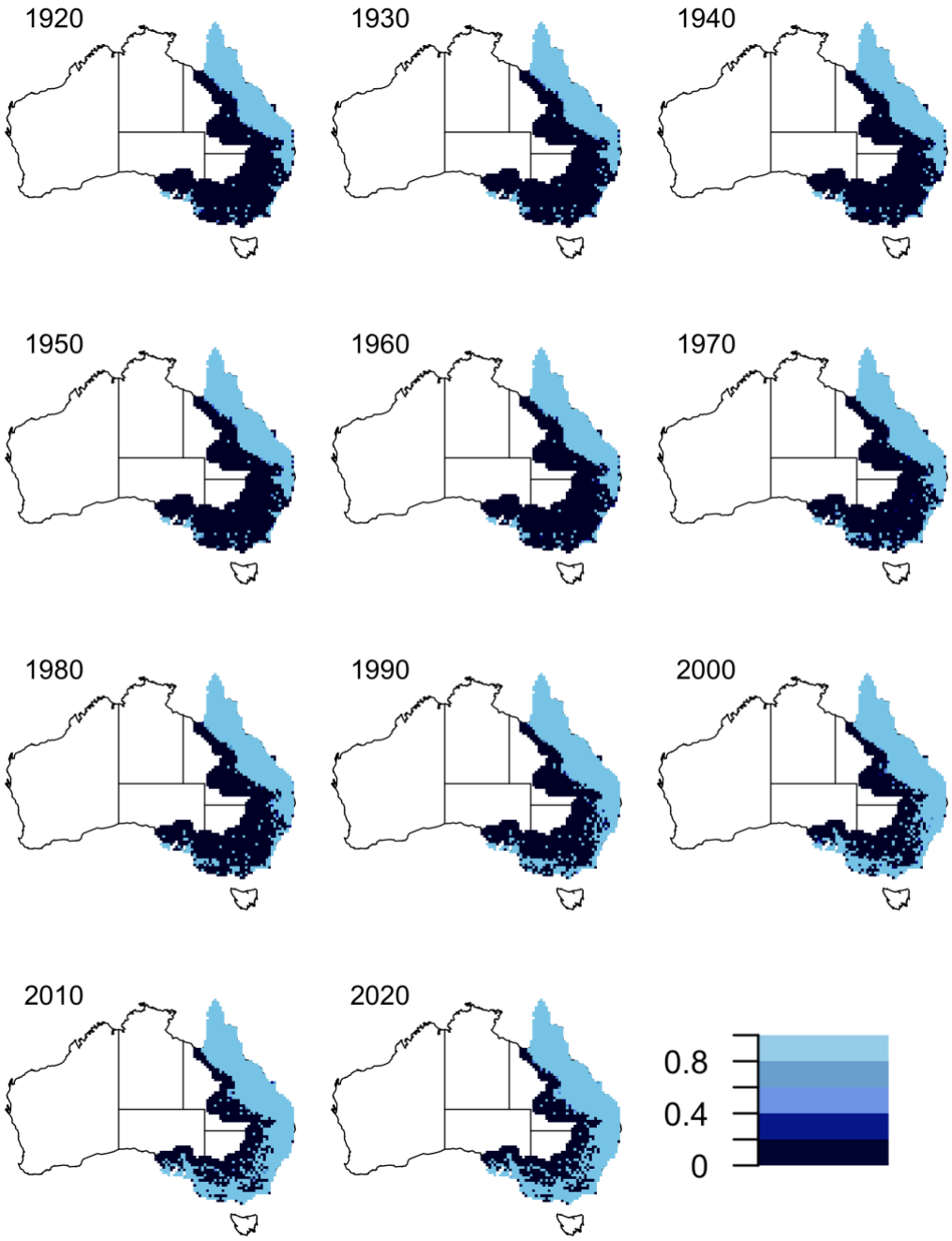

Figure 6. Spread of Rainbow Lorikeets from 1900-2020, under a 40km resolution over the study region of mainland eastern Australia. Spread is quantified by probability of occupancy continuously. Data shows bimodal distribution, with most values at either end of the spectrum, the darkest blue at zero (not occupied) or the lightest blue at one (occupied). This lack of variation shows the model has high certainty.

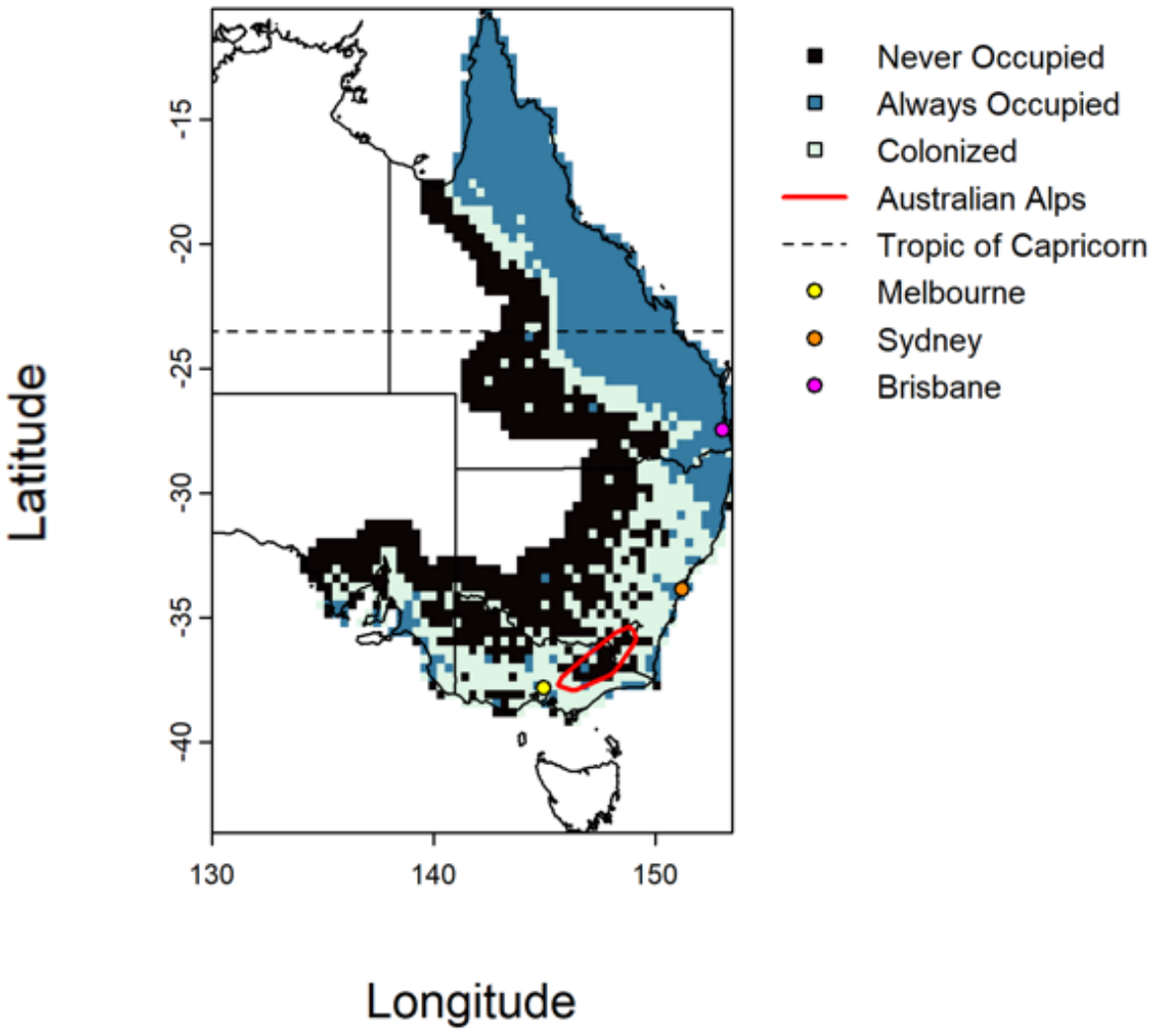

Figure 7. Rainbow Lorikeet Occupancy under a 40km resolution, classified into three categories – 'Never Occupied', 'Always occupied' and 'Colonised' in study area of eastern Australian distribution, with geographic landmarks in legend.

4.2 Post Hoc Analyses

4.2.1 Model Selection

Model selection was based on Akaike's Information Criterion (AIC). The top-ranked model with the lowest AIC value included all predictor variables considered: precipitation, mean temperature, elevation, agriculture, and urban variables.

Models that included only bioclimatic variables (elevation, precipitation and temperature) were considerably weaker, with the lowest ranked models only including these variables. The addition of anthropogenic variables (agriculture and urban) consistently improved model fit (Table 2).

A substantial difference was observed between the top-ranked model and the second-best model, as indicated by a large delta AIC of 23.1 (Table 2). The difference between these models is that the top model includes elevation. The top model has a model weight of almost one, meaning that it explains the largest proportion of variation in the data (Table 2).

Table 2. Model selection showing the ten most parsimonious Rainbow Lorikeet occupancy multinomial models ranked by Akaike Information Criterion (AIC). The number of parameters and log-likelihood for each model is provided. Delta (Δ) AIC shows the difference between the AIC of the model and the AIC of the most parsimonious model. Lastly, all model weights add to 1, so the higher the model weight, the larger proportion of variation in the data is explained by the model.

Ranking	***Variables***	*Number of parameters*	*Log-likelihood*	*AIC*	*Δ AIC*	*Model weight*
1	Annual Precipitation, Mean Temperature, Elevation, Agriculture, Urban	12	-1223.11	2470.39	0	0.999989979
2	Annual Precipitation, Mean Temperature, Agriculture, Urban	10	-1236.68	2493.49	23.1	< 0.01
3	Annual Precipitation, Mean Temperature, Elevation, Urban	10	-1239.9	2499.93	29.54	< 0.01
4	Annual Precipitation, Mean Temperature, Urban	8	-1250.19	2516.46	46.07	< 0.01
5	Annual Precipitation, Mean Temperature, Elevation, Human Footprint	10	-1259.99	2540.09	69.7	< 0.01
6	Annual Precipitation, Mean Temperature, Elevation, Agriculture	10	-1264.13	2548.38	77.99	< 0.01
7	Annual Precipitation, Mean Temperature, Human Footprint	8	-1268.84	2553.77	83.38	< 0.01
8	Annual Precipitation, Mean Temperature, Agriculture	8	-1272.19	2560.46	90.07	< 0.01
9	Annual Precipitation, Mean Temperature, Elevation	8	-1285.91	2587.89	117.5	< 0.01
10	Annual Precipitation, Mean Temperature	6	-1292.39	2596.82	126.43	< 0.01

4.2.2 Factors Associated with Colonisation

Coefficient estimates for the colonisation model were derived from the top-ranked model identified in the AIC-based model selection process, using the 'never occupied' category as the reference baseline.

Predictor variables in this model had predominantly low p-values, reflecting their associations with cell colonisation (Table 3). However, not all variables were significant. Mean temperature and elevation had p-values above the conventional 0.05 threshold (Table 3).

In terms of effect size, the predictors with the largest positive coefficients were urban proportion (4.85) and precipitation (3.71), indicating that increasing values of these variables are strongly associated with a higher likelihood of a cell being classified as 'colonised' (Table 3). Agriculture had the next largest effect size, also contributing significantly to the model with a coefficient estimate of 0.68. (Table 3). All coefficients had positive values except for mean temperature, which was negatively associated with colonisation (Table 3). This suggests that as temperature increases, the likelihood of colonisation decreases.

Table 3. Model table showing contributions of predictor variables to the top-ranked Rainbow Lorikeet multinomial model. The 'never occupied' classification was used as a reference baseline. Coefficient estimates indicate the magnitude of effect on the top 'colonised' model, with higher values indicative of a stronger effect/contribution to the model. P values shown, with $p < 0.05$ indicating significance in bold. Standard Error (SE) indicates the statistical accuracy of an estimate.

	Coefficient Estimate	***Standard Error***	***P-Value***
Intercept	0.476806725	0.130379816	**<0.001**
Annual Precipitation	3.712541	0.340573	**<0.001**
Mean Temperature	-0.16647	0.196059	0.395848
Elevation	0.186005	0.178337	0.296948
Agriculture	0.680961	0.156604	**<0.001**
Urban	4.85465	0.839563	**<0.001**

Model predictions were made using the top-ranked occupancy model to visualize how each predictor variable influenced the probability of a cell being classified into one of the three occupancy categories: 'never occupied', 'colonised', or 'always occupied'. 'Always occupied' cells were associated with high levels of annual precipitation, while 'never occupied' areas had low precipitation values, likely below the threshold needed to support Rainbow Lorikeet populations (Figure 8). 'Colonised' cells tended to

occur in areas with mid-range precipitation, around 500 mm annually, suggesting that expansion is occurring in moderately suitable, previously unoccupied climates (Figure 8).

Mean temperature also showed distinct differences between the curves of each category. 'Always occupied' regions had significantly higher temperatures, with high probability of classification with temperatures upwards of 25^{o}C. Cells with high probability of being classified as 'never occupied' had significantly lower temperatures, and likely outside the species' tolerance. 'Colonised' cells tended to be from cooler climates, matching the spread into areas of southern NSW, Victoria and South Australia (Figure 8).

The elevation variable displayed a less dramatic but still discernible pattern. 'Colonised' and 'never occupied' cells had very similar elevation ranges, both significantly lower than the always occupied category (Figure 8). The probability of classification of 'always occupied' was highest at over 1000 metre elevations. The downward slope of both 'colonised' and 'never occupied' categories suggests that higher elevation may have reduced probability of colonisation. Elevation may be a less influential factor in determining colonisation compared to other covariates, although it may still interact with other ecological drivers (i.e. mean temperature).

The rate of expansion was relatively rapid, particularly when considering expansion into climatically distinct areas (Figure 6). This may suggest that climatic suitability alone does not account for the observed distributional shifts, given the divergent climatic profiles of novel areas of expansion. 'Always occupied' cells were associated with high agricultural land cover proportions, while 'never occupied' cells had consistently low agricultural land use proportion (Figure 8). 'Colonised' cells again fell in the mid to high range, with cells holding the highest probability of being classified as 'colonised' at around 75% agricultural proportion. The urban land cover variable exhibited the strongest pattern, with the three categories diverging the most across the urban proportion gradient (Figure 8). 'Never occupied' cells had minimal urban proportion, while 'always occupied' cells were strongly associated with high urban proportions, as the Rainbow Lorikeet's historical range is now within some highly urbanised areas. 'Colonised' areas peaked at moderate levels of urbanization, approximately 10% urban cell proportion (Figure 8). An overarching pattern emerging from the multinomial modelling was that predictor variable values for colonised cells were typically situated at the transition margins between 'always occupied' and 'never occupied' cells.

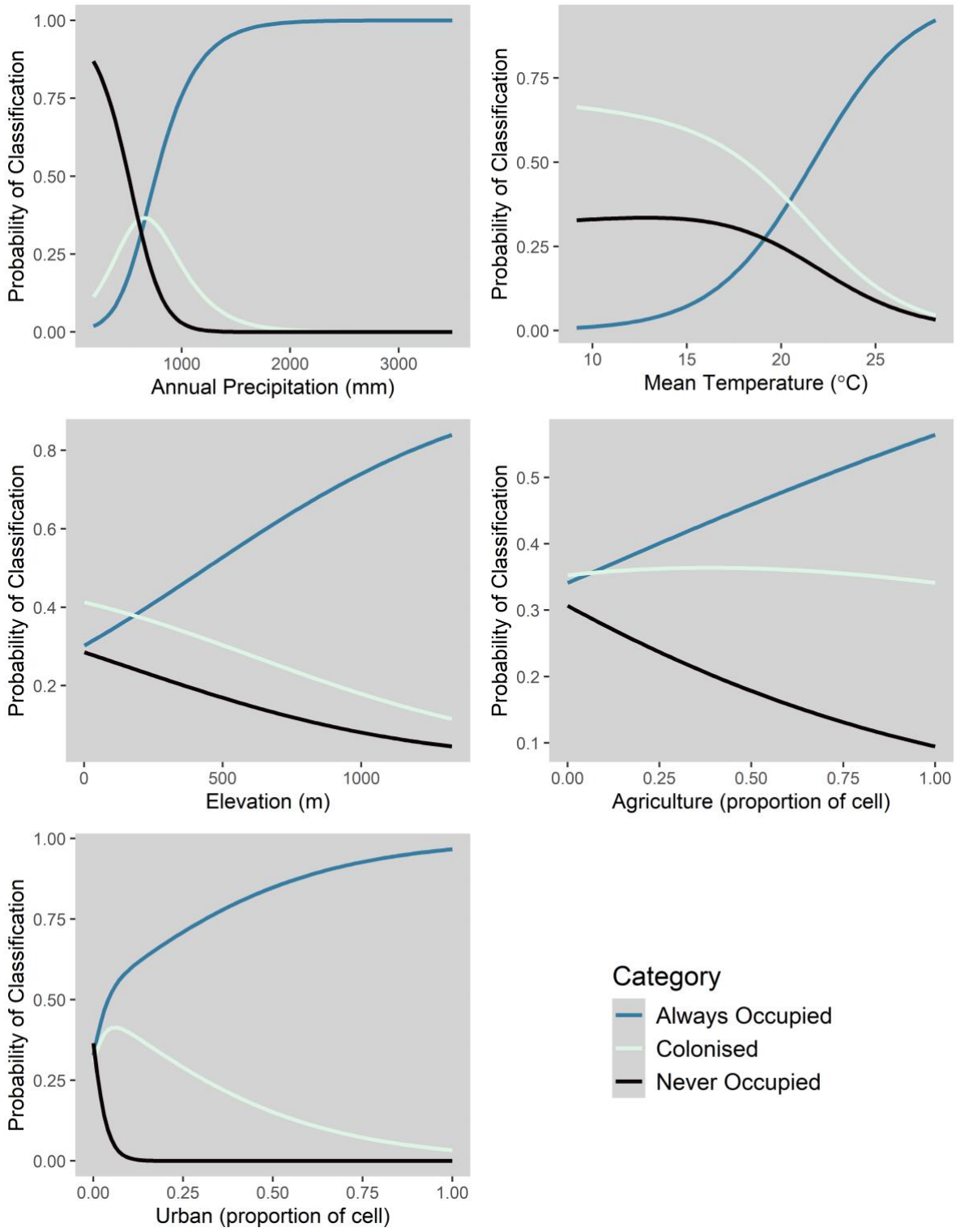

Figure 8. Model predictions from the top multinomial model. Predicted probability of classification into each of the three cell categories on the Y axes (seen in legend), and five predictor variable proportions on the X axes.

Chapter 5: Discussion

In an era of profound global change characterised by major reductions in many species' distributions, some species are experiencing major increases in their distribution (Lawlor et al. 2024, Britnell et al. 2023, Wingfield et al. 2015). While many of these expansions have been anecdotally reported, they lack robust empirical quantification. One group of species that is notable for numerous reports of range expansion are birds in eastern Australia (Campbell et al. 2022, Stewart et al. 2022). In this thesis, I have quantified the range expansion of the Rainbow Lorikeet from 1890 to 2020. This species has experienced particularly rapid expansion post-1960. Using dynamic occupancy models, I identified areas where the species has expanded, areas that have been consistently occupied through time, as well as areas uncolonised by the species despite being adjacent to occupied areas. I then examined ecological and anthropogenic factors associated with colonisation and found strong associations between areas colonised and those under urban and agricultural land uses. Furthermore, I demonstrate that the expansion of the Rainbow Lorikeet has occurred into novel environmental conditions, particularly areas at lower temperatures and reduced rainfall. My findings have important implications for future research and conservation in this field.

5.1 Rainbow Lorikeet Expansion

My quantification of widespread range expansion over time for the Rainbow Lorikeet aligns with observational literature reporting a marked increase for the species, particularly in urban and suburban areas across eastern Australia (Cobden et al. 2021, Rogers and Kark 2021). In quantifying temporal patterns of occupancy (Figure 6,7), my results are compatible with suggestions in the literature that the Rainbow Lorikeet has expanded significantly in recent decades, particularly since the 1960s (Chapman 2005, Rogers and Kark 2021). My results support the anecdotal consensus that Rainbow Lorikeet expansion is particularly pronounced in landscapes modified by humans, that offer novel resources and shelter (Davis et al. 2015, Smith and Lill 2008, Rogers and Kark 2021). Other authors have highlighted large brain size and behavioural flexibility as factors that may significantly contribute to the expansion success of certain native parrot species like the Rainbow Lorikeet (Rogers and Kark 2021, Sayol et al. 2020, Sayol et al. 2018).

I also found colonisation in unexpected areas. For example, expansion into semi-arid areas with less surface water. These expansions may be explained by the availability of key resources, particularly food sources such as fruiting trees planted in human-altered landscapes (i.e., irrigation areas along inland river systems), suggesting the importance of local resource availability in facilitating expansion. Notable areas of expansion also occurred in forested landscapes, not subject to agricultural or urban land uses. Overall, while there was an increased probability of cell colonisation in areas under urban

and agricultural land uses, major areas of expansion also occurred outside these areas. This result illustrates a general pattern of broadscale range expansion which can only be in part attributed to changes in human land use.

5.2 Environmental Drivers Role in Colonisation Patterns

Bird species have specific upper and lower temperature limits associated with physiological tolerances (Huntley et al. 2006), with increasing temperatures having been suggested as aiding Rainbow Lorikeet establishment in Tasmania (Robinson et al. 2020). Temperature can indirectly support or restrict species expansion through its influence on other factors like water availability (Lawlor et al. 2024, Huntley et al. 2006). Examples important for Rainbow Lorikeets include surface water availability or the timing of resource availability such as flowering events (Davis et al. 2012, Shukuroglou and McCarthy 2009, Rogers and Kark, 2021). Higher minimum temperatures, heat-island effects and reduced occurrence of frost in cities like Melbourne have made their climate more comparable to the original subtropical and tropical range of Rainbow Lorikeets, which may have contributed to their range expansion (Shukuroglou and Mccarthy 2009). However, of the bioclimatic variables studied in modelling, temperature was the sole variable to exhibit a negative colonised coefficient estimate in the top performing model, meaning that colonisation reduces with increasing temperature. This may be due to the species' historical distribution being in warmer, tropical and subtropical regions, where occupancy has long been established (Shukuroglou and Mccarthy 2009). Hence, these warmer regions would fall into the 'always occupied' category. In contrast, 'colonised' areas fell in cooler climatic zones than Rainbow Lorikeets have occupied historically, particularly in southern Australia. Temperature characteristics of never occupied cells may represent areas that are beyond the temperature tolerances of the species, like the mainland Australian Alps. Interestingly, Rainbow Lorikeets have not colonised the Australian Alps despite colonising surrounding subalpine areas (Figure 7). The 'always occupied' cells generally fall within a window or 15 to 35 ºC. The mean annual temperatures of the Australian Alps are significantly lower than the rest of mainland eastern Australia, ranging from 3°C to 12°C, with minimum average monthly temperatures between -7°C and -4°C for the coolest month (Fick and Hijmans 2017). Thus, the lack of expansion in this region may suggest that the Alps are either outside the thermal tolerances of the species or there is a lack of access to suitable food resources.

Precipitation has a key role in determining many bird species realised niches (Tingley et al. 2009). Rainfall has been thought to significantly positively influence Rainbow Lorikeets expansion (Davis et al. 2011). Areas with consistent, high rainfall within the species' historical range had consistently high probability of being classified as 'always occupied'. 'Colonised' areas typically had intermediate precipitation levels, with at least approximately 500 mm annually, suggesting that Rainbow Lorikeets can expand into new areas even when rainfall is substantially lower than areas historically occupied,

although colonisation appeared limited in areas with less than 500 mm annually. This is consistent with broader patterns observed in other bird species, which tend to expand toward wetter areas when possible, especially nectivorous species, as wet conditions promote abundant flowering resources (Tingley et al. 2009). Short term rainfall deficiencies in inland areas have been linked to increased relative abundance of certain inland parrot species in urban landscapes (Davis et al. 2011), indicating that variability in precipitation may not only influence habitat suitability but may also drive shifts in species dispersal toward more mesic urban environments.

Elevation is commonly correlated with climatic factors such as temperature and precipitation, which in turn govern the distribution patterns of flora and fauna (Lee et al. 2004). Bird species' responses to elevation vary widely as altitude gradients often see zonation of ecological conditions (Patterson et al. 1998). Elevated areas typically have higher rainfall and cooler temperatures (McCain 2009, Jin et al. 2024). My results show that lower elevation areas are more likely to be newly colonised by Rainbow Lorikeets, likely due to their accessibility and fewer temperature constraints. Much of the higher elevation areas had high probability of being in the 'always occupied' category, particularly those with favourable rainfall conditions that support lorikeet persistence. Elevation was identified as a key variable in the top multinomial models (see the difference between top and second models, Table 2), emphasising its importance alongside climatic and anthropogenic factors in predicting Rainbow Lorikeet occupancy. While Rainbow Lorikeets appear constrained in high-elevation areas in southern Australia due to low temperatures, these regions may also pose additional ecological challenges, including reduced resource availability, increased competition, or environmental conditions that exceed the species' physiological limits. While the species' southern expansion may reflect a niche shift toward cooler, wetter conditions, as suggested by Tingley et al. (2009), their absence from colder subalpine zones underscores the ongoing role of climatic thresholds in limiting the expansion of even generalist, adaptable species.

My results indicate that the Rainbow Lorikeet is now inhabiting regions beyond its historical climatic range, suggesting the species has expanded its climatic niche. This is evidenced by 'colonised' areas being characterised by cooler, drier conditions. However, the rate of range expansion and the occupation of climatically dissimilar regions imply that climate alone is not the primary driver of distribution change. For example, major cities across eastern Australia show increasing occupancy of Rainbow Lorikeets (Campbell et al. 2022, Chapman 2005), despite having divergent environmental conditions (Maheshwari et al. 2020). For example, in comparing Brisbane, 'always occupied' by Rainbow Lorikeets (Stanford and Lill 2008), and Melbourne, where Rainbow Lorikeets have colonised in the last few decades (Chapman 2005, Cobden et al. 2021), we see that these two cities differ substantially in temperature, rainfall, and elevation (Maheshwari et al. 2020).

Surprisingly, I documented Rainbow Lorikeet expansion into some areas that appear substantially drier than those commonly occupied. An example of this is seen in the colonised corridor along the Murray River (Figure 7) (Walker 1992). Whilst Rainbow Lorikeet distribution is not formally recognised in this region (Menkhorst et al. 2017), they have proven ability to travel large distances for food, enabling them to utilise dispersed resources effectively (Jaggard et al. 2015). Fruit availability and abundance have also been shown to be important drivers of habitat use (Shukuroglou and McCarthy 2006). Key resources from intensive land use in this semiarid region in the form of irrigated orchards including citrus and viticulture (Walker 1992, Cochrane 1960), may support occupancy despite challenging macroscale climatic conditions. Overall, the expansion I document into semi-arid areas may be explained by the availability of key resources, suggesting the importance of local resource availability in facilitating expansion in climatically marginal areas.

5.3 Importance of Anthropogenic Variables

While bioclimatic factors are generally thought to be most important for determining a species ecological niche, anthropogenic factors have been recognised as particularly pertinent for a range of parrot species (Calzada 2024). Environmental change may give rise to other conditions that cumulate with bioclimatic factors to create optimal novel conditions and resources for select native Australian species (Valentine et al. 2020, Rogers and Kark 2021). Rainbow Lorikeets persistence and even expansion in some arid zones provides further evidence that climatic factors alone do not fully explain distribution patterns. Patterns in my results show that Rainbow Lorikeets are occupying different climatic conditions than historically, suggesting occupation of a unique bioclimatic niche. However, it appears this range expansion is not solely climatically driven but also shaped by the presence of novel ecological resources or conditions. While my results identified clear associations with bioclimatic variables, anthropogenic land use emerged as the most influential factors predicting colonisation probability.

The rapid expansion of anthropogenically modified areas since mid-20th century has emerged as a major disruption to patterns of species occurrence (Legge et al. 2023). Bird species experience novel ecological dynamics under land use change and disturbance (Iglesias-Carrasco et al. 2022). Results supported scientific contention that land use change is a primary driver of ecological niche expansions in bird species (Avidad et al. 2025, Liu et al. 2025, Livezey 2009b). Urban and agricultural land proportion were both included in the top-ranked models, with cells containing a mid to high level of agricultural and urban proportion being associated with the colonisation category. This suggests that areas modified by humans like city fringes and farming areas support Rainbow Lorikeet colonisation (Rogers and Kark 2021).

As agriculture expands to support growing human populations, it is expected to have increased impacts on bird species globally (Teyseddre and Couvet 2007). Perhaps the most significant resource provided in agricultural areas is drinking water (Davis et al. 2011). Changes in vegetation associated with agriculture may also provide unique foraging opportunities for a range of parrot species, enabling their colonisation (Livezey 2009b). There is evidence that parrots may exploit mosaics of fragmented habitats for reduced predators and increased foraging opportunities.

Urban habitats, with modified vegetation structures and warmer microclimates, provide novel conditions that support parrot populations beyond their traditional ranges (Stanford and Lill 2008, Smith and Lill 2008). Urbanisation is a significant driver of environmental change and can lead to increases in species abundance (Le Louarn et al. 2018). Urban landscapes give rise to above average rainfall and elevated temperatures that often result in prolonged flowering (Davis et al. 2012). The increasing occurrence of select parrot species in Australia has been suggested to relate to cascading interspecies and environmental interactions across time and space (Shukuroglou and Mccarthy 2009). On a smaller spatial scale, species like the Rainbow Lorikeet have found success in urban areas due to plants in suburban gardens, providing nectar, fruits and seeds year-round (Davis et al. 2015, Ikin et al. 2014, Shukuroglou and McCarthy 2006). Urban areas tend to feature a higher density of non-native plant species, which can serve as food sources and nesting sites, and have been reported as being positively associated with expanding bird densities (Mills et al. 1989). Nectivorous species like the Rainbow Lorikeet and the Noisy Miner (M*anorina melanocephala*) have benefited from these exotic planting choices in urban areas (Beggs 2020, Campbell et al. 2022, Shukuroglou and McCarthy 2006). At a landscape scale, predators such as raptors are often less abundant in urban areas, which may lower predation pressure on Rainbow Lorikeets and support their establishment in cities (Shukuroglou and McCarthy 2009). There is also evidence that at macroecological scales, bird species have utilised metropolitan areas as refuges under extreme environmental disturbance like droughts or wildfires (Rogers and Kark 2021).

Anthropogenic variables were the most significant in my top ranked multinomial model, highlighting the centrality of land use change, particularly urban and agricultural areas. Landscape scale land use change can modify resource availability and habitat suitability, effectively shifting the environmental limits historically constraining parrot species (Jaggard et al. 2015). My results support evidence that human disturbance can aid adaptable species' expansion and support the idea that agricultural landscapes may provide consistent food resources and habitat structure conducive to colonisation.

5.4 Limitations

This study has several important limitations that must be acknowledged. First, analysing macroecological patterns across large spatial and temporal scales presents significant challenges,

especially when using data collected over several decades with varying levels of certainty (Campbell et al. 2022). Although dynamic occupancy modelling accounts for imperfect detection (Mackenzie et al. 2003, Mackenzie and Royle 2005), using presence-only records requires caution. More than half of the Atlas of Living Australia's records are from citizen science projects and platforms like iNaturalist (ALA 2024). While using occurrence records largely attained from citizen science data facilitates analysis of patterns over wide spatial and temporal scales, it can also come with biases and errors to consider (Johnston et al. 2023). An example of this is the spatial bias, where accessible and populated areas present more observations, with uneven geographic coverage leading to underrepresentation of remote or less-visited regions (Johnston et al. 2023). This was addressed in my methods by accounting for sampling effort. However, given the relatively coarse 40km resolution for my occupancy modelling, there could still be biases that may overlook local ecological colonisation patterns in my research.

In my post-hoc multinomial analysis, predictor variables were selected based on their availability for use in a national-scale framework, which necessitated the use of broad bioclimatic measures (e.g., annual mean temperature) and simplified anthropogenic variables such as land use type. While this approach allowed for the identification of macroecological patterns of Rainbow Lorikeet expansion, it was limited in the ability to pinpoint specific drivers of colonisation. Though flowering vegetation, and hollow bearing trees have been identified as strong predictors of lorikeet occupancy (Dalladay 2018, Davis et al. 2014), national-scale, high-resolution vegetation data were not accessible within the time constraints of this study. Fine-scale information on food resources could be particularly pertinent for species like the Rainbow Lorikeet, which rely on nectar and fruit as primary food sources and nest in tree hollows (Rogers and Kark 2021, Davis et al. 2014, Gibbons and Lindenmayer 2002). Future studies could model the presence of flowering or fruiting trees, specific agricultural practices, or the availability of nesting sites against occurrence to refine understanding of colonisation drivers. The primary aim of my study was to identify broad macroecological patterns of expansion, rather than to quantify the potentially complex and context-dependent interactions between variables. More complex models may be fitted in the future at finer scales to address these possible generalisations and interactive effects. These variables provide a snapshot of the characteristics of novel conditions the Rainbow Lorikeet is occupying, but not the exact driving context-dependent mechanisms behind expansion.

While the dynamic occupancy modelling approach that I used quantified changes in Rainbow Lorikeet distribution over decadal timescales, for the post hoc analysis I compared changes from just two time points, 1930 and 2010. This approach may miss areas currently undergoing new colonisation and does not capture historical occupancy patterns that may shape the patterns seen today. For example, some sources suggest that Rainbow Lorikeets may have been abundant in the Sydney region during early European colonisation, but experienced noticeable reductions in the late 19th century, and subsequently re-established in Sydney in the early 20th century (Stanford and Lill 2008, Waterhouse 1997). Stanford and Lill (2008) term the expansion seen in Sydney today as 'recolonisation'. My methods do not capture

fine scale changes like this example that have occurred across the last two centuries in eastern Australia. This project thus does not stive to represent either the complete history of Rainbow Lorikeet occupancy, or the endpoint of the species range expansion, but instead is focussed on changes within the last century. By providing a snapshot between these years rather than a continuous view of expansion, this may underestimate or misrepresent areas currently undergoing colonisation, as Rainbow Lorikeet expansion is ongoing.

It is important to note that the methods did not directly assess the influence of climate change on range shifts. This is because the climate variables used were static, and do not represent the larger phenomena of climate change. Expansion into cities like Melbourne or Adelaide should not be interpreted as evidence that these areas are now climatically similar to the species' original range. Instead, land use mechanisms are likely important with changing climatic conditions through time also potentially playing a role (although I did not examine these factors). Lastly, multinomial analyses did not incorporate interactions between variables. The consideration of interactive and additive effects of predictor variables is an important choice in modelling (Harrison et al. 2018). In this study, an example of a potential interactive effect could be between the species potentially being able to occupy lower rainfall areas but only in areas with lower temperatures and rainfall. I made the decision to not include interactive effects in my modelling to simplify interpretation and reduced model complexity.

5.5 Implications and Directions for Future Research

Under environmental change, the distributions of numerous species are rapidly changing. My research used Rainbow Lorikeets as a widely recognised representative example species. However, as mentioned in the literature review, there is growing evidence that several other native birds are expanding in Australia (Campbell et al. 2022). This includes other examples like the Musk Lorikeet, Galah, Noisy Miners and Eastern Koels (Beggs 2019, Davis et al. 2012, Engelhard et al. 2015). While native Australian bird species like these are known to be expanding, the full extent of their colonisation into new areas remains unstudied (Rogers and Kark 2021). In fact, many Australian bird population trends are not currently being analysed at all (Campbell et al. 2022).

One key contribution of my thesis is that the approach taken to quantify distribution change, and to compare characteristics of long occupied, newly occupied and unoccupied areas respectively, is widely applicable to investigating species range shifts under environmental change. This approach could be easily replicated for other expanding species and may be especially useful for understanding understudied native species expansion, considering the aforementioned historical focus on exotic expanding species analysis. Whilst, local-scale invasions of Rainbow Lorikeets are studied, like patterns in Perth and Tasmania (Robinson et al. 2020, Chapman 2005, Cobden et al. 2021), this thesis provides

an example of a macroscale trend analysis of a native expander, and to the best of my knowledge is unique within the literature. The method I applied could contribute to systematically addressing specific questions surrounding range expansion patterns in birds in eastern Australia. More broadly, it may also provide the opportunity to explore changes in ecological communities under environmental change, like expansion and contraction in other taxonomic groups. The key implication of this research is the importance of these patterns being robustly quantified, to inform conservation of Australian avian communities, and the ecosystem functions that rely on them.

5.5.1 Are Rainbow Lorikeets a Pest Species to be Managed?

Under environmental change, a small but notable portion of native species have experienced dramatic increases in abundance, in some cases to the detriment of other native species and human infrastructure (Kennedy et al. 2022, Pecl et al. 2017, Woinarski 2019). Although there has not been robust quantifications undertaken of the agricultural costs associated with Rainbow Lorikeet damage of infrastructure and food crops (Chapman 2005), the species is widely considered a critical pest to agricultural assets in Australia (Cobden et al. 2021, Rogers and Kark 2021). In agricultural contexts, they are known to cause damage to commercial crops as they feed on ripening fruits (Tracey et al. 2007). Rainbow Lorikeets are also known to carry Psittacine beak and feather disease, which can spread quickly to other species (Ritchie et al. 2003, Raidal et al. 2015). In urban environments, their aggressive behaviour and dominance at feeding and nesting sites have been linked to the displacement of other less populous native species by outcompeting them for food and hollow-bearing trees used for nesting (Davis et al. 2014). The expansion success of the Rainbow Lorikeet into urban and agricultural areas in recent decades, as quantified in my results (Figure 6,7), comes with ongoing significant impact on human systems. The rate and breadth of this expansion mean that human communities may not be adequately equipped to manage the presence of an assertive and highly mobile species.

Rainbow Lorikeets require management to mitigate these agricultural costs, but also due to their ability to displace smaller native species (Cobden et al. 2021). This is particularly true in Perth and Tasmania, areas outside of my study area, where the species has been actively managed to some degree (Cobden et al. 2021, Robinson et al. 2020). For example, in Western Australia, Rainbow Lorikeets are listed as acclimatised fauna, cannot be legally released in the southern parts of the state, and can be lethally controlled without a permit on private land (DPIRD 2021). This means that private, municipal and state government landholders are responsible for the control of lorikeets on their land. Sporadic organised management using trapping and shooting methods has been used in Western Australia and Tasmania (Cobden et al. 2021, Robinson et al. 2020). However, understanding and research surrounding effective methods to control Rainbow Lorikeet populations remains scarce (Cobden et al. 2021).

Areas with high land use heterogeneity or ‘management mosaics’, create practical difficulties in addressing invasions (Epanchin-Niell et al. 2010). This is because the responsibility of conservation and management of invasive species lies with multiple disconnected landowners and governments across landscapes (Epanchin-Niell et al. 2010). This is particularly pertinent is Australia, with over 60 percent of land being privatised (Richardson et al. 2023). When there is a lack of control of invasive species by any one landowner, this may decrease incentives of surrounding landowners to address the invasion as the cost increases with the invasion severity (Epanchin-Niell et al. 2010). For the Rainbow Lorikeet, effective management is further challenged by the species’ high dispersal capacity and breeding success, which may undermine localised control efforts and facilitate ongoing range expansion (DPIRD 2021).

There are also ethical considerations surrounding Rainbow Lorikeet management as lethal control of native species gives rise to a moral dilemma for communities (Woinarski 2019). Whilst lethal control of exotic species is established in policy and common practice in Australia, regulations surrounding the control of native invasive species are much less developed (Woinarski 2019). Management of native, widely recognised Australian parrots like Rainbow Lorikeets comes with contention, as it raises ethical concerns about managing a native species that have found success under anthropogenically modified conditions (Kennedy et al. 2022). While they provide some ecosystem services like pollination (Sazima and Sazima 2024), their success may come at the expense of other native birds, prompting debate over whether they are drivers of ecological change or merely passengers benefiting from urbanised landscapes (MacDougall and Turkington 2005). I suggest that Rainbow Lorikeets can act as both drivers and passengers of ecological change, actively influencing ecosystems by outcompeting native species for food and nesting sites, while also expanding their range in response to urbanisation and environmental changes that facilitates their spread, without them directly causing those changes (Cobden et al. 2021, MacDougall and Turkington 2005). While Rainbow Lorikeets are widely recognised as a pest in urban and agricultural settings in Australia, management methods to effectively address their invasion are still unclear and carry ethical and ecological concerns.

5.5.2 Changing Structure of Bird Communities in Urban Australia

Increasingly modified landscapes are driving changes in avian community assemblages in Australia (Campbell et al. 2022, Joyce et al. 2018). There is evidence that in urban areas the density of breeding birds commonly increases, but species richness (the diversity of bird species) is significantly reduced (Chase and Walsh 2006). Through competition and predation mechanisms, many urban areas have patterns of high breeding rates in a few select dominant bird species (Chase and Walsh 2006, Campbell et al. 2022). In eastern Australia, introduced species such as the Common Myna (*Acridotheres tristis*) have dominated many urban bird assemblages in recent decades, but their prevalence has declined

recently (Birdlife Australia 2021). While they are still present, a subset of native species like the Rainbow Lorikeet have taken their place in many instances (Campbell et al. 2022). This leads to the question, what mechanisms are facilitating the dominance of expanding species like the Rainbow Lorikeet in urban areas? Understanding competition mechanisms may help contribute to understanding the answer to questions like these (Guillamet and Russell 2022).

Rainbow Lorikeets are highly effective urban exploiters and have been linked to the decline of other native species through competition (Campbell et al. 2022). Rainbow Lorikeets are known to compete aggressively for nesting hollows and food resources, particularly with other lorikeet species and cavity-nesting birds such as the EPBC listed swift parrot (*Lathamus discolor*) and the endemic Green Rosella (*Platycercus caledonicus*) in Tasmania (Latitude 42 2011, Stanford and Lill 2008). This case parallels global examples where similar ecological dynamics are displayed. For instance, the Barred Owl (*Strix varia*) in North America, which has expanded its range and displaced other species through similar mechanisms of ecological generalism and competitive dominance (Long and Wolfe 2019, Livezey 2009b, Dumbacher and Franklin 2024.) Both Rainbow Lorikeets and Barred Owls have found success in highly modified landscapes by outcompeting native and exotic birds alike for key resources such as food and nesting sites (Stanford and Lill 2008, Livezey 2009a, Livezey 2009b).

In the case of the Barred Owl, increased tree cover in previously open grassland areas due to urbanisation, fire suppression, and agricultural plantings is recognised as the main driver of its significant westward expansion, contributing to the decline of the endangered Northern Spotted Owl (*Strix occidentalis caurina*) (Livezey 2009b, Long and Wolfe 2019). The two expanding species also converge in their aggressive behaviour towards other species, their ability to effectively utilise both exotic and native vegetation types for food and nesting, and their increased tolerance of human-modified landscapes including edge, peri-urban and fragmented habitat types (Long and Wolfe 2019, Dumbacher and Franklin 2024). The expansion of the Barred Owl into areas it previously did not occupy is thought to be the main mechanism driving the decline of native species like the endangered Northern Spotted Owl (Dumbacher and Franklin 2024, Long and Wolfe 2019). This may mirror what is occurring for Rainbow Lorikeets and other native species in Australia. For the Rainbow Lorikeet, the fine scale landscape characteristics, like the increase of tree cover in the instance of the Barred Owl, is not known. However, like the Barred Owl, my results demonstrate that modified landscapes, highlighted by the importance of agricultural and urban land uses in my results, can be a key determinant of expansion.

Tree hollows for nesting are a critical and potentially limiting resource for many bird species in southern Australia (Ford et al. 2001, Gibbons and Lindenmayer 2002). There are significant hollow shortages, particularly in urban and farmland areas (Davis et al. 2013, Treby and Castley 2015). This issue is projected to continue, with increasing urban sprawl and agricultural intensification, leading to the removal of old, hollow-bearing trees and increasing competition between bird species for nesting

hollows (Treby 2014, Gibbons and Lindenmayer 2002). Tree hollow scarcity, and increasing abundance of the few highly competitive, adaptable, and mobile larger avian species, places increasing competitive stress on endangered birds in Australia (Ford et al. 2001, Guillaumet and Russell 2022). Strong competition for nest-sites has contributed to the decline of species like the Regent Parrot (*Polytelis anthopeplu*s) (Ford et al. 2001, Lewis et al. 2019). With increasing competition from species like the Rainbow Lorikeet under land use change, less competitive species may decline, leading to reduced bird species diversity in highly modified areas. Further research should be undertaken to determine the potential competitive impacts of Rainbow Lorikeets on other co-occurring endangered species, particularly in urban landscapes.

Although substantial range expansion of Rainbow Lorikeets was apparent in my results across eastern and southern regions, their distribution notably remains relatively stable in the north-western portion of their range. This spatial disparity suggests the presence of limiting mechanisms, with one potential factor being interspecific competition. While the Rainbow Lorikeet has successfully expanded into many novel environments, its absence from north-western Queensland may reflect competitive exclusion by the Red Collared Lorikeet (*Trichoglossus rubritorquis*), a closely related species native to northern Australia (Menkhorst et al. 2017). Despite some ecological similarities, these two species currently exhibit little to no range overlap (eBird 2025), raising the possibility that competitive interactions at range margins may be preventing further westward expansion. Such biotic interactions are increasingly recognised as important drivers of range limits, particularly where environmental tolerances alone do not account for distributional boundaries (Case et al. 2005). Further investigation is needed to assess whether behavioural dominance, resource partitioning, or interspecific aggression could be acting as constraints on Rainbow Lorikeet expansion into areas currently occupied by Red Collared Lorikeets. An alternative explanation is the effects of Carpentarian biogeographic barrier between these species being impermeable for dispersing Rainbow Lorikeets (Umbrello et al. 2024).

The expansion of Rainbow Lorikeets that I document may be reflective of a broader ecological trend; the increasing dominance of select large-brained, generalist parrot species across eastern Australia (Callaghan et al. 2019, Campbell et al. 2022, Sol et al. 2005). Results from my analysis are indicative that the recent expansion of Rainbow Lorikeets is primarily driven by land use changes. However, the interplay between urban development, climate variability, and ecological factors creates a complex matrix influencing their distribution (Uchida et al. 2021). Significant gaps remain regarding the ecological consequences of such range shifts, including their long-term impacts on urban ecosystems (Ives et al. 2016). Further robust analyses surrounding changes in species distributions, particularly in relation to shifts in realised niche occupation, would enhance understanding of how native species are responding to accelerating environmental change. Finer scale, systematic research on this well observed

pattern could further support evidence-based conservation planning in an increasingly urbanised Australia.

Chapter 6: Conclusion

I aimed to explore the range expansion of the Rainbow Lorikeet, and to contribute to the understanding of the mechanisms behind the pattern of expanding native parrots observed across eastern Australia. My research sought to address questions surrounding how the expansion of native Australian bird species like the Rainbow Lorikeet may be quantified, and what variables may best predict these colonisation patterns. I provided a robust empirical quantification of the range expansion of the Rainbow Lorikeet, which bolsters observations and reports of the significantly increased distribution and abundance of this species. My analysis identified that the probability of an area becoming colonised by Rainbow Lorikeets was associated with urban and agricultural land uses and that the expansion has occurred into bioclimatic conditions that were not commonly occupied in this species' historical distribution. The changes in occupied bioclimatic and anthropogenic conditions in my results are suggestive of a change in the realised niche of this species. The extent and pattern of expansion that I documented is indicative of a substantial degree of ecological flexibility and a broad fundamental niche. A key insight of my research is the identification of urban and agricultural land use as significant predictors of Rainbow Lorikeet colonisation. These findings highlight that anthropogenic habitat modification, rather than shifts in climatic suitability alone, plays a central role in facilitating the expansion of this species. Hence, my hypothesis that Rainbow Lorikeets are expanding in geographic distribution throughout eastern Australia in response to environmental change was supported by my results.

My thesis also sought to address gaps in current literature. While most studies of range shifts have focused on contractions or expanding exotic species due to the prevalence of these patterns under environmental change, this thesis offers an analysis of a native expanding species exploiting environmental change to its advantage. In the context of Australian birds, this perspective is particularly valuable, offering insight into the contrasting outcomes of shared environmental stressors across different species.

The key implication of this research is the need to better understand the potential implications of this dramatic range expansion in terms of how it may reshape the distribution of other co-occurring species. As Rainbow Lorikeets and other dominant species expand their range, there is a pressing need to understand how their presence may alter the structure and composition of existing avian communities, potentially displacing or reshaping the distribution of co-occurring species. More broadly, my thesis underscored that while anecdotal reports of expansion are common in several other eastern Australian bird species, systematic effort to quantify these changes in distribution and realised niche space use across a broad range of species is justified and urgent under ongoing environmental change. As birds continue to serve as indicators of broader ecological transformations, the study of their distributional changes will remain a vital tool for anticipating and managing future biodiversity outcomes.

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