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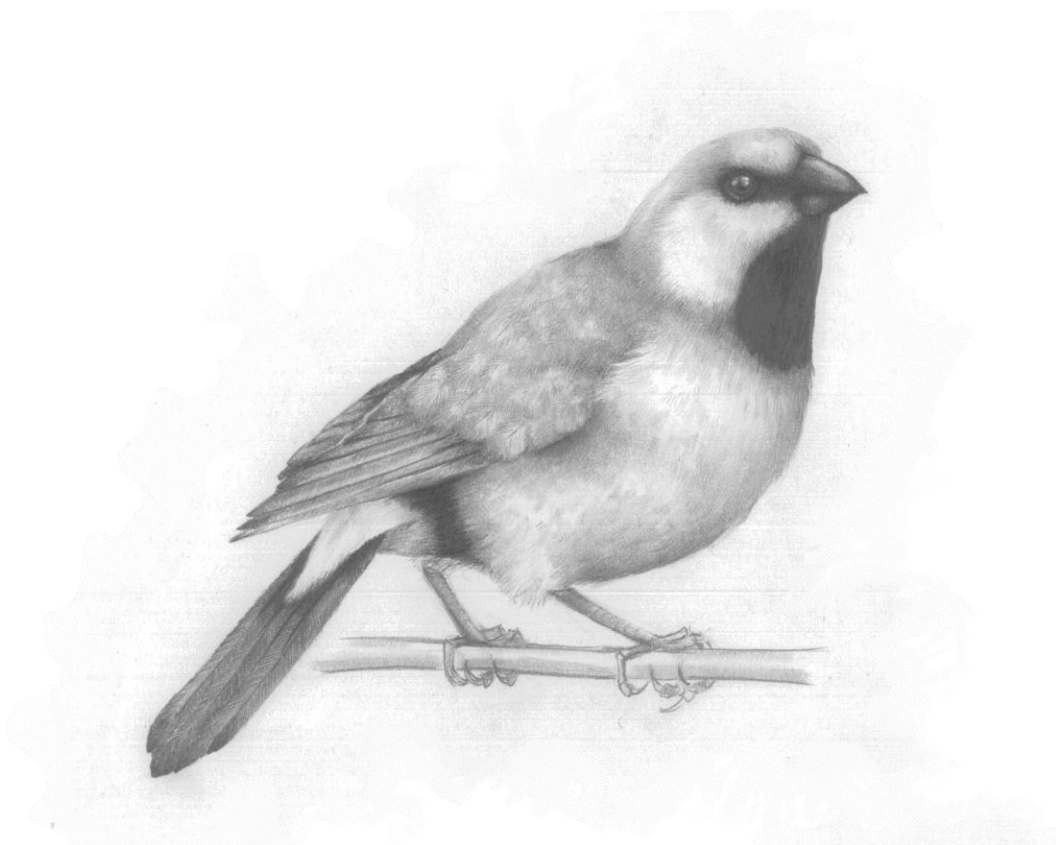
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# **Understanding uncertainty to inform conservation**

**Tools to protect the endangered black-throated finch  
southern subspecies.**



Thesis submitted by

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For the degree of Doctor of Philosophy in the  
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Artwork by Catherine Kelly

# Preface

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I and the rest of co-authors declare no conflict of interests in any of the work included in this thesis. Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

The following publications have come to light as a result of this thesis.

**Chapter 2 – Published as:** Mula-Laguna, J., Reside, A. E., Kutt, A., Grice, A. C., Buosi, P., Vanderduys, E. P., Taylor, M., & Schwarzkopf, L. (2019). Conserving the endangered Black-throated Finch southern subspecies: what do we need to know? *Emu - Austral Ornithology*, 119(4), 331–345. <https://doi.org/10.1080/01584197.2019.1605830>

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**Chapter 4 – Under review as:** Mula-Laguna, J., Schwarzkopf, L., Pintor, A. F., Reside, A. E. Under review. Finding stable areas for conservation in a dynamic environment. *Biological Conservation*.

**Chapter 5 – Prepared for publication as:** Mula-Laguna, J., Griffith S. C., Reside, A. E., Pintor, A. F., DiSibio, S., Schwarzkopf, L. Manuscript in preparation. Picky finches? Ruling out dietary specialisation as a driver of the decline of the endangered southern black-throated finch (*Poephila cincta cincta*).

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# Statement of contributions and Ethics declaration

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## **Statement of contributions of others**

Lin Schwarzkopf (James Cook University) supervised all of the content in this thesis and provided editorial assistance for all written work. She co-authored all data chapters, contributing to their conception and design. Lin provided statistical advice when needed, particularly during chapter 5. April Reside (University of Queensland) supervised all of the content in this thesis and provided editorial assistance for all written work. She co-authored all data chapters, contributing to their conception and design. April provided statistical advice when needed, particularly during chapter 4. Anna Pintor (James Cook University) supervised all of the content in this thesis and provided editorial assistance for all written work. She co-authored chapters 3, 4 and 5, participating in their conception and design. Anna assisted in the collection of data for chapter 3, and provided substantial statistical advice for chapter 4 and 5. Alex Kutt (Bush Heritage Australia at the time of the collaboration), Tony Grice (James Cook University), Peter Buosi (NRA Environmental Consultants), and Eric Vanderduys (CSIRO) provided bibliographical sources and figures for chapter 2, and participated in the review of the manuscript for publication. Martin Taylor provided data for chapter 2, and also reviewed the manuscript prior to submission. Iadine Chadès (CSIRO), acted as a main supervisor during chapter 3, participating in the design, data collection, analysis and manuscript review for chapter 3. Sam Nicol provided methodological advice and reviewed early versions chapter 3. Simon Griffith (Macquarie University) participated in the experimental design, the provision of infrastructure, and the review of the manuscript for chapter 5. Samantha DiSibio assisted in the collection of data for chapter 5. The resulting samples were processed by Rishab Pillai, Christina Baldwin, Elliot Budd and Jodie Nordine.

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**Ethics declaration**

Ethics clearance for expert elicitation in chapter 3 was obtained from the CSIRO Social Science Human Research Ethics Committee (approval 047/18). Experts were asked to sign a consent prior to their participation in the study and were given the option to withdraw at any point.

We obtained ethics approval to conduct foraging experiments on live captive finches from the Macquarie University Animal Ethics Committee (2018/028), in accordance with the Australian code of practice for the care and use of animals for scientific purposes (8th edition, 2013). Finches were provided with food and water at all times, and were only handled when necessary to ensure minimal disturbance. Additionally, we had access to trained personnel, who performed regular health checks on the finches.



# Abstract

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The effective protection of species at risk of extinction requires outcome-oriented decisions. Effective decisions are based on accurate information, yet in many cases, threatened species are rare and hard to study, creating a trade-off between investing time and resources in obtaining information, and acting quickly to halt further declines. Balancing this choice is essential for the persistence of threatened species, while multidisciplinary approaches that can obtain key information without relying on field data, may offer a cost-effective alternative to complement the limitations of studying rare species.

This thesis is a detailed examination of the case of the endangered southern subspecies of the black-throated finch (*Poephila cincta cincta*; BTFS). This granivorous bird endemic to open woodland areas in north-eastern Australia, has lost 88% of its former range due to vegetation clearing and processes associated to pastoralism, becoming rare where they occur. Since the establishment of a Recovery Plan in 2007, there has been a strong focus on collecting more information on the finch's ecology to support management. However, its rarity and inconspicuousness has limited the outputs from research, and our lack of understanding of BTFS's requirements and threats is still viewed as an impediment to effective conservation.

Here I present a multidisciplinary approach to the case of the BTFS to provide detailed information that can be used to inform their protection, while exploring tools that can be applied to the conservation of rare and hard-to-study species. First I evaluated the priorities for BTFS conservation through a review of knowledge and the use of quantitative decision making tools, to then tackle two of the major issues identified: finding priority areas for protection in a temporally variable environment, and assessing the role of certain aspects of BTFS diet as potential risk factors.

In my initial review, I compiled available knowledge on BTFS's ecology and discussed the limitations and gaps in our current understanding of BTFS's requirements and threats. I used this review to create a list of eight research priorities for the conservation of the BTFS, which revolved around monitoring remaining populations, and assessing the effectiveness of management practices in pastoral lands.

Following this review, I applied Value of Information analysis to the case of the BTFS as a decision-making tool to prioritise management and research investment. Value of Information (VoI) analysis is

a framework that uses expert estimates to quantify the difference in outcomes between acting with current uncertainty, and investing in obtaining more information before making a decision. The results are a measure of the value of new information, and can help determine which management and research actions provide a greater benefit for conservation. The study revealed that sparing land for conservation is the most effective action to protect the BTFS. Value of new information was marginal, as the effectiveness of this action did not depend on resolving current uncertainty. However, implementing land sparing at a distribution scale was perceived as unfeasible due to socioeconomic constraints. To identify the best choice in a scenario where land sparing is not possible, I replicated the analysis after removing this action. In this scenario, I found that new information could substantially improve management effectiveness, warranting the investment in further research. Most research value was assigned to understanding the impacts of a potential decline in the availability of seeds, and changes in the configuration of resources in the landscape. Despite these findings, the overall outcomes of this second scenario were lower than implementing land sparing with current uncertainty. This highlights the risks of disregarding effective actions due to socioeconomic constraints, which can lead to inefficient decisions with little benefit.

In reality, the partial implementation of land sparing through the prioritisation of areas of high quality habitat might be the most effective option to stop the decline of the BTFS. However, measuring the value of BTFS habitat can be complex. Savanna habitats are characterised by irregular weather patterns which drive the availability of resources in the landscape, creating periods of local shortages. In response, species such as the BTFS can undertake temporal resource-tracking movements to make use of alternative habitat patches. Therefore, incorporating this dynamic component is key to the evaluation of habitat, as areas that are less exposed to stochastic resource shortages, and are within flight distance of alternative suitable habitat, can provide higher security.

I used 20 years of BTFS occurrence data to fit a dynamic species distribution model trained on monthly short-term climate variables, to generate projections of habitat suitability for each month between 1998 and 2017. The outputs were used to identify temporal patterns and create a classification of habitat stability based on the number of months an area remained suitable, and the distance to alternative suitable areas. I found that although the condition of BTFS habitat tends to follow a seasonal pattern, the extreme differences between years create uncertainty about the availability of suitable habitat at any given time. Of all areas that were considered as suitable at some point, only 30% remained consistently suitable, which should be targeted for protection.

For my last study, I focused on the impacts of a possible decline in the availability of seeds by learning more about BTFS's dietary behaviour. Dietary specialisation is cited as one of the main factors contributing to species' risk of extinction, as it can often limit adaptive capacity. I conducted a comparative study of dietary behaviour using captive bred individuals of four taxa of Estrildid finches endemic to Australian savannas: both the southern (*P. cincta cincta*) and northern subspecies (*P. cincta atropygialis*) of the black-throated finch, the long-tailed finch (*Poephila acuticauda*), and the zebra finch (*Taeniopygia guttata*). I explored two aspects of their diet that may influence dietary adaptability: selectivity, or the display of strong dietary preferences, and willingness to explore and consume novel seed types. BTFS were not substantially more selective than the other taxa, and also showed highly exploratory behaviours. Contrary to my initial hypotheses, zebra finches, the most widespread species of Estrildid finch in Australia, displayed stronger preferences and a reluctance to try novel seed types.

Although I did not find evidence to suggest a higher susceptibility of BTFS based on these traits, I found that BTFS were the only taxon that substantially changed their foraging behaviour depending on the presentation of the seeds. BTFS became more selective when seeds were presented separately than when they were presented mixed, suggesting that their diet might be strongly defined by factors such as resource availability or energetic cost. Although this behaviour could have implications for the conservation of BTFS, the specific mechanisms behind them remain unclear.

In this thesis I provide critical information to guide research, management, and spatial prioritisation for the effective conservation of the BTFS. My results reveal key insights about the habitat and diet of this endangered finch, which can help in the mitigation of threats and the design of management plans. Beyond these findings, my research offers a prime example on how to address problems related to the conservation of rare and hard to study species, and the tools shown here can be applied to a wide variety of cases across the globe.

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# Chapter 1

## Introduction

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Anthropogenic changes are driving the decline and extinction of species at an alarming rate (Barnosky et al. 2011). The International Union for Conservation of Nature estimates that across the globe more than 30,000 species are threatened to some degree (IUCN, 2019), while many other taxa require protection at a regional level. Protecting species at such a large scale requires rapid and effective responses, yet the resources available for conservation are limited. In this context, effective decisions that can target key threats and support species recovery, while making the most of the resources available, are a key piece in the success of conservation action, and a fundamental step to guide conservation research (Maxwell et al. 2015).

Effective decisions require information. Yet in many cases, threatened species are rare, hampering the collection of ecological field data for conservation purposes. Studying rare species is often costly and time consuming, and the outcomes that can be obtained tend to be limited by small sample sizes and the local characteristics of the study population (Raphael and Molina 2013). This situation can create a dilemma between investing time and resources into obtaining information to improve our decisions or acting in time to prevent further declines. Balancing these choices requires a critical process, as additional data does not always result in better management, and the opportunity costs can be too high (Martin et al. 2012, 2016). At the same time, multidisciplinary approaches that can make use of available data to obtain novel information, or identify important patterns without relying on field observations, can provide alternatives to help to complement the limitations presented by rare species.

This thesis is a close examination of the case of the endangered southern subspecies of the Black-throated finch (*Poephila cincta cincta*), a taxon that has recently become a flagship for conservation in Australia due to the high public profile of some of its threats. The southern black-throated finch (hereafter BTFS) is a granivorous bird endemic to open woodland habitats in north-eastern Australia that has lost 88% of its former range over the last 40 years. Remaining BTFS have been pushed to the northern edge of their distribution in Queensland, and have now become rare, as most populations

occur sparsely, loosely concentrated in two major strongholds around Townsville and the Desert Uplands bioregion (Black-throated Finch Recovery Plan 2007; Laguna et al. 2019).

The decline of the BTFS is strongly linked to the widespread clearing of vegetation in the southernmost areas of its distribution, a threat that is still removing important habitat where remaining populations occur (Reside et al. 2019). In addition to clearing, it is generally hypothesized that processes associated with land use changes, most prominently due the spread of pastoralism in Australian savannas, might have contributed to this decline. Poor grazing management, changes in the frequency and intensity of fires, and the introduction of invasive vegetation, are known threats species closely-related to the BTFS, and the broader group of granivorous birds of northern Australia (Bonnet et al. 2010; Franklin et al. 2005; Weier et al. 2017). However, the magnitude of their contribution, and the best way to manage them, remains uncertain.

To protect the BTFS, a dedicated Recovery Plan was designed and published in 2007 (Black-throated Finch Recovery Plan, 2007). This document contains information on the biology and threats to the BTFS, and proposes a list of objectives aimed at improving its conservation status. Yet, the significant gaps in knowledge about the BTFS's total population, and aspects of its fundamental ecology and requirements, resulted in a general demand for further research and monitoring. Since then, there has been an increase in the number of studies targeting the BTFS, revealing critical aspects of its ecology. However, BTFS's small size, inconspicuousness, and rarity, occurring in low density throughout extensive areas of open savanna, have limited the collection of field data, and most knowledge is still incomplete or very localised (Laguna et al. 2019).

Within this context, and the pressing need to take urgent decisions to prevent further declines, I set out to use the case of the BTFS as an example of how novel techniques and diverse sources of information can inform the conservation of rare and hard-to-study species. The leading thread of this thesis is the BTFS, yet, the following pages are also a detailed description of methods that can be applied to a broad spectrum of conservation cases. The outcomes of this work are intended to provide a balance between sufficiently nuanced information to support case-specific planning and management of the BTFS, while also appealing to an international audience of ecologists and conservation scientists that can use our case as an example of how to apply these tools, or improve them based on my results. This premise can be better summarised as two separate but complimentary aims:

1. Generate useful outputs to support the protection of BTFS, by improving the efficacy of conservation decisions and filling key gaps in current ecological knowledge.
2. Provide tools for conservation that can make use of alternative sources of information, when the collection of field data is limited due to urgency, resource costs, or species' rarity and inaccessibility

The thesis will follow a deductive structure, in which the findings of the first chapters are used as a basis and motivation for the following ones. However, all chapters are also independent studies designed to be published in international scientific journals. Given the diversity of topics addressed, I will give a brief background description for each chapter in the thesis, which consists of four standalone studies and a final synthesis and conclusion.

To lay a foundation for the rest of the thesis, chapter 2 is a review of all available knowledge on the status, ecology and threats to the BTFS. Despite the identification of their decline more than two decades ago (Franklin 1999), information about the BTFS population, life history and ecological requirements has historically been scarce, limiting effective conservation action. Dedicated research efforts after the establishment of the Black-throated Finch Recovery Plan have provided more information about their occurrence, main habitat characteristics, or movements, among other aspects of their ecology and potential threats (Maute 2011; Rechetelo 2015; Tang 2017; Vanderduys et al. 2016). However, much of this new knowledge has been scattered among academic, policy and private documents (including consultancy reports and Environmental Impact Assessments), creating small discrepancies, as well as some uncertainty about the accuracy of our assumptions. My aim with this review was to compile in a single source all information on BTFS that could prove useful for its conservation, while providing critical commentary on the limitations of our current knowledge, and pointing out major gaps. Based on this review and with the assistance of other authors who are part of the Black-throated Finch Recovery Team, I created a list of eight research and monitoring priorities aimed to obtain key information to assess the conservation status of the BTFS, evaluate the impact of uncertain threats, and provide useful ecological information to inform management.

While chapter 2 provides the theoretical foundation for the rest of the thesis, chapter 3 is the quantitative basis on which I decided which research questions should be addressed in my remaining chapters. Here I explored the use of Value of Information analysis applied to the case of the BTFS, as a tool to improve the effectiveness of conservation decisions. Value of Information (VoI) analysis can

be described as a quantitative framework designed to measure the value of new information based on current knowledge. It originates from economic assessments of risk investment (Raiffa and Schlaifer 1961), but has been successfully applied to complex conservation decisions as a way to optimise the investment trade-off between research and management (Keisler et al. 2014). Vol is calculated on estimates provided by a group of experts that represent the best available knowledge on the study system. The results are a measure of the difference between the conservation outcomes of implementing management actions with current uncertainty, or after investing time and resources in removing said uncertainty. Furthermore, Vol can be broken down to identify which particular management and research actions accumulate more value for conservation and should be prioritised.

The results of chapter 3 helped to clarify the benefits of investing in the research objectives suggested in chapter 2, some of which we address in this thesis, and highlight which management actions should be prioritised in an impending update of the Black-throated Finch Recovery Plan. In addition to the specific implications for BTFS conservation, this study provides a prime example on how Vol can help in the elaboration of conservation planning documents, and offers a novel insight into the risks of disregarding effective conservation actions that might be perceived as unfeasible due to socioeconomic constraints.

One of the key findings of chapter 3 was that land sparing is the safest and most effective action to prevent further declines of remaining BTFS populations. Yet again, the selection of areas for the protection of species requires careful planning to make the most of the resources available. In this prioritisation process, the first step is to determine which areas offer a higher value for conservation. This evaluation is typically carried out by surveying habitat and determining its suitability according to its ecological factors and the requirements of the target species or community. However, BTFS habitats present a few particularities that can be an obstacle for the evaluation of suitability.

Australian savannas are known for their irregular weather patterns that can drive the availability of ephemeral resources, such as water and grass seeds (Garnett and Williamson 2010). As a response, many savanna species have developed adaptations to shortage periods, making use of alternative resources or temporarily moving to areas that are more suitable. Previous studies have shown that, although BTFS prefer to maintain small home ranges, they are also capable to disperse for distances of up to 17 km (Rechetelo 2015). The causes of these movements have not been clearly established, but observations suggest that they might be a response to shortages caused by extreme weather events. Therefore, the correct assessment of the value of BTFS habitat should incorporate these

temporal shifts, measuring suitability as dynamic variable, where factors like stability and access to alternative areas of suitable habitat are key to the persistence of local populations.

In chapter 4, I used a Dynamic Species Distribution model, a variation of traditional species distribution models replacing long-term climate data by monthly weather conditions, to generate monthly maps of BTFS habitat suitability for the period 1998-2017. I used the results to examine temporal patterns in the availability of suitable habitat, and create a classification of habitat stability according to the number of months an area was estimated to be suitable, as well as the distance to alternative areas, that could act as a safety net during shortage periods. The outcomes of this chapter provide a guide for spatial conservation planning that can combine our habitat mapping with additional factors to decide on priority areas for the protection of BTFS. Furthermore, we demonstrate how Dynamic Species Distribution models can be used to identify irregular spatiotemporal patterns in ecological studies and optimize habitat protection in highly variable environments.

Another key conservation priority identified in our Vol analysis was to resolve current uncertainty on the potential impacts of declines in seed availability on BTFS. This is a complex question that requires a better understanding of potential risk factors in the diet of BTFS, as well as the processes affecting the quantity and access to seed. Traits associated with a higher dietary specialisation have been traditionally linked to species' risk of extinction (Purvis et al. 2000). Their dependence on a small variety of food types can make dietary specialists less resilient to changes in the availability of their preferred resources. Furthermore, specific behavioural traits such as the display of strong dietary preferences, or a reluctance to explore novel food items, can limit their adaptability if alternative resources become abundant.

Habitat modifications and the introduction of invasive species are recognised as two of the most prominent threats in Australian savannas (Grice et al. 2013; Whitehead, Russell-Smith, and Woinarski 2005). Processes such as cattle grazing and changes in fire regimes can modify the native grass community, along with the types of seeds available to granivorous species. Likewise, invasive grasses have become prevalent throughout savanna habitats (Cook and Grice 2013), and in some areas, they can dominate the community, replacing familiar seeds with novel types. While there is some information about the diet of BTFS showing that they may be able to adapt to changes in seed availability, not much is known about their level of specialisation and their responses to exotic seed types. As my last standalone study, in chapter 5, I explored aspects of the foraging behaviour of BTFS that could have increased their susceptibility to environmental changes. To do so, I compared foraging

selectivity, and willingness to explore novel seed types between BTFS and three closely-related taxa of Estrildid finches. The results clarify prior hypotheses about the role of diet in the decline of the BTFS, while offering details about the particularities of their dietary behaviour. Furthermore, the study provides a more general insight into the assumptions around the ecology of and threats to dietary specialists, which may be conditioned by a plethora of factors.

In my sixth and final chapter, I summarise the key findings of each data chapter and discuss the case-specific implications for the conservation of the BTFS. I conclude the thesis highlighting the lessons learned and listing my recommendations on possible future for BTFS conservation and research.

My work provides a comprehensive source of information on the ecology and threats of BTFS, and addresses key questions to guide efficient research and management investment. This thesis offers a solid foundation for an update of the Black-throated Finch Recovery Plan that can provide the best advice for the protection of this endangered finch.



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# Chapter 2

## Conserving the endangered black-throated finch southern subspecies: what do we need to know?

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### Abstract

Successful conservation of threatened species requires judicious allocation of limited resources. The threatened black-throated finch southern subspecies (*Poephila cincta cincta*), endemic to north-eastern Australia, has suffered an 80% contraction in its historical range. Stemming ongoing habitat loss is the main priority in its conservation, but remaining areas where habitat has been degraded require active management. However, the scarce information about the subspecies' ecology has inhibited effective conservation planning. In this paper, we gather and review current knowledge on the Black-throated finch southern subspecies' ecology and threats and propose a list of research priorities aimed to support conservation management. We highlight how available knowledge could lead to false assumptions due to the limited temporal scope of most studies and their focus on a substantially modified area within its current range. There is a shortage of information on the present population size and distribution of the subspecies, which creates uncertainty about its conservation status. Our top three priority actions are focused on monitoring the remaining populations and evaluating the effects of management practices in pastoral land. We expect this paper to serve as a first step to create a cohesive framework for researchers and stakeholders when deciding to invest in the conservation of this iconic finch.

**Keywords:** black-throated finch; threatened species; conservation planning; habitat loss; granivorous birds.

## Introduction

Ongoing declines and extinctions of species worldwide require effective conservation action (Barnosky *et al.*, 2011). Australia is recognized as a globally significant region for conservation (Rodrigues *et al.* 2014), but it presents an unusual case, in that it has high extinction rates, yet many declines and extinctions have occurred in remote areas, often regarded as relatively unmodified (Woinarski, Burbidge, & Harrison, 2015). Strong support for hypotheses behind these declines has only surfaced in the last decade, pointing at the expansion of pastoralism and introduced predators after European settlement as the leading threats (Kutt & Woinarski, 2007; Frank *et al.*, 2014; Woinarski, Burbidge, & Harrison, 2015).

Endemic granivorous birds are one of the most prominent groups affected by changes in Australian savannas. One species, the Paradise Parrot (*Psephotus pulcherrimus*) was declared extinct in the 20<sup>th</sup> century, and many taxa show long-standing trends of decline (Franklin, 1999; 2005). Among them, Estrildid Finches have drawn particular attention, with four species currently listed as threatened at some taxonomic level under *Australia's Commonwealth Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act).

Habitat loss is recognised as the top threat for Australian declining finches, primarily caused by clearing and other widespread processes transforming the landscape, such as stock grazing, altered fire regimes, and the spread of exotic plants (Tidemann, 1996; Garnett *et al.*, 2005; O'Malley, 2006; Black-throated finch Recovery Team (BTFRT), 2007; Legge *et al.*, 2015). These changes involve intricate ecological interactions, which are poorly understood and generate much uncertainty for conservation management.

Targeted research on the Gouldian Finch (*Erythrura gouldiae*), one of the most iconic species in the group, has proven useful to understand its responses to complex dynamics such as fire (Legge *et al.*, 2015). However, information for other species is scarce, and often context dependant. More conservation-oriented research is needed, but acquiring knowledge is costly and time consuming, and given the limited resources available for conservation, it is important to weigh up the benefits of investing in species research against implementing management actions (Maxwell *et al.*, 2015).

Another species of Estrildid finch, the black-throated finch (*Poephila cincta*) offers a particularly dramatic example of the shortcomings of a lack of ecological information that can be applied to conservation. Its southern subspecies (*Poephila cincta cincta*), one of the two genetically distinct

subspecies (Tang, 2017), suffered an 80% reduction of its extent of occurrence over the last two decades of the 20<sup>th</sup> century (Threatened Species Scientific Committee, 2005; BTFRT, 2007; NRA, 2007). Due to this contraction, it is currently considered as ‘Presumed Extinct’ in New South Wales under the *Biodiversity Conservation Act 2016*, and ‘Endangered’ both in Queensland and nationally under the *Nature Conservation Act 1992* and the EPBC Act.

Despite the early identification of this decline (Franklin, 1999), the conservation of the black-throated finch southern subspecies (hereafter BTFS) has been hampered by a lack of knowledge around the subspecies’ ecology. As a response, a dedicated Recovery Plan was completed in 2007 (BTFRT, 2007). Recovery Plans aim to identify research and management actions to conserve threatened species and ecological communities listed under Australia’s EPBC Act. However, regardless of recent research efforts (Isles, 2007; NRA, 2007; 2009; 2011; Whatmough, 2010; Maute, 2011; Rechetelo, 2016, Vanderduys *et al.*, 2016; Melton, 2017; Tang, 2017), few conservation gains have been achieved eleven years after the initial plan (Reside *et al.* 2019), and there is still much uncertainty around the state of knowledge of the BTFS or best management guidelines.

A list of clear research questions aimed to inform the management of the BTFS is the first step to improve the effectivity of conservation efforts. In this paper, we review the case of the BTFS, one of the most alarming examples of decline of Australian granivores. We present a critical examination of all available information of the BTFS’s ecology and threats, highlighting the main gaps and areas of possible bias that generate uncertainty for conservation planning. Our final aim is to outline research priorities that can be used as guidelines for future studies, optimising conservation investment.

## **Ecology of the black-throated finch southern subspecies**

### *Distribution and abundance*

The BTFS historically occurred in an area up to 500 km inland from north-eastern New South Wales to a broad hybridization zone with the northern subspecies (*Poephila cincta atropygialis*) between the headwaters of the Burdekin and Lynd Rivers in north-eastern Queensland (Morris *et al.*, 1981; Ford, 1986; Ley & Cook, 2001) (Fig. 2.1).

Post-2000 sightings indicate a significant contraction towards the northern edge of their distribution, and most records concentrate within two stronghold areas (Fig. 2.1). These roughly correspond to the Townsville Coastal Plain subregion on the northern border of the Brigalow

Belt Bioregion, and the eastern half of the Desert Uplands Bioregion (as described by the Department of the Environment, Interim Biogeographic Regionalisation for Australia version 7, 2012).

Recent bird surveys in the Desert Uplands eastern edge record the highest abundance of BTFS per unit effort (GHD Pty Ltd, 2012; 2013; 2014), which suggests that the area supports the largest remaining BTFS population. However, there is no reliable estimate of the total number of remaining BTFS in the wild and the lack of systematic long-term monitoring creates uncertainty about ongoing population trends. The longest running monitoring program for the BTFS is an annual count conducted at waterholes in the area surrounding the city of Townsville since 2003. However, results are likely to be biased by water availability at waterholes depending on patterns of preceding rainfall.

Distribution-wide, opportunistic observations reveal that the number of big flocks has decreased in favour of smaller ones both in the Townsville Coastal Plain and the Desert Uplands (Fig. 2.2). While this could be an artefact of a likely increase in fragmentation due to habitat loss and the non-systematic origin of the data, it raises concerns about an ongoing population decline within both remaining BTFS strongholds.

The scarcity and inconspicuousness of the BTFS, and its distribution across extensive, rarely-surveyed rangelands, poses a significant challenge for the collection of accurate occurrence and abundance data. As a consequence, it is likely that current knowledge of its extent of occurrence and area of occupancy is incomplete. Available habitat suitability models (Vanderduys *et al.*, 2016) provide useful information about remaining suitable areas, but these should be treated carefully, as a lack of field data can create a false impression of the true extent of occupied habitat (Cosgrove, McWhorter & Maron, 2017). The shortage of data about the BTFS abundance and distribution limits the accurate assessment of the conservation status of the subspecies, which in turn limits strategic planning.

### *Habitat*

BTFS mainly inhabit tropical open woodlands dominated by tree species in the genera *Eucalyptus*, *Corymbia* and *Melaleuca* (Isles, 2007; NRA, 2007; GHD Pty Ltd, 2012; 2013; Rechetelo, 2016). These habitats combine areas of sparse woody vegetation used for nesting, resting, or as vantage points, with a ground layer of grass with patches of bare ground on which to forage (Mitchell, 1996; Rechetelo, 2016). Their occurrence is associated with areas in the

vicinity of permanent sources of drinking water, such as streams or waterholes, which they visit daily (NRA, 2005; 2009; Rechetelo, 2016). Ephemeral water sources are also used (GHD Pty Ltd, 2013), and may be critical to allow dispersion and sustain populations year-round. BTFS also occur in denser woodland and open forests with riverine vegetation (Baldwin, 1976; Morris *et al.*, 1981; Immelman, 1982), but the use of riparian areas has been less often reported within their current range.

A significant part of BTFS habitat is currently restricted to pastoral lands (NRA, 2009; 2011; GHD Pty Ltd, 2012). Such areas are often exposed to high grazing pressure and the presence of non-native vegetation, which is likely to result in sub-optimal habitat (BTFRT, 2007). BTFS prefer areas of lightly grazed or ungrazed native grasses (GHD Pty Ltd, 2012; 2013; Rechetelo, 2016), while heavily grazed sites are avoided (GHD Pty Ltd, 2012; 2013). Furthermore, BTFS on pastoral land show significantly higher hormonal indicators of stress compared to individuals of the northern subspecies in protected areas (Maute, 2011).

In species conservation, understanding the key habitat features determining suitable habitat is an essential component to guide on-site management practices and identify high quality areas that need to be protected. This is particularly important in cases like the BTFS's, where the extent of remaining suitable habitat is already limited. Due to the lack of quality data from regions other than the highly modified Townsville Coastal Plain (Table S2.1), it is likely that our knowledge of the optimal habitat requirements of the BTFS is biased or incomplete. Information from the Desert Uplands is scarce and relies on broad vegetation classifications and plant inventories (GHD Pty Ltd 2012; 2013). Likewise, the absence of long-term studies (Table S2.1) limits our understanding of seasonal changes in the habitat, which is critical to design management plans to ensure persistence throughout the year.

#### *Movement ecology*

BTFS is generally described as “sedentary” or “resident” (Higgins *et al.*, 2006; Garnett *et al.*, 2011). Individuals often occupy the same site for 100 to 600 days (Rechetelo, 2016), which suggests that they may inhabit the same areas throughout their life. Genetic population structuring can occur over a distance of 10-20 km, seemingly limited by habitat fragmentation and the presence of dispersal barriers, such as large water bodies (Tang, 2017).

Locally, BTFS perform daily foraging and drinking movements, which tend to be restricted to less than 350 m from their roost (Isles, 2007). Nonetheless, there are records of individuals moving

up to 1.5 km in a day (Mitchell, 1996). Most daylight hours are spent foraging or perching, moving in small groups early in the morning and aggregating into bigger flocks later (Mitchell, 1996; Rechetelo, 2016), often mixing with other species (GHD Pty Ltd, 2012; 2013; 2014; Vanderduys *et al.*, 2012).

Home range estimates show that, during the dry season, BTFS use an area of 50.79 ha (min = 25.15; max = 120.88) (Rechetelo, 2016). Alternatively, pairs forage in an area of 12 ha during the breeding season (NRA, 2005); while shortly after breeding, this area may be as small as 2.3 ha (Isles, 2007). However, these results remain inconclusive, as they are based on scarce, short-term data, and due to disparities among methods, they are not comparable (Table S2.2).

Despite their seemingly sedentary habits, BTFS have been recorded moving more than 16 km in a minimum of 49 days (Rechetelo, 2016). There is no information on the frequency and drivers of these movements, although it has been suggested that they might be triggered by weather events (Baldwin, 1976; McCutcheon, 1976; Passmore, 1982; Mitchell, 1996). This behaviour is common in other Estrildid finches, which have developed partially nomadic habits, performing long-range resource-tracking movements as a response to local bottlenecks (Higgins *et al.*, 2006).

Given the difficulties in tracking the movements of BTFS and obtaining systematic data, there is still much uncertainty about their movement ecology. The limited information available has been exclusively collected in the Townsville Coastal Plain, where the landscape is highly fragmented; a factor that might bias our interpretation of the BTFS's behaviour in other contexts. Further investigation on the home range and long distance movements of the BTFS is needed to understand its fundamental spatial requirements, which can help inform spatial planning.

#### *Diet and foraging behaviour*

BTFS primarily forage on fallen seeds of grasses, sedges and legumes (Mitchell, 1996; NRA, 2005; GHD Pty Ltd, 2012; Rechetelo, 2016). Systematic diet observations are scarce (Table S2.3), and most information on species consumed originates from opportunistic records and indirect sources such as plant composition at foraging patches (Table S2.5). There is an apparent preference for native grasses (Rechetelo, 2016), but seeds of non-native species are often consumed (Table S5) and could, in particular cases, provide the bulk of their diet (Mitchell, 1996).



The high variability in seasonal and inter-annual weather patterns typical within tropical savannas leads to large fluctuations in plant composition and condition of foraging habitat (Crowley & Garnett, 1999; Crowley & Garnett, 2001). Resource bottlenecks might occur at the end of the dry season, when productivity is low, or at the onset of the wet season, when seeds are germinating or inaccessible due to flooding (Mitchell, 1996). In response to these bottlenecks, BTFS can shift their dietary habits, widening the diversity of seeds consumed (Isles, 2007; Meyer & Agnew, 2012; Mitchell, 1996), changing their foraging strategies (Mitchell, 1996), or preying on termites and other insects (Rechetelo, 2016).

Uncertainties about the role of specific grasses common within BTFS habitat (Rechetelo, 2016) need to be clarified. Habitat management plans should aim to identify and promote local seeding species that can provide suitable seed, while allowing a patchy ground layer where BTFS can forage (BTFRT, 2007). A better understanding of the causes and impacts of seed shortages can also prove useful to inform adaptive management that can minimise the risk of seasonal population declines.

#### *Nesting and breeding*

BTFS aggregate in loose colonies to breed, building their nests within the foliage, forks, hollows or mistletoes in the outer branches of trees (North, 1901-14; Roberts, 1955; Campbell, 1974; Baldwin, 1976; NRA, 2005; Rechetelo, 2016). Preferred nesting trees include species in the genera *Eucalyptus*, *Corymbia* and *Melaleuca* (GHD Pty Ltd, 2013; Rechetelo, 2016), rarely found more than 400 m away from a permanent water source (Isles, 2007). Nests are made out of woven grass (North, 1901-14; Campbell, 1974), and can be used for breeding or roosting, often serving both purposes (NRA, 2005). Pairs are socially monogamous and show site fidelity, often using the same nest in consecutive years (NRA, 2005; Isles, 2007).

BTFS can breed at any time of year (Forshaw *et al.*, 2012) (Table S2.4), though peaks in breeding activity seem to coincide with periods of high food availability, which, in the Townsville Coastal Plain, tend to occur two months after substantial rainfall (Mitchell, 1996). BTFS lay 5 to 6 eggs per clutch (North, 1901-14; Campbell, 1974), and juveniles remain with their family group months after becoming fully independent (Forshaw *et al.*, 2012). There is a shortage of information about the BTFS's life cycle in the wild, but captive individuals reach sexual maturity after 6 months, while life expectancy is 4 to 6 years (Shephard, 1989).

Factors influencing breeding success in the BTFS are still largely unknown. In other Estrildids, competition over high-quality sites can cause a reduction in reproductive success (Brazill-Boast, Pryke, & Griffith, 2010, 2013; Brazill-Boast *et al.*, 2011). In the case of the BTFS, limited access to foraging resources is a more likely cause for breeding failure. Seed shortages can lead to the abandonment of their nesting areas (NRA, 2005). Understanding the factors driving to breeding success is essential to manage populations and support their recovery.

### **Main threats to the black-throated finch southern subspecies**

#### *Habitat destruction: land clearing*

Land clearing is recognised as the leading historical cause for the decline of the BTFS (BTFRT, 2007; Reside *et al.* 2019). BTFS habitat loss due to clearing has been more intense in the southern parts of its former range, particularly affecting riparian woodlands (BTFRT, 2007; NRA, 2007; Reside *et al.*, 2017). The Brigalow Belt Bioregion, which encompasses the Townsville Coastal Plain, one of the two BTFS strongholds, has one of the highest current and historic rates of clearing in Queensland, with more than 50% of its area already cleared (Accad *et al.*, 2017; Reside *et al.*, 2017).

Ongoing urban expansion around Townsville further threatens to remove BTFS habitat. Since European settlement, the estimated average size of habitat patches available to BTFS in the region has dropped from 168 ha to 33 ha (Whatmough, 2010). In 2010, proposals for development of the Townsville Coastal Plain were predicted to cause the further loss of 3,190 ha of BTFS habitat (Whatmough, 2010), some of which has already occurred.

Globally, more than 36,000 ha of BTFS habitat were cleared between 2013 and 2015, and another 120,000 ha have been slated for clearing for agriculture (Department of Science, Information Technology and Innovation of Queensland, 2015; 2016). Further habitat loss in areas that might be crucial to the persistence of surrounding populations, either as seasonal resource refuges, or as stepping stones, might lead to a collapse of BTFS populations (Saura, Bodin & Fortin, 2014). Habitat suitability models predict that 56.9 % of remaining BTFS habitat falls within resource extraction or exploration tenures (Fig. 2.3; Vanderduys *et al.*, 2016). Within these, currently approved plans for extensive areas of open-cut and underground mining within the Desert Uplands (Hancock Prospecting Pty Ltd, 2010; Macmines Australia Pty Ltd, 2012; AMCI Pty Ltd & Alpha Coal Pty Ltd, 2012) would remove almost 50% of BTFS habitat within the region (Vanderduys *et al.*, 2016).

Most described projects propose to individually mitigate their impacts through offsetting (Ecological Australia, 2012, EHP, 2013). However, the limited area of suitable BTFS habitat remaining, the poor condition of selected offsets, and the lack of a BTFS-specific cumulative impact assessment, or a coordinated plan for development, makes offsets unlikely to compensate for the losses caused by clearing (Vanderduys *et al.*, 2016; Melton, 2017).

#### *Habitat modification: changes in grazing and fire regimes*

Widespread livestock farming has led to significant changes in habitat condition within BTFS range, often resulting in a degradation of available habitat (BTFRT, 2007). Increased grazing pressure and trampling removes biomass from the grass layer, decreasing seed production and altering the composition of the community (Woinarski & Ash, 2002, Read & Cunningham, 2010). The severity of these threats has been greater in the southern parts of the BTFS's historical range, coinciding with a predominance of sheep grazing rather than cattle, and larger rabbit populations (Garnett, 1993; Franklin, 1999), which might help explain past patterns of disappearance.

Changes in fire regimes are known to affect Australian bird communities (Woinarski, 1990; Woinarski & Legge, 2013). Intensive grazing regimes often result in a reduction of natural fuel loads (Roques, O'Connor, & Watkinson, 2001). Additionally, fire management practices in small pastoral properties of northern Australia typically involve exclusion (Fensham, 1997). As a result, there is likely to have been an overall reduction in fire frequency and intensity within BTFS habitat, favouring the predominance of shrubs and low stratum woody vegetation (Moreira, 2000), which compete with grasses (Scholes, & Archer, 1997).

#### *Habitat modification: introduced plant species*

Pastoralism has contributed to the spread of non-native plant species in Australia (Grice *et al.*, 2013). Invasive shrubs such as chinese apple (*Ziziphus mauritiana*) and lantana (*Lantana camara*) often form thickets, dominating the landscape (Smith, 2002). The proliferation of both species in areas inhabited by BTFS coincides with a decrease in BTFS abundance (Rechetelo, 2016), suggesting that they are negatively impacted by invasive shrub species.

The impacts of introduced grasses are less well understood. Some species may be less suitable food sources when compared to native grasses (NRA, 2007; Grice *et al.*, 2013), and BTFS tend to avoid foraging patches where introduced species, such as grader grass (*Themeda quadrivalvis*), are abundant (Rechetelo, 2016). However, other non-native species such as sabi grass (*Urochloa*

*mosambicensis*) and southern crabgrass (*Digitaria ciliaris*) can be dietary resources (Mitchell, 1996).

#### *Other threats*

Other threats might have contributed to local extinctions, aggravating the impacts of habitat loss. Introduced predators such as cats (*Felis catus*), are known to prey on Estrildid finches (Barratt, 1997; Paltridge, 2002), including BTFS (Woinarski *et al.*, 2017). However, specific records on predated BTFS are anecdotal, leading to uncertainty about the magnitude of this threat.

Droughts and other catastrophic phenomena, such as tropical cyclones or storms typical of north-eastern Queensland, can lead to abandonment of nests and deterioration of suitable habitat (NRA, 2005). These phenomena might become a severe threat in areas where fragmentation is greater, as access to alternative suitable habitat is limited, and may result in mortality events.

Aviculture might also negatively affect BTFS populations (BTFRT, 2007). Trapping is likely to have led to local extinctions in the past, although it is unlikely to be a substantial threat in the present (Roberts, 1979; Garnett *et al.*, 2011). Likewise, hybridisation with escapees can be detrimental for the genetic stock of small populations (BTFRT, 2007), but little is known about hybridisation rates in the wild.

#### **Future research aims**

There is still much uncertainty around the status and ecological requirements of the BTFS. While its decline was identified decades ago, available data on the abundance and distribution of the BTFS are scarce. Establishing adequate monitoring programs is a top priority to assess the true status of the BTFS, identify the impact of ongoing threats and the outcomes of management actions.

Further ecological studies should target information necessary to implement effective management actions. The current partial understanding of many aspects of the BTFS's ecology could lead to inefficient allocation of resources, or even result in perverse conservation outcomes (e.g. Game, Kareiva, & Possingham, 2013). Many of the gaps in BTFS knowledge are a result of the difficulties associated with collecting data on a rare and inconspicuous species, as well as the limited spatial and temporal scope of past studies.

With these priorities in mind, we propose the following list of research actions:

(i) Monitor BTFS population trends by implementing adequate long-term count schemes, prioritising the two known strongholds. A combination of techniques, such as waterhole surveys, active searches and camera trapping, have shown to improve accuracy (GHD Pty Ltd, 2012; 2013).

(ii) Map the current area of occupancy of the BTFS and monitor possible contractions. Surveying for presence throughout its potential extent of occurrence using methods as described in research action (i) can improve detection, but passive techniques such as bioacoustic monitoring should be tested, as they might provide an inexpensive alternative.

(iii) Conduct field experiments to identify the best grazing and fire management regimes to provide management recommendations that can ensure BTFS persistence in pastoral lands.

(iv) Improve our understanding of the main habitat features determining suitability. Comparative habitat studies between the two strongholds can prove particularly informative especially focusing in the role of vegetation structure.

(v) Evaluate the effects of fragmentation on population size and viability. Similar to action (iv), a the study should focus on possible differences between the highly fragmented Townsville Coastal Plain, and the less modified Desert Uplands region.

(vi) Determine dietary preferences by conducting seed choice experiments, as well as investigate the local role of specific grass species to inform vegetation management. This information might prove hard to obtain in the field, but captive individuals can help to clarify current uncertainties.

(vii) Investigate the spatial requirements of the BTFS by acquiring long-term systematic movement data that can help refine current home range estimates and reveal the drivers for longer distance movements.

(viii) Identify the main drivers of reproductive success, targeting the effects of the most likely limiting factors, such as food resource bottlenecks.

The proposed list of research actions is ranked according to our qualitative assessment of pressing knowledge needs. However, given the limited resources available for conservation, it is important to evaluate the costs and benefits of investing in ecological research against threat abatement (Maxwell *et al.*, 2015). Any research should be conducted while obvious threats are halted or minimised, the most prominent being habitat clearing.

We recommend further quantitative evaluation of research priorities to determine the value of obtaining new information. For this purpose, we suggest performing a value of information analysis, a decision-making tool used to quantify the expected management gains of investing in reducing uncertainty (Runge, Converse & Lyons, 2011). The results of such study can help setting up an objective framework for resource allocation that can be implemented in structured decision-making and adaptive management plans (Moore & Runge, 2012; Saura, Bodin & Fortin, 2014)

We expect that this review and our recommendations will add valuable information to previous and ongoing conservation efforts such as the upcoming update of the black-throated finch Recovery Plan, leading towards more cohesive planning and the successful conservation of the BTFS. Much of the knowledge gained by our recommendation is likely to be relevant to other declining granivorous birds, and also for other components of declining woodland bird communities (Fraser *et al* 2019). Further understanding the effect of different management regimes, particularly for grazing and fire, are still research priorities for woodland birds across Australia (Ford 2011).

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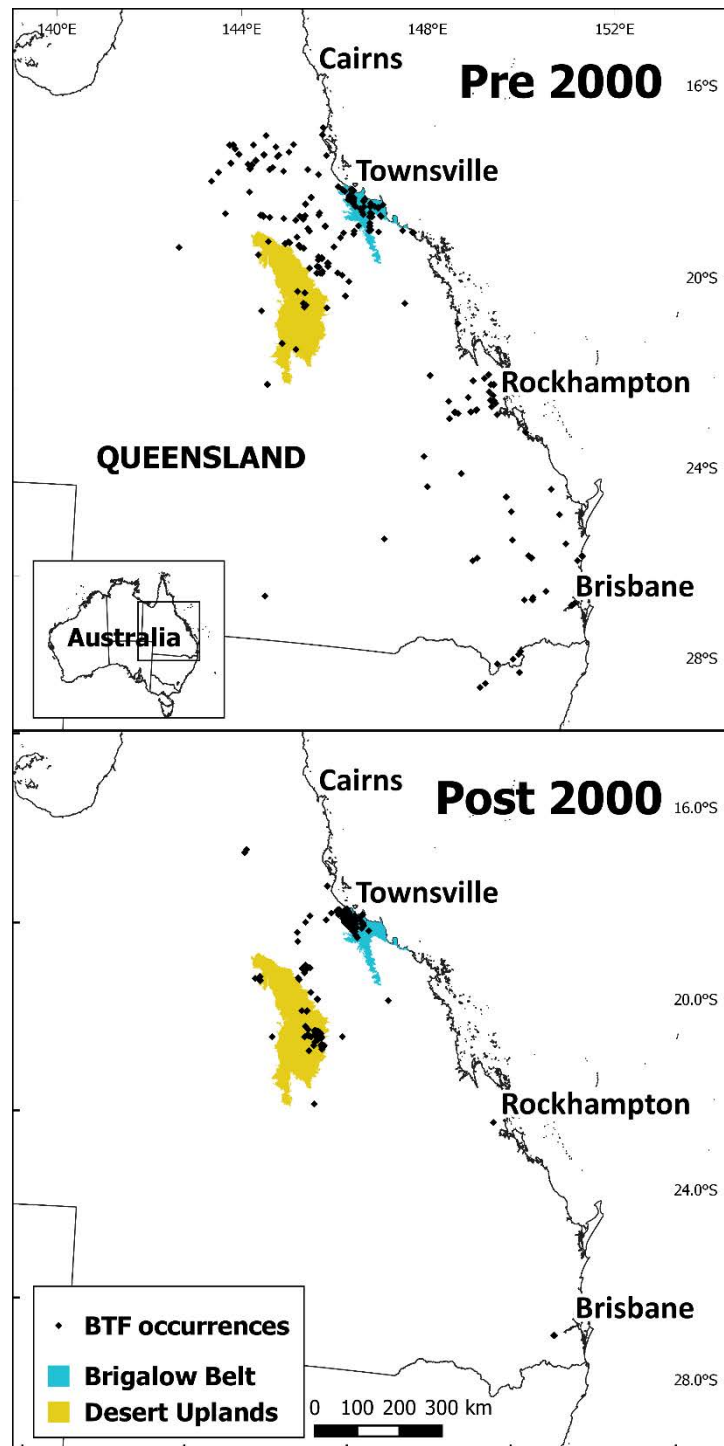
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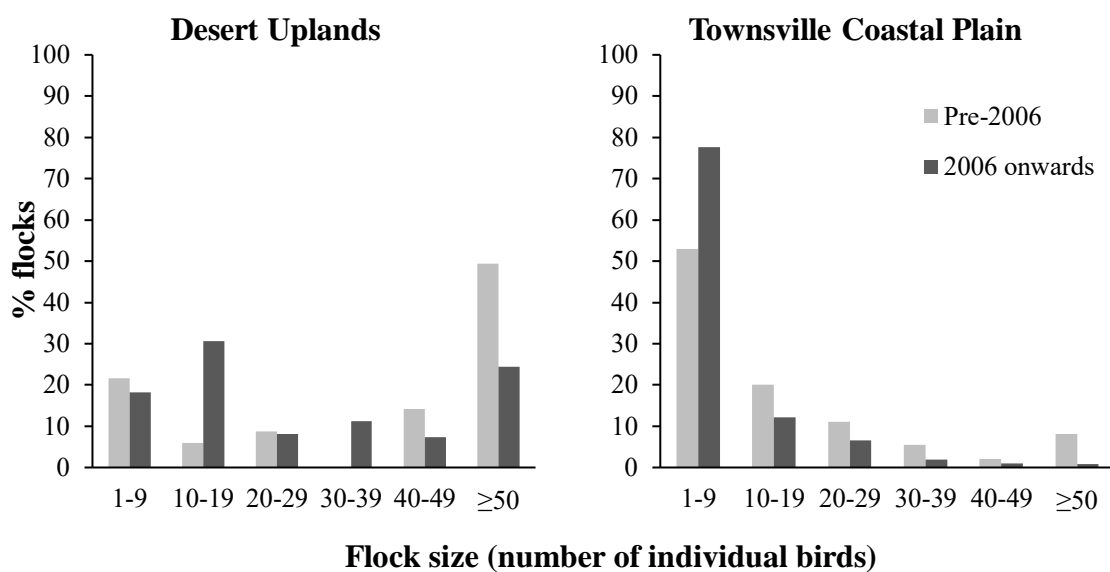
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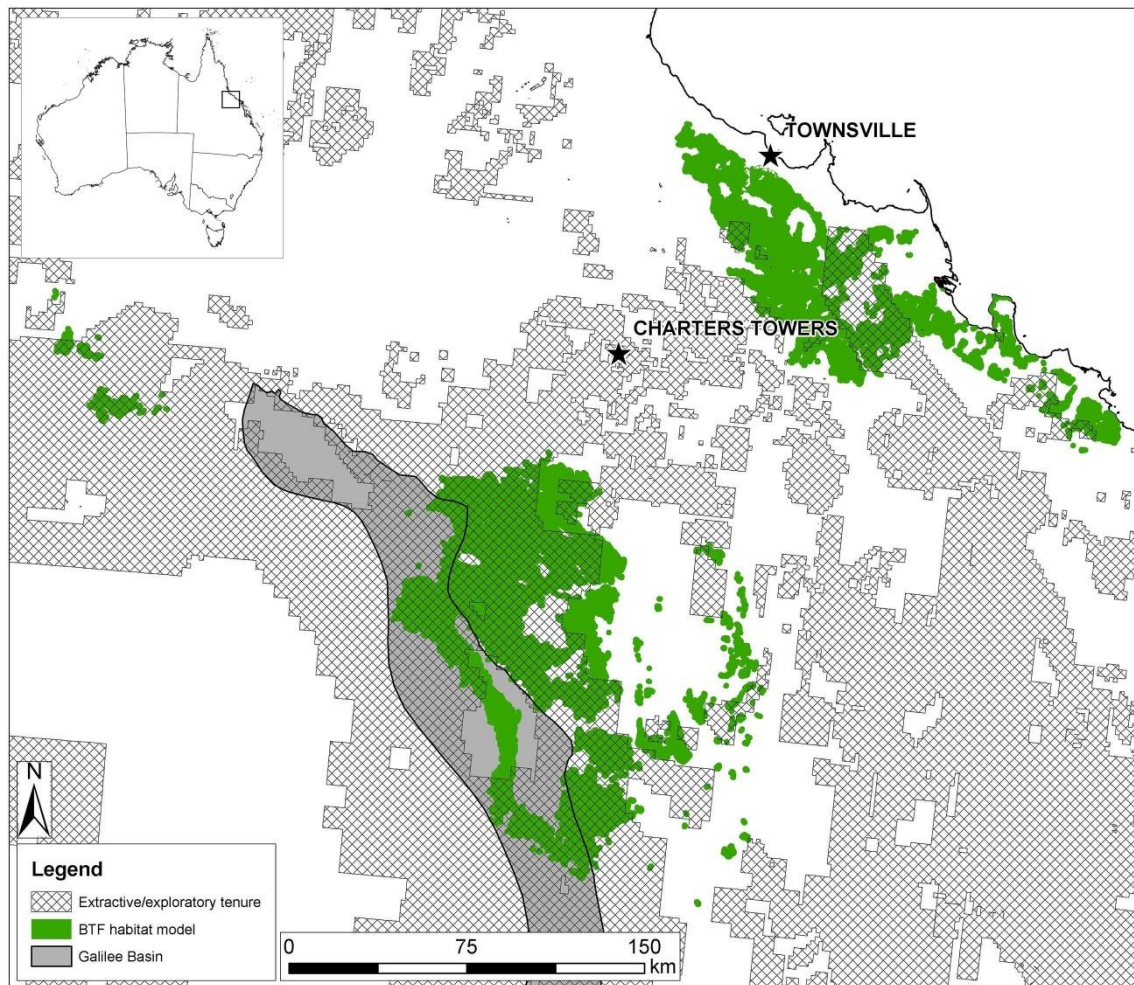
## Figures



**Figure 2.1.** Decline in occurrences of black-throated finch southern subspecies (BTFS). Data from the BTFS Recovery Team Database. BTFS records pre 2000 (top) and post 2000 (bottom). Coloured areas indicate the two main stronghold bioregions in Queensland, Australia where the BTFS occurs: Townsville Coastal Plain in blue and Desert Uplands in yellow (maps accessed from <https://www.environment.gov.au/land/nrs/science/ibra>).



**Figure 2.2.** Black-Throated finch southern subspecies (BTFS) flock sizes pre- and post-2006 in the two its remaining stronghold areas in Queensland Australia: the Townsville Coastal Plain and the Desert Uplands. Data from the BTFS Recovery Team Database (BTfRT, unpublished)



**Figure 2.3.** Predictive model showing remaining suitable habitat for the black-throated finch southern subspecies (green). Hashed area represents tenures with granted extractive or exploratory permits and susceptible of clearing. The grey area marks the Galilee Basin, which encompasses properties with approved plans for open-cut coal mining. Source: Vanderduys *et al.*, 2016. Used under a CC BY license, with permission from Eric Vanderduys, original copyright 2015.



# Chapter 3

## Clarifying the value of unfeasible actions for species recovery

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### Abstract

- 1) Globally more than 32,000 species are threatened with extinction, and securing them requires efficient allocation of the resources available for conservation. However, the lack of information on species' needs is a common obstacle for their protection. While research can help improve the effectiveness of management, the delay of conservation action can result in irreplaceable losses.
- 2) Value of information (Vol) analysis calculates the relative benefits of obtaining new information before acting, against acting with current uncertainty. While Vol has been proposed as a best practice approach to guide research investment, it has not been applied in the design of key conservation documents such as recovery plans, which establish research and management priorities for the protection of species and communities.
- 3) The endangered southern subspecies of the black-throated finch (*Poephila cincta cincta*) has lost 88% of its range over the last four decades. Although a recovery plan is in place, conservation action has been delayed by uncertainty around the finch's ecological requirements as well as other socioeconomic factors. Here, we used this case to present an example of how Vol can help to prioritize contested investment in conservation planning.
- 4) We found that there is little gain to be obtained from new information. Land sparing was considered the best action to minimize the decline of the southern black-throated finch. However, implementing land sparing at a general scale was regarded as unfeasible in the current socioeconomic context. After excluding land sparing from the analysis, we found that research could substantially improve the effectiveness of alternative management actions. Yet, the potential benefits of these actions remained lower than implementing land sparing without further research, which highlights the inefficiency of this alternative.
- 5) **Synthesis and applications.** This study highlights the applications of Vol as a tool to optimize conservation investment under limited information. Vol analysis offers a structured quantitative framework that can help improve the efficacy of recovery plans. Our results present a novel perspective on the risks of ignoring effective management actions that may

be regarded as unfeasible due to factors beyond conservation, which could lead to the adoption of inefficient conservation strategies.

**Keywords:** Value of information, conservation decisions, decision-making tools, expert elicitation, recovery plans, black-throated finch, endangered species.

## Introduction

The successful conservation of species facing a high risk of extinction is a critical process that requires outcome-oriented decisions (Keene & Pullin, 2011). In 2020, the International Union for Conservation of Nature listed 32,441 species as threatened (IUCN, 2020), and many other taxa are nominated for protection at a national or regional level. To tackle this issue, countries like the United States, Canada, New Zealand and Australia have adopted the concept of recovery plans, or strategies, case-specific documents designed to identify the causes for the decline of threatened species, and recommend research and management actions to improve their conservation status. The utility of these plans relies on prioritizing investment options that can make the most of the resources available (Bottrill et al., 2011). However, their true efficacy has been criticized (Bottrill et al., 2011; Taylor et al., 2011). The recovery planning process is time consuming (Walsh et al., 2013), and their evaluation of threats and proposed actions tends to be vague due to inadequate funding and/or lack of fundamental ecological data (Clark et al., 2002). Given the inherent complexity of natural systems, this lack of baseline ecological knowledge is a common hurdle for conservation planners, who need to assess the uncertainties around their choices before deciding for a best course of action (Polasky et al., 2000).

Gathering information can help avoid investing in ineffective, or counter-productive management actions (Marlow et al., 2015). Yet, the cost of delayed action can be higher than the benefits of investing in research (Martin et al., 2012, 2016). Conservation funding is typically insufficient, and threatened species often present emergency scenarios, where ongoing declines or unsustainably small populations create an urgent need to act (Maxwell et al., 2015). This emergency context requires critical evaluation of the trade-offs between investing in obtaining new information or implementing management based on limited knowledge (Grantham et al., 2009; Iacona et al., 2017).

Not all planning approaches necessarily trade off research and management. Adaptive management plans, for example, integrate management and monitoring actions, which can reduce uncertainty as conservation outcomes are achieved (McCarthy & Possingham, 2007). Yet, such approaches are costly, and can incur suboptimal resource investment, since they may lack *a priori* evaluations of the main

sources of uncertainty, or the expected benefits of management (Runge et al., 2011). To reduce these shortcomings, decision-making tools such as value of information analysis has been proposed as an effective and inexpensive method to optimize the choice between investing in research or managing with uncertainty (Bolam et al., 2019).

Value of information (Vol) analysis originates from economic applications of investment risk analysis (Raiffa & Schlaifer, 1961), and has been widely used in the field of health research for the prioritization of information gathering (Claxton & Sculpher, 2006; Tuffaha et al., 2014). More recently, Vol has been applied to support effective decision-making in biological conservation (Keisler et al., 2014); assisting in the design of conservation strategies for single-species populations (Johnson, Hagan, et al., 2014; Johnson, Jensen, et al., 2014; Maxwell et al., 2015; Runge et al., 2011; Tulloch et al., 2017), multi-specific communities (Moore & Runge, 2012; Nicol et al., 2018), or statewide threat management in Australia (Nicol et al., 2019).

Tools such as Vol can assist conservation planning paralyzed by uncertainty, by providing a structured decision framework and guiding resource investment. Here we demonstrate how these tools can be used to assess the value of research and management actions, and inform the design of conservation documents such as recovery plans. We focus on the case of the endangered southern subspecies of the black-throated finch (*Poephila cincta cincta*), an Australian bird that has lost more than 88% of its historical extent of occurrence (Reside et al., 2019). In response to this decline, a Black-throated Finch Recovery Plan was completed in 2007. However, conservation outcomes have been hindered by the lack of funding for actions, and an unwillingness to protect key habitat from development (Reside et al., 2019). Most recently, funding for conservation has become available as compensation for development of the BTFS's habitat, yet the key investment priorities are to be articulated and evaluated.

Our results offer a revealing comparison on the value of management actions that may be seen as unfeasible due to socioeconomic constraints, and the potential implications of systematically excluding them from the conservation decision-making process.

## **Materials and methods**

### *Case study*

The southern black-throated finch (hereafter BTFS) is a granivorous bird endemic to tropical and subtropical regions in northeastern Australia. BTFS once occupied open woodlands and savannas

across the eastern half of the state of Queensland and the northeastern edge of New South Wales. Yet, their range has severely declined over the last 40 years (Fig. 3.1), and BTFS are now listed as 'Presumed Extinct' in New South Wales under the *Biodiversity Conservation Act, 2016*, and 'Endangered' both in Queensland and nationally under the *Nature Conservation Act, 1992* and the *EPBC Act, 1999* respectively.

The historical decline of the BTFS is mainly attributed to the high vegetation clearing rates within its range, which are primarily associated with the expansion of pastoralism after European settlement in Australia (Laguna et al., 2019). Additionally, processes derived from pastoral land uses, such as changes in grazing pressure, fire regimes, and the introduction of invasive vegetation, may have resulted in the progressive degradation of habitat, although the magnitude of these impacts is still unknown (Laguna et al., 2019). BTFS threats remain largely unmitigated, and ongoing developments linked to urbanization and extractive industries threaten to remove high quality BTFS habitat from its already constrained range (Reside et al., 2019).

The uncertainty surrounding the finch's ecological needs and best management practices (Laguna et al., 2019), has led to investing most of the funding that has been made available for its conservation into research (Queensland Government, 2014). Given the significant gaps in our knowledge of BTFS, it is reasonable to think that effective management would require additional research. Yet, the BTFS's urgent conservation needs, added to its inconspicuousness and increasing rarity, which can increase the costs of research, warrant the critical evaluation of any further research investment.

#### *Vol analysis: Expected Value of Perfect Information*

Vol is formally calculated as the 'Expected Value of Perfect Information' (EVPI), an estimate of the potential investment gain derived from obtaining new information (Yokota & Thompson, 2004). EVPI is the difference in the return value between making an investment when more information is available, against making an investment with current information (equation 1). In our case, EVPI can quantify the expected conservation gain of investing in management after improving our understanding of the ecology of and threats to BTFS, against the expected gain of investing in management with current uncertainty. These two concepts are commonly known as the expected value under certainty ( $EV_{certainty}$ ) and the expected value under uncertainty ( $EV_{uncertainty}$ ):

$$EVPI = EV_{certainty} - EV_{uncertainty} \quad (\text{eqn 1})$$

The prospective nature of the decision-making process implies that the outcomes of acting are unknown at the time of the decision. Therefore, the numeric values behind the EVPI are necessarily based on estimates of the future made with the best knowledge available at the time of the analysis. These estimates are not expected to be an accurate forecast of the future, but rather provide comparable figures for the calculation of metrics within a structured analytical framework. Constructing this framework requires three components:

- Objectives (and metrics): one or more goals with defined deadlines, each associated with a quantitative metric to estimate and measure future outcomes;
- Hypotheses: the main sources of uncertainty, processes operating in the target system that are expected to influence future outcomes;
- Actions: a list of actions designed to change the outcomes of the hypotheses considered.

Thus, the two terms necessary for the EVPI calculation (eqn 1) can be calculated as:

$$EV_{certainty} = \sum_h [p_h \times \max_a V(a, h)] \quad (\text{eqn 2})$$

$$EV_{uncertainty} = \max_a [\sum_h W_h \times V(a, h)] \quad (\text{eqn 3})$$

Where  $h$  is a given hypothesis,  $W_h$  is a weighting factor that represents the expected impact of hypothesis  $h$  in the system,  $a$  is a given action, and  $V(a, h)$  is the estimated outcome given a scenario defined by action  $a$  and hypothesis  $h$ . More intuitively,  $EV_{certainty}$  is the accumulated value of choosing the best action for each hypothesis, while  $EV_{uncertainty}$  is the accumulated value of the action regarded as the most beneficial, regardless of the hypothesis. Therefore, when EVPI is high, we benefit the most from investing in research to resolve uncertainty on which hypotheses have more impact in the system and how to address them, before deciding the best management action.

EVPI alone however, does not offer an individual measure of which hypotheses accumulate most uncertainty, both in their impacts or how to mitigate them. Alternatively, the ‘Expected Value of Partial Information’ (EVPXI) measures the value of undertaking actions under each hypothesis, allowing us to estimate the relative contribution of each hypothesis to the system’s uncertainty, and prioritize research according to its potential benefits.

### *Vol analysis: Expected Value of Partial Information*

Similar to EVPI, EVPXI is calculated as the difference between the expected value of resolving uncertainty versus acting based on current knowledge, with the distinction that each source of uncertainty is assessed individually, as if only one hypothesis was affecting the system at a time. Therefore, the first term of equation (1) is replaced by:

$$EVX_{certainty} = p_{x=true} \max_a V(a, x) + (1 - p_{x=true}) \max_a \sum_{h \in H \setminus h} p_{h|x=false} \times V(a, h) \text{ (eqn 4)}$$

Where  $x$  is the selected hypothesis for the calculation of the EVPXI,  $p_{x=true}$  is the weight of  $x$ , and  $p_{h|x=false}$  is the normalized weight over hypotheses given hypothesis  $x$  is false.

### *Vol analysis: Expert elicitation and analysis*

To ensure that our analysis included the best knowledge available on BTFS, we assembled a panel of 16 experts to participate in a structured elicitation process. The panel consisted of individuals with substantial expertise on the ecology and threats of BTFS from multiple stakeholder groups, including local and state government, government researchers (CSIRO), university researchers, environmental consultants, Natural Resource Management groups and conservation non-government organizations.

Following a method adapted from (Nicol et al., 2018), the elicitation process was conducted in two phases to (i) establish the analysis' components, and (ii) provide outcome estimates. All experts participated in the selection of objectives, hypotheses and actions during two separate one-day workshops. To minimize the bias inherent in group decisions, we followed an adapted Delphi method (Mukherjee et al., 2015), in which the outcomes of the workshops were compiled and summarized by the facilitators, and the summary was then presented to the experts to provide individual feedback and establish the final components.

Eleven of the 16 experts also participated in the second phase, which was carried out *via* individual email consultation. In this consultation, experts were given a decision matrix displaying all unique combinations of the selected hypotheses and actions. For each combination, experts were asked to provide future outcome estimates as if only those factors influenced the system. The outcomes were provided using quantitative metrics and a future time deadline associated with the chosen conservation objectives. To control for individual uncertainty, estimates were collected using a three-point estimate format (Thompson et al., 1992), including a most optimistic, most pessimistic, and most likely estimate within a pre-established 80% confidence interval. The range provided by the three

estimates was used to create a beta-distribution of each response, and extract 10,000 random data arrays. We used each array as an independent dataset to calculate 10,000 iterations of EVPI and EVPXI, following a Monte-Carlo simulation method (Papadopoulos & Yeung, 2001).

We used additional Kruskal-Wallis H and pairwise Wilcoxon Rank-Sum tests to evaluate differences among the results and other responses obtained. All analyses were performed in R version 3.5.2 (R Core Team, 2018).

### *Analysis' components*

#### *Objectives*

In the context of Vol analysis, objectives require two critical factors: a quantitative metric and a timeframe. An appropriate metric should be intuitive enough to facilitate the estimation of outcomes during the expert elicitation phase, while also being precise enough to allow the future monitoring of management outcomes in the real world. In turn, the timeframe should allow enough time for actions to have observable outcomes, while not being too far into the future to obstruct the elicitation process. The expert panel settled on three conservation objectives for BTFS:

- O1. Maintain the area of occupancy of BTFS for the next 10 years, measured as the percentage of the present area of occupancy (=100%) remaining in 10 years.
- O2. Maintain the extent of occurrence of the BTFS for the next 10 years, measured as the percentage of the present extent of occurrence (=100%) remaining in 10 years.
- O3. Secure the local persistence of representative BTFS populations for the next 10 years, measured as percentage of change in the trend of a hypothetical local population in 10 years (no change = 0%).

The first two objectives were designed to measure changes in the range of BTFS. Given the absence of an accurate estimate on the number of remaining BTFS, measuring changes in range extent was considered the best option to predict large-scale effects of conservation. However, this measure fails to evaluate possible outcomes at a local scale, where the impacts of management are more evident. Despite their acute decline, BTFS still occupy a large range within Queensland; yet, their occurrence is sparse, and most population numbers are concentrated in two main strongholds (Laguna et al., 2019). A significant population decline in these strongholds might prove more damaging than the loss of a

small isolated population, something that might be overlooked by general range estimates. To account for that, experts selected a third objective focused on the effect of threats and management on local populations.

### *Hypotheses*

Hypotheses are the main sources of uncertainty for the decision. In conservation applications of Vol, these are often roughly equivalent to threats, factors limiting the achievement of the conservation objectives. During the workshops, experts identified a list of 16 hypotheses that could contribute to the decline of the BTFS. Calculating Vol also requires measuring the relative importance of each hypothesis based on the knowledge available. To do so, we asked experts to weight the 16 hypotheses by assigning a percentage of importance to each. We then used the average weight to remove low impact hypotheses, so only the top 10 most relevant were considered in the final analysis:

- H1. Urban encroachment. Ongoing urban expansion concentrated in the Townsville Plains subregion is responsible for the loss of important BTFS habitat within one of its main strongholds.
- H2. Large-scale mining. Approved development plans for surface mining in the Desert Uplands bioregion threaten to remove large areas of important BTFS habitat within one of its main strongholds.
- H3. Small-scale clearing. Widespread small-scale clearing for agriculture or other extractive industries (e.g. metalliferous mining) is responsible for the cumulative loss of suitable BTFS habitat throughout its range.
- H4. Connectivity loss. Increased fragmentation due to habitat loss reduces connectivity among BTFS populations and areas of suitable habitat, which increases the risk of local extinctions.
- H5. Seed productivity. Grazing pressure, fire regimes and other vegetation changes associated with pastoralism result in a reduction in the overall production of suitable seeds, which limits the amount of food available to BTFS.



- H6. Seed continuity. Grazing pressure, fire regimes and other vegetation changes associated with pastoralism contribute to seed shortages during periods prone to resource bottlenecks, which limits the amount of food available to BTFS at critical times of the year.
- H7. Seed quality. Vegetation changes associated with pastoralism result in severe modifications in the composition of native plant communities, changing the types of seed available, which overall are less suitable for BTFS.
- H8. Vegetation structure. Vegetation changes associated with pastoralism result in severe modifications in the composition of native plant communities, changing the structural characteristics of habitat and limiting access to seed due to reduced visibility and physical access to the ground.
- H9. Landscape configuration. Vegetation changes associated with pastoralism result in severe modifications in the spatial configuration of the landscape, which increases the dispersion of essential resources like seed, water and nesting trees, limiting access due to distance.
- H10. Nesting spots. Vegetation changes associated with pastoralism result in a decrease of suitable nesting resources and spots, which limits successful breeding.

### *Actions*

We asked experts to propose adequate management actions to address one or several of the selected hypotheses. The panel initially selected 17 actions, which were vetted to keep only those chosen to address at least one of the final list of 10 hypotheses. Additionally, we included an option where no action is taken, acting as a baseline scenario. This resulted in a total of 11 actions:

- A0. No action. None of the proposed conservation actions is undertaken.
- A1. Land sparing. Secure areas of habitat where BTFS occur (through purchase, covenant or financial agreements with landowners) and dedicate them to conservation and research.
- A2. Clearing restrictions. Map critical BTFS habitat and use it as a basis to enforce restrictions on clearing and thinning, particularly in remnant and regrowth areas.

- A3. Deter pastoralism. At non-grazed properties maintaining BTFS populations, use economic incentives to deter pastoral land uses.
- A4. Cattle removal. At lightly grazed pastoral properties maintaining known BTFS populations (where cattle might not be a main source of income), use economic incentives to promote gradual cattle removal.
- A5. Grazing management. At pastoral properties maintaining BTFS populations, provide information to landowners and incentivize them to apply appropriate grazing regimes that encourage the persistence of perennial grasses and can maintain a seed stock accessible to BTFS.
- A6. Fire management. At publicly managed land and pastoral properties maintaining BTFS populations, provide information to landowners and incentivize them to apply appropriate fire regimes that encourage the persistence of perennial grasses and can maintain an accessible seed stock.
- A7. Manage habitat structure. At publicly managed land and pastoral properties maintaining BTFS populations, provide information to landowners and incentivize them to apply appropriate management techniques that can maintain a suitable vegetation structure and spatial composition to facilitate access to foraging and breeding resources.
- A8. Manage exotic grasses. At publicly managed land and pastoral properties maintaining BTFS populations, provide information to landowners and incentivize them to apply appropriate management techniques that can maintain a healthy stock of local grass species, minimize weed proliferation and discourage intentional sowing of exotic species.
- A9. Remove exotic shrubs. At publicly managed land and pastoral properties maintaining BTFS populations, incentivize landowners to remove exotic shrubs.
- A10. Incentives for native grasses. Facilitate the use of local grass species in pastoral lands by funding and maintaining a commercial farm that can supply local grasses and seeds to landowners.

## **Results**

### *Most likely hypothesis*

Experts considered large-scale mining (H2) as the main hypothesis threatening the BTFS (Fig. 3.2). Small-scale clearing (H3) and urban expansion (H1) ranked closely, such that the three hypotheses directly related to land clearing comprised an accumulated 45.5% of the total weight of the 10 hypotheses. Landscape configuration (H9) and seed productivity (H5) also ranked high, with average weights above 10% each. Conversely, nesting spots (H10) and seed quality (H7) were not thought to have a substantial impact on the conservation of BTFS (<3.5%).

### *Best management actions under current uncertainty*

The expected value under uncertainty ( $EV_{uncertainty}$ ) reveals which management actions are considered most effective for conservation with current knowledge (Tables S1-S3). Experts did not provide positive estimates for any unique combination of objectives, hypotheses and actions (i.e. all estimates are below 100, the current reference value). This result indicates that no action alone is expected to fully neutralize the impacts of any of the threats considered, implying an expected decline of BTFS over the next 10 years, regardless of the management choice. Of all actions, experts agreed that land sparing (A1) had the highest conservation benefits across the three objectives. Land sparing was considered the best choice for every hypothesis in objectives 1 and 2, and six out of 10 hypotheses in objective 3. Furthermore, when averaging all hypotheses, land sparing was the only action with significantly different outcomes from the no action alternative (A0) (Pairwise Wilcoxon Rank-Sum Test for each objective,  $p < 0.005$ ).

Although land sparing was regarded as the best management action for the conservation of the BTFS, its implementation on a broad scale was also considered unfeasible due to lack of funding and competing interests such as mining, agriculture and urban development. Given its dominance over the rest of actions, disregarding land sparing could significantly change the outcomes of Vol. To measure these changes, we replicated our analysis for two scenarios, one where land sparing was included and one where it was not. In the second scenario, identifying the best action became more dependent on the target hypothesis (Table S3.1-S3.3). Overall, actions based on deterring clearing and pastoral uses (A2 to A4) were expected to have greater conservation outcomes than actions focused on habitat management (A5 to A10). Enforcing clearing restrictions (A2) was the most valuable action to address clearing and fragmentation hypotheses (H1 to H4), while partial cattle removals (A4) were more beneficial for most of the remaining hypotheses. There were only a few exceptions when active fire and habitat structure management became the better option, specifically to address changes in vegetation structure (H8) and a possible reduction in nesting spots (H10).

### *Expected Value of Perfect Information*

For the scenario including land sparing, EVPI was below 1% for all three objectives, 0.4% on average (Table 3.1). This value is marginal when compared to the 12.19% benefit (averaged for all objectives, Fig. 3.3) that can be achieved from choosing the best action under current uncertainty. Therefore, there is little conservation gain to be obtained from research compared to implementing land sparing, regardless of which objective is prioritized or which hypothesis is more relevant.

When land sparing was not considered, EVPI increased significantly for all three objectives (Pairwise Wilcoxon Rank-Sum Test for each objective,  $p < 0.005$ ). Conversely, the margin of acting with current uncertainty decreased to 5.45% (averaged for all objectives, Fig. 3.3). At an average EVPI gain of 4.17%, when land sparing is not possible, investing in obtaining perfect information can increase the benefits of choosing the best management action with current knowledge by 77%. This significant benefit margin can warrant an investment to obtain further information. However, the absolute conservation margin that can be obtained from making a decision with perfect information is still lower than the benefit gained from implementing land sparing without further research (Fig. 3.3).

### *Expected Value of Partial Information*

The EVPXI revealed how the value of investing in reducing uncertainty was distributed across hypotheses and scenarios (Table 3.1). When land sparing was possible, the similarities between objectives 1 and 2, measuring changes in the range of BTFS, resulted in comparable EVPXI. In both objectives, most value was concentrated around seed-related hypotheses, including a possible loss of seed productivity (H5), quality (H7) and continuity (H6) (in this order as averaged for objective 1 and 2). Contrary to the other two objectives, EVPXI was substantially different for objective 3, aimed at measuring local population trends. In this case, most value was concentrated in resolving the uncertainty around the effect of clearing caused by urban expansion (H1) and large-scale mining (H2). Overall, due to the marginal EVPI when land sparing is a possibility, hypothesis-specific EVPXI was equally negligible, with no substantial benefits that can justify research into any of the hypotheses.

Alternatively, in a no land sparing scenario, the increment in EVPI also increased the EVPXI of all hypotheses. Hypotheses linked to access to resources, due to changes in their spatial distribution in the landscape (H9), or a specific reduction in seed productivity (H5) and continuity through the year (H6), ranked consistently high for all objectives. Measuring the impacts of these changes on existing BTFS populations, and experimenting with appropriate resource management regimes can

substantially improve the effectivity of conservation action, and is an effective choice when implementing land sparing is not possible.

Additionally, although there was little uncertainty in the role of clearing as a threat to BTFS, the three clearing-related hypotheses (H1 to H3) accumulated high EVPXI for objectives 1 and 2. This result suggests that there is substantial value in clarifying which specific motivations (urbanization, mining, or other small developments), have a higher impact in the decline of BTFS's range, as well as which areas should be prioritized for protection.

## **Discussion**

The uncertainty created by shortages in species' ecological data is often an obstacle for efficient conservation investment. While there are multiple reasons to strive for a better understanding of natural systems, conservation-oriented decisions should only prioritize research when resolving uncertainty can significantly improve the value of management (Martin et al., 2012). In an attempt to measure the value of new information, Vol analysis provides a robust method that can assess the conservation outputs of research, while serving as a structured framework to prioritize investment based on the best knowledge available (Morris, 2017; Nicol et al., 2019). The case of the endangered BTFS offers an excellent opportunity for the application of Vol analysis to evaluate the impact of contested conservation investment. Despite its evident decline, the lack of fundamental information about BTFS ecology and the magnitude of certain threats creates uncertainty about the main conservation priorities (Laguna et al., 2019). Our results revealed that sparing BTFS habitat from clearing, and dedicating those areas to conservation, is the most efficient choice to stop further decline. Yet, the perceived unfeasibility of implementing land sparing at a general scale made us consider two scenarios, one where land sparing was possible, and another where it was not, in order to find investment alternatives. We found that discarding effective actions such as land sparing due to their perceived unfeasibility, can lead to an inefficient use of resources, which warrants the consideration of this type actions in planning and Vol as a way to assess the true effectiveness of all management options.

In contrast with the general demand for additional research to fill the gaps in our knowledge of BTFS, we found that the value of new information was marginal when land sparing was a possibility. Low Vol can occur in conservation cases where, despite a high uncertainty on the species ecological requirements, the most relevant threats are already identified, and managing them does not depend on collecting further data (Bal et al., 2018). Based on their responses, experts agreed that addressing

clearing-related hypotheses could have the highest impact on preserving the BTFS. A perspective supported by the substantial body of evidence pointing at clearing as the leading historical and ongoing threat to BTFS (Reside et al., 2019), and reinforced by the recent approval of mining developments within the region harboring the largest known BTFS population (Vanderduys et al., 2016).

Land sparing was considered the best action to protect BTFS habitat from clearing, while also being a highly effective option to address most other hypotheses (Tables S1 to S3). The fact that on average, only land sparing was expected to have significant benefits compared to not acting at all, reveals that although alternative actions could outperform land sparing at solving specific threats, these threats need to be clearly identified as priorities before acting is worth. This conclusion aligns with the results for our scenario excluding land sparing, which showed that additional research can significantly improve the effectiveness of management actions. Yet, even with perfect information, the potential conservation outputs of these actions are estimated to be lower than land sparing. These findings highlight the overall inefficiency of actions other than land sparing, which would require investing valuable time and resources in research to decide the optimal management strategy, while we could achieve higher benefits from land sparing without the need of gathering further information.

Despite our clear findings, we acknowledge that in the context of realistic conservation management, investment cannot be reduced to a unique choice. Calculating Vol requires a simplification of the system, assuming that only one action can be taken at a time. Large-scale management scenarios are more nuanced, and often involve the simultaneous implementation of a diverse range of research and management actions according to local factors and socioeconomic constraints. A more realistic approach to the case of the BTFS can combine the protection of critical areas, with additional management to ensure the persistence of populations occurring in pastoral lands. We encourage decision-makers to prioritize land sparing whenever possible, with the alternative of conducting research to determine the impact and best management choices to address threats related to seed availability and changes in the distribution of resources through the landscape.

The use of Vol can increase the effectiveness of recovery plans and other prominent strategic conservation documents, such as the Species Action Plans prepared by the IUCN and the European Union. These plans can benefit from the outcome-oriented perspective and the structured decision-making framework offered by Vol analysis. Our study presents an applied example of these tools, and

its outcomes can provide a quantitative foundation to inform a pending update of the Black-throated Finch Recovery Plan and support the conservation of this endangered finch.

Beyond our findings specific to the case of BTFS, this study provides a novel perspective on the risks of disregarding conservation actions because of factors other than their efficacy. Conservationists should be aware of the limitations of their proposed actions to ensure their real world applicability (Knight et al., 2008; Mills et al., 2013). Yet, the systematic exclusion of actions regarded as difficult to implement from the conservation planning process might enforce the selection of alternatives due to their low cost or ease of establishment. This can ultimately lead to a highly inefficient use of resources with residual gains for conservation (Devillers et al., 2015; Vieira et al., 2019). We argue that using tools such as Vol to assess the outcomes of actions regarded as unfeasible, can help to highlight the irreplaceable value of effective solutions that may otherwise be limited by inadequate policies or funding.

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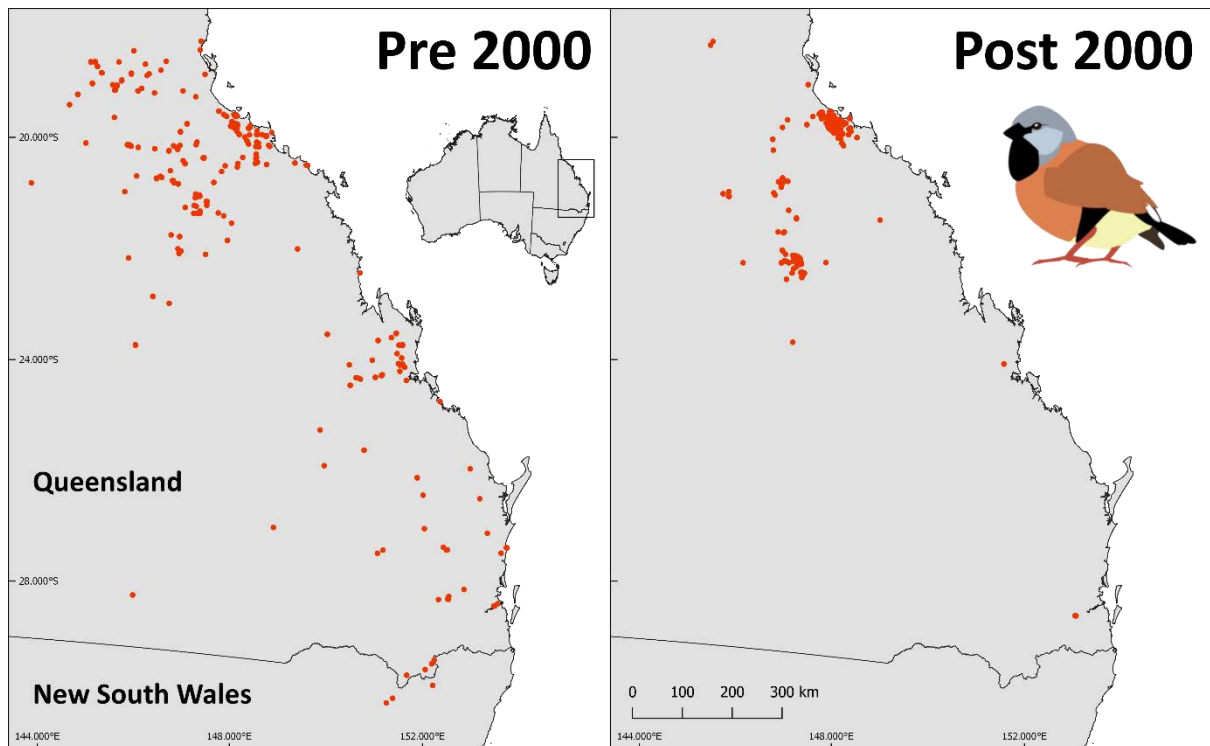
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## Tables

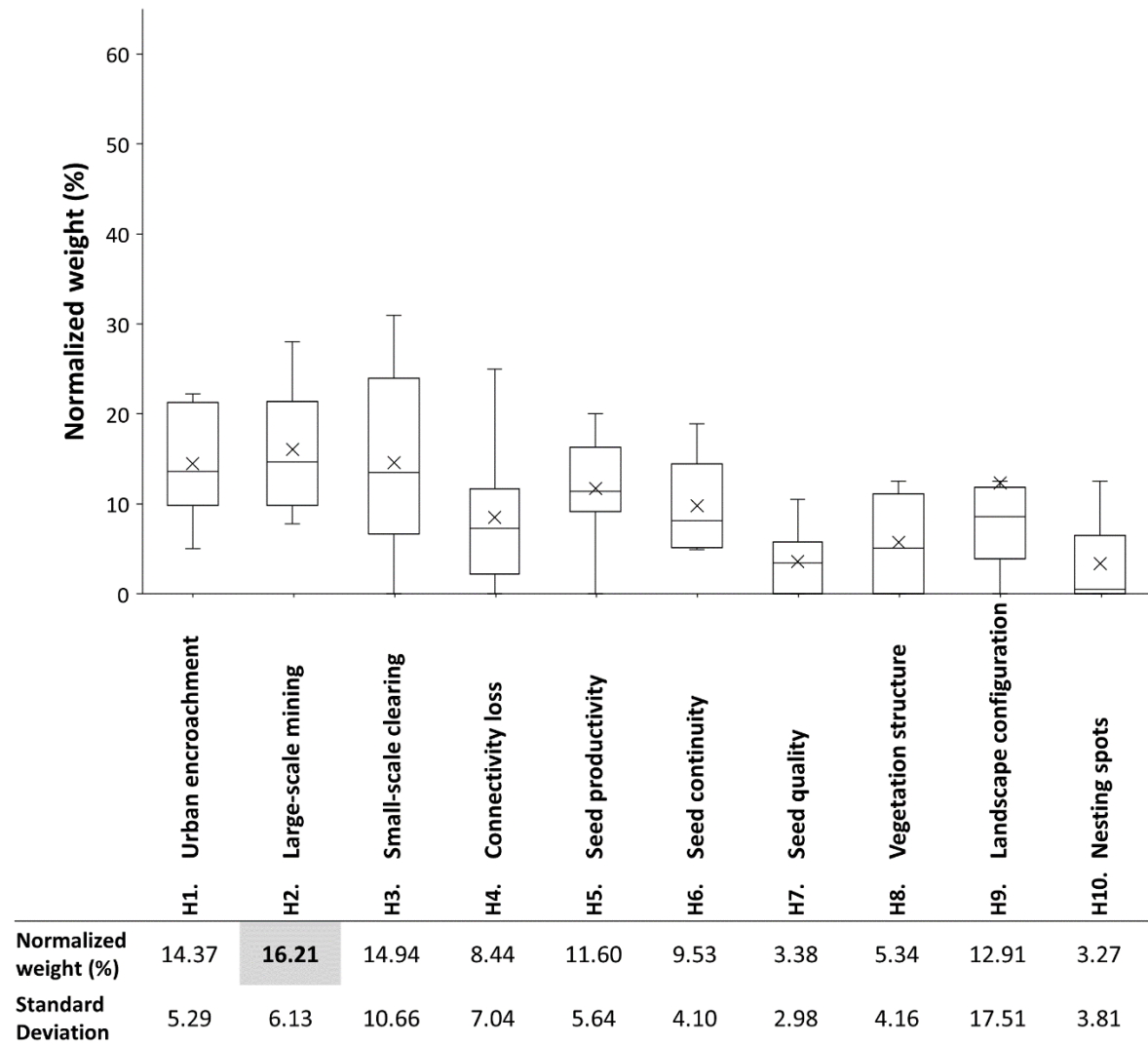
**Table 3.1.** Expected Value of Partial Information (EVPXI). The intensity of yellow shade indicates a higher value for the objective and scenario combination (rows). Bold values highlight the highest value within the row.

Objective	Scenario	H1 Urban encroachment	H2 Large-scale mining	H3 Small-scale clearing	H4 Connectivity loss	H5 Seed productivity	H6 Seed continuity	H7 Seed quality	H8 Vegetation structure	H9 Landscape configuration	H10 Nesting spots	EVPI
1	No sparing	0.00	0.00	0.01	0.00	<b>0.06</b>	0.03	0.06	0.00	0.01	0.02	<b>0.19</b>
	No sparing	0.80	<b>1.36</b>	1.23	0.32	0.94	0.57	0.18	0.34	1.23	0.15	<b>4.62</b>
2	Sparing	0.00	0.00	0.00	0.00	<b>0.07</b>	0.06	0.05	0.00	0.01	0.02	<b>0.21</b>
	No sparing	0.61	0.76	0.86	0.15	<b>1.12</b>	0.80	0.27	0.38	1.09	0.17	<b>4.19</b>
3	Sparing	<b>0.30</b>	0.19	0.02	0.01	0.01	0.02	0.07	0.09	0.10	0.00	<b>0.81</b>
	No sparing	0.00	0.00	0.00	0.00	<b>1.04</b>	0.80	0.23	0.44	1.00	0.19	<b>3.69</b>
AVG	Sparing	<b>0.10</b>	0.06	0.01	0.00	0.05	0.03	0.06	0.03	0.04	0.01	<b>0.40</b>
	No sparing	0.47	0.71	0.70	0.15	1.03	0.72	0.23	0.39	<b>1.11</b>	0.17	<b>4.17</b>

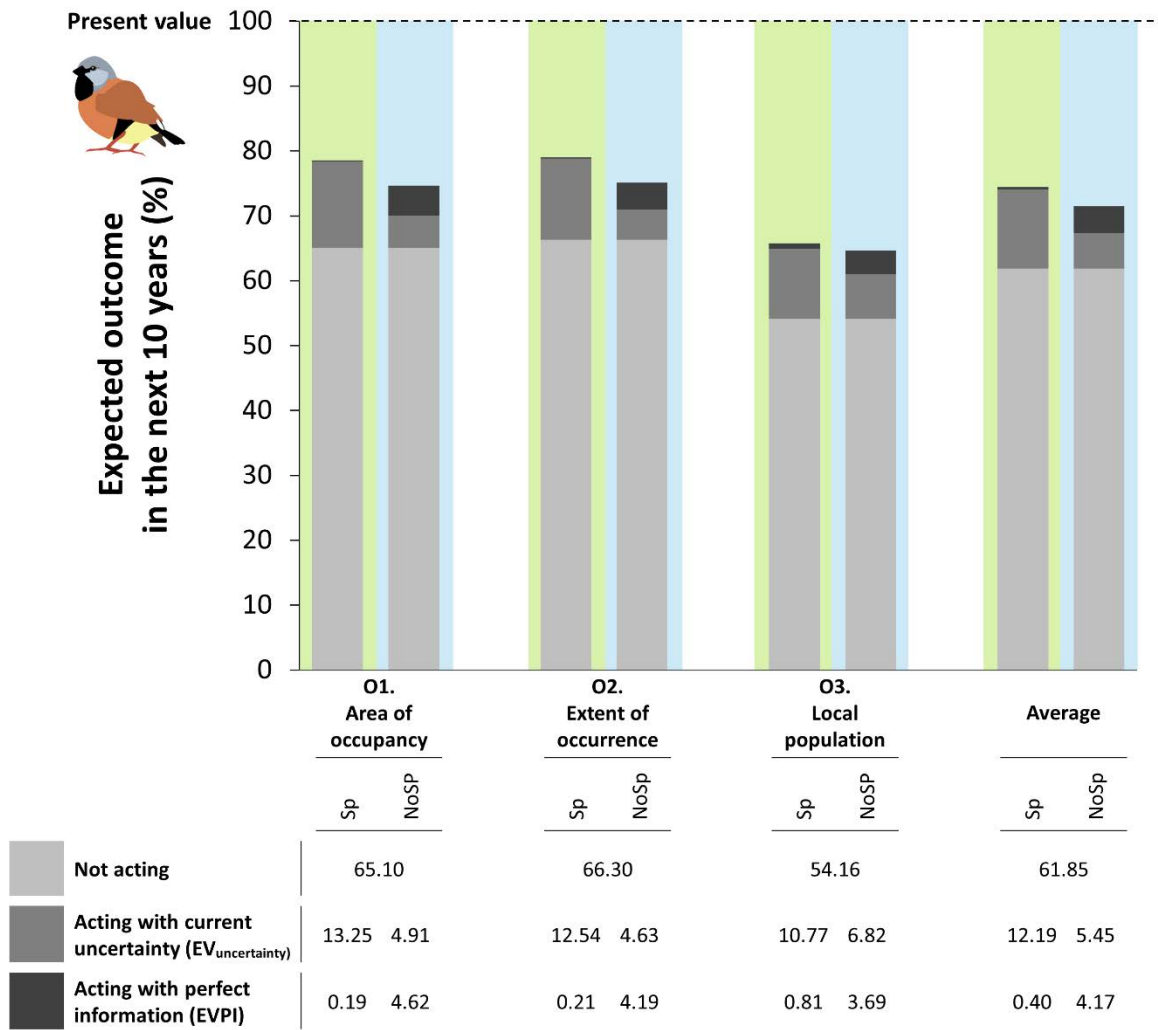
## Figures



**Figure 3.1.** Occurrences of Black-throated Finch southern subspecies before (left) and after (right) the year 2000.



**Figure 3.2.** Perceived relative impact of the top 10 hypotheses influencing the decline of the BTFS. Top 10 hypotheses were selected out of 16 options based on the average weight provided by eleven experts. Normalized weight % was recalculated after removing the six lowest ranking hypotheses.



**Figure 3.3.** Expected conservation outcomes of research and management in the next 10 years by objective and management scenario. The dotted line indicates the reference (present) conservation value for each objective, and any values below it can be interpreted as a net loss. ‘Not acting’ represents the expected conservation outcome if no management action is undertaken.  $EV_{uncertainty}$  (Expected Value Under Uncertainty) represents the expected gain of applying the best management action with current uncertainty. EVPI (Expected Value of Perfect Information) represents the potential gain of applying the best management action after investing time and resources in resolving current uncertainty. The two columns for each objective represent two management scenarios, one where land sparing is a viable management action (Sp, green) and another where it is not (NoSp, blue).

# Chapter 4

## Finding stable areas for conservation in a dynamic environment

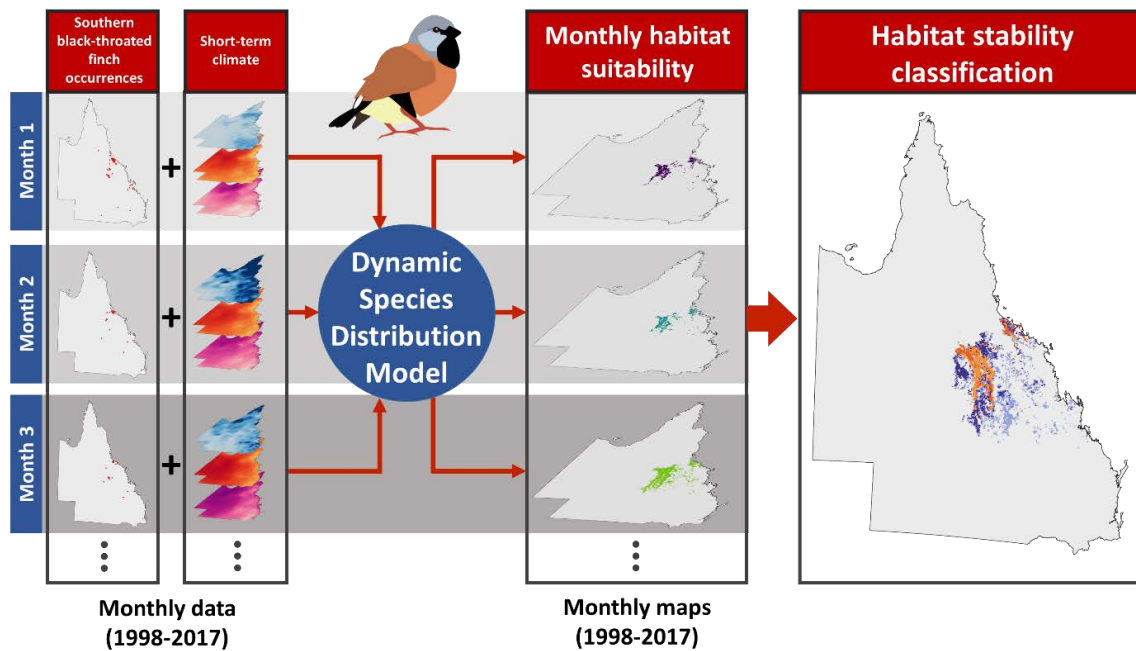
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### Abstract

The dynamic nature of many ecological processes creates uncertainty for conservation planning. Unpredictable shifts in habitat condition and species' subsequent responses can change the value of habitat patches, creating challenges for the prioritization of conservation areas. Here, we demonstrate the need to quantify unpredictable variation in habitat suitability, and propose a method to incorporate this uncertainty in conservation strategies. We used the case of the endangered southern black-throated finch (*Poephila cincta cincta*), to fit a dynamic species distribution model trained on short-term climate data, and generated monthly projections of habitat suitability over 20 years. We examined temporal patterns in the extent of suitable habitat and created a classification of habitat based on the number of months an area was considered suitable, and the availability of alternative suitable areas within accessible distance. Our results showed that southern black-throated finches are exposed to extreme fluctuations in the condition of their habitat. While we identified a consistent seasonal pattern, the large interannual differences create uncertainty about the extent of suitable area at any given time. 'Core' areas that remained consistently suitable represented less than 30% of the extent that was considered suitable at some point during the time series. We encourage halting further habitat destruction, and use our habitat classification to guide surveying and establish a network of secure, stable sites dedicated to conservation. Additionally, we propose the adoption of similar methods as a way to account for dynamic factors in the protection of species influenced by highly variable and unpredictable habitat conditions.





**Keywords:** dynamic species distribution model; resource shortages; extreme weather events; black-throated finch; nomadism; threatened species

## Introduction

Given the limited resources available for biodiversity conservation and the competing interests over land use, conservation planners must identify priority areas for protection and management (Kukkala and Moilanen, 2013). However, considering the plethora of factors involved in systematic planning, assessing the value of areas for conservation action can be a difficult task (Margules and Pressey, 2000). Among them, the dynamic character of many ecological processes is a common source of uncertainty that poses major challenges to the design of effective conservation strategies (Pressey et al., 2007).

Fluctuations in habitat condition and resource availability have led to a wide diversity of species adaptations. For example, seasonal migrants undertake movements to make use of spatially disjunct areas throughout the year according to resource availability and habitat condition (Runge et al., 2014). Access to these temporally important habitats is crucial for the survival of species with mobile strategies (Runge et al., 2015b). Yet, the global impact of habitat loss, fragmentation, and climate change can limit timely access to important areas, jeopardizing the persistence of these species (Both et al., 2006; Lampila et al., 2005).

Conserving highly mobile species requires identifying and preserving key areas that allow them to meet their spatial needs (Martin et al., 2007). However, identifying these areas is particularly challenging when targeting species with irregular movements (Cottee-Jones et al., 2016). Species in highly variable habitats that depend on ephemeral resources, often driven by irregular weather events, can make use of extensive areas without a predictable pattern. In one of the most extreme examples, Mongolian Gazelles (*Procapra gutturosa*) roam average areas of more than 19 000 km<sup>2</sup> within a single year looking for pastures, a range that can vary as much as three times among years, as individuals use vastly different locations without a clear seasonal pattern (Nandintsetseg et al., 2019).

To deal with this uncertainty, many assessments of the value of species' habitat have moved beyond static perspectives of habitat suitability in favor of incorporating spatiotemporal dynamics (Grantham et al., 2011; Johst et al., 2014; Runge et al., 2016). With this purpose, species distribution models based on short-term climate conditions can be used to examine and quantify changes in the suitability of species' habitat. These methods have proven particularly useful to determine the distribution of highly mobile, episodic and nomadic species and assess their risk of extinction (Mordecai et al., 2011; Reside et al., 2010; Runge et al., 2015a). Furthermore, this information can help to identify priority areas for conservation when targeting unpredictable species and habitats (Runge et al., 2016; Van Teeffelen et al., 2012).

Despite the efficacy of these methods, there are limited examples of ways to incorporate dynamic habitat suitability information on conservation programs for endangered species (Webb et al., 2017). We investigated how spatiotemporal patterns in habitat suitability can inform the conservation of an endangered bird with irregular and poorly-known movements, the black-throated finch southern subspecies (*Poephila cincta cincta*). Southern black-throated finches (hereafter BTFS) inhabit savanna areas of northeastern Australia. These habitats are characterized by a large variability in weather patterns (Garnett and Williamson, 2010), which drive the availability of water and grass seeds on which BTFS forage (Orr and O'Reagain, 2011; Setterfield, 2002). This variability exposes BTFS to intermittent resource shortages (Mitchell, 1996), which might force them to temporarily move to areas that provide suitable habitat during periods of unfavorable conditions.

BTFS have lost 88% of their historic extent of occurrence (Fig. 4.4.1) due to habitat clearing and modification (Reside et al., 2019b), and are now listed as 'Endangered' (EPBC Act, 1999; Nature Conservation Act, 1992). With only a small proportion of their range remaining, establishing areas for

urgent protection is crucial for BTFS persistence. However, the unpredictability of resource shortage periods poses significant complexities for the prioritization of areas for conservation. We hypothesize that the widespread habitat loss and fragmentation within BTFS range limits the availability of suitable habitat within their preferred dispersal distance, increasing the likelihood of local extinctions during shortage periods. Quantifying the probability of an area to remain suitable over time can help identify sites that are less likely to experience resource shortages. We created a dynamic species distribution model based on monthly climate conditions over a 20-year period to measure spatiotemporal changes in BTFS habitat suitability. We used this model to examine temporal patterns and propose a classification of BTFS habitat value according to the recurrence of periods of unsuitable habitat conditions, and potential access to alternative habitat.

This study demonstrates how dynamic distribution models can be used to inform the conservation of poorly-known species in highly variable habitats. Our aim is to present a case example that can be applied to other species and systems, while also to providing useful outputs for the management and protection of the BTFS.

## **Material and methods**

### **Case study**

Southern black-throated finches are granivorous birds endemic to tropical and subtropical savannas of north-eastern Australia (Laguna et al., 2019). Their habitats are primarily characterized by the presence of permanent water sources, a sparse tree layer, and an understory of grasses mixed with patches of bare ground that provide easy access to fallen seeds (Rechetelo, 2015).

The decline of BTFS has been primarily linked to the clearing of vegetation resulting from the expansion of pastoralism and other land use changes since European settlement in Australia (Laguna et al., 2019). This threat is still ongoing, as there are multiple plans from extractive industries that have been granted permission to clear important areas of BTFS habitat (Reside et al., 2019b). Furthermore, changes in grazing and fire regimes are also likely to contribute to the modification of BTFS habitat, as evidenced by the negative impacts on similar species like the Gouldian Finch (*Erythrura gouldiae*) (Weier et al., 2017).

BTFS movements are poorly described. Their declining flock and population sizes make them hard to detect, and their vast, patchy distribution is almost entirely restricted to private pastoral holdings with low accessibility to bird watchers and researchers (Laguna et al., 2019). Furthermore, their small

physical size limits the applicability of most movement tracking techniques available (Laguna et al., 2019). The only radio-tracking study on BTFS movement concluded that individuals tend to occupy small average home ranges of 0.5 km<sup>2</sup> (Rechetelo et al., 2016). However, there are records of BTFS flocks using habitat patches 1.4 km apart within the same day, and groups establishing in areas more than 3 km apart from their former home range to make use of seasonal resources (Mitchell, 1996). In the most extreme examples of BTFS dispersal, individuals have been re-sighted 16 km away from their initial banding location after 49 days, or 17 km in 132 days (Rechetelo et al., 2016). Without further data, the drivers and regularity of such movements remain uncertain. Yet, historical observations (Laguna et al., 2019), and the example of other closely related granivorous finches in the region suggests that these responses might be triggered during periods of resource shortages.

#### Dynamic habitat suitability model

We fitted a dynamic species distribution model trained on short-term climate data for the month and location of each occurrence (Reside et al., 2010), replacing the more traditional approach of using 30-year climate averages. This model was then projected onto monthly time slices for the 20-year period between 1998 and 2017, obtaining 240 monthly BTFS habitat suitability maps based on short-term climate conditions.

#### Environmental variables

We obtained 0.05° (~28.5 km<sup>2</sup>) resolution grids of Queensland for monthly average temperature maxima, minima, and total monthly rainfall in the period 1998 to 2017 (Australian Water Availability Project; Jones et al., 2007; Grant et al., 2008). For each of the three variables, we calculated nine additional grids: conditions of the previous month, average for the last three, six, nine and twelve months, and seasonality measured as the coefficient of variation also for last three, six, nine and twelve months. Additionally, we included the monthly normalized difference vegetation index (NDVI) (Australian Water Availability Project; Jones et al., 2007; Grant et al., 2008), a measure of vegetation greenness; and two static layers to inform the model about the community type: lithology (Global Lithological Map; Hartmann & Moosdorf, 2015) and vegetation type (Broad vegetation groups - pre-clearing and 2017 remnant; Neldner *et al.*, 2019). As a result, we obtained a set of 33 environmental variables for every month in the twenty-year period (Table S4.1).

We then thinned the initial set of variables to avoid model overfitting. Highly correlated variables ( $R^2 > 0.8$ ) were discarded, favoring those that showed lower correlation with the rest of variables in the matrix. We conducted a stepwise model selection fitting the model with the remaining variables and

removed the lowest one based on permutation importance. This process was repeated with one variable at a time until all variables had at least a minimum percent contribution of 1% (Table 4.1). This process restricted the initial set of 33 variables to 12.

#### Occurrence data

We obtained BTFS occurrences from a database managed by the Black-throated Finch Recovery Team (Black-throated Finch Recovery Team, 2017), including data from yearly targeted counts at waterholes, multiple non-specific surveys and verified incidental records. For our model, we restricted these occurrences to BTFS records from Queensland during our study period (1998-2017), and removed any occurrences north of 17.5° or west of 143.6° (outside the known range and likely to correspond to the northern subspecies).

The final dataset showed a potential bias in BTFS occurrences towards densely populated areas or easily accessible locations (e.g., next to roads), a common issue in datasets including a significant number incidental and opportunistic records. To minimize the impact of this bias we used a 0.05° resolution grid, matching the format of the environmental data, to limit presence points to a single occurrence per cell for each unique month and year combination. The final presence dataset included 534 BTFS occurrences.

#### Modelling protocol

Due to the scarce data on BTFS absence, we selected MAXENT as our modelling algorithm (Phillips et al., 2006). MAXENT is a widely used technique due to its robust performance modelling habitat suitability using presence-only datasets. Rather than relying on true absences to inform the model, MAXENT uses a 'background' of points representing available environmental conditions (Phillips et al., 2017). In the standard approach, background points are selected at random within the defined environmental space. However, to correct for the spatial and temporal bias in our BTFS occurrences, we used a target-group method, which replaces the standard selection of random background points with occurrences of other species that can act as proxies for survey effort on the target species (Phillips et al., 2006).

Following Vanderduys et al., 2016, we used seven bird species for our target-group background points, which were selected for fulfilling one or more of the following conditions: common species that associate with BTFS; species that require similar sampling methods (small size, cryptic or rare); or species strongly associated with humans that could represent sampling bias around highly populated

areas or roads. Presence points for all background species were downloaded from the Atlas of Living Australia. Similar to our occurrences, the background dataset was restricted to records in Queensland for the period 1998-2017, and then vetted to a 0.05° resolution grid per month. Additionally, we removed points that were more than 250 km around any BTFS presence, to exclude areas not representative of BTFS environmental niche (VanDerWal et al., 2009). A total of 31 485 background points were included in the model.

The MAXENT model was run using a 10-fold cross-validation process, and model performance was evaluated using the average area under the receiver operating characteristic curve (AUC). We projected this model over each calendar month between 1998 and 2017, obtaining a set of 240 habitat suitability maps.

We identified a tendency of our model to over-predict BTFS habitat beyond its distribution, particularly during highly suitable months. This over-prediction is likely a result of niche similarities with the northern subspecies, and the short-term character of our climate variables, which might produce transient forecasts of suitable habitat where BTFS do not occur due to generally unsuitable conditions, dispersal barriers and other biogeographic constraints. To improve the accuracy of our projections, we filtered unsuitable areas using Queensland's Regional Ecosystems mapping, a detailed habitat classification based on vegetation communities according to bioregion, geology, landform and soil (Department of the Environment, 2012). To create this filter, we identified all Regional Ecosystem types with five or more historical BTFS occurrences, and added a buffer of 1118 m to reflect 'edge' habitat: modified or generally unsuitable areas that BTFS often use to access resources (Vanderduys et al., 2016). This buffer distance was chosen according to daily movement patterns recorded through a telemetry study of 15 individuals (Rechetelo et al., 2016). We clipped our projections to these areas in the post-modeling stage to preserve the high resolution of Regional Ecosystem classifications, mapped at a much finer scale than our 0.05° resolution grid.

#### Weather pattern analyses

We analyzed the projected monthly fluctuations in suitable BTFS area to test for possible temporal patterns. We used time series decomposition (West, 1997) as implemented in the core stats package for R (R Core Team, 2018), to isolate two basic time patterns: the recurring seasonal component that occurs from year to year, and the overall trend component that indicates the accumulated change over the extent of the time series. We then conducted specific tests to determine the significance of both components. To analyze the seasonal effect we used a Webel-Ollech overall seasonality test

included in the 'seastests' package in R (Ollech, 2019), and the trend effect was analyzed using a non-parametric Spearman test in the 'trend.test' function of the 'pastecs' package (Grosjean & Ibanez, 2018).

Additionally, we performed Dunn's pairwise comparison tests (Dunn, 1964), as implemented in the FSA package for R (Ogle, Wheeler, & Dinno, 2019), to determine significant differences among months and years with the intent of identifying extreme fluctuations in extent of BTFS habitat.

#### Habitat value classification

We used our monthly projections to create a spatial classification of habitat value for the BTFS. We hypothesize that given the predominantly sedentary behavior of BTFS and their dependence on ephemeral, climate-driven resources, areas that (1) remain consistently suitable and (2) are within BTFS dispersal distance of alternative, consistently suitable habitat, offer greater resilience against occasional unsuitable conditions. Hence, by using a measure of suitability consistency over time, we aim to represent BTFS habitat value more accurately than using an average of suitability score, which could mask cases of extreme variability.

We defined consistency according to the number of months a single cell qualified as 'suitable' or 'unsuitable' within our study period. To establish the difference between 'suitable/unsuitable', we transformed our projections of continuous habitat suitability scores to a binary classification using the maximum test sensitivity plus specificity threshold provided by our MAXENT model. This threshold minimizes the number of false positives (sensitivity) and false negatives (specificity), and is often used in conservation literature to avoid overconfident estimates (Vale et al., 2014).

The number of suitable months was then used to establish four classifications cells according to suitability consistency: 'core' ( $\geq 180$  suitable months), 'occasional' (179 to 120 suitable months), 'marginal' (119 to 60 suitable months) and 'negligible' ( $<60$  to 1 suitable months). Cells that were not suitable for at least 1 month were considered unsuitable and removed.

Large, short-term expansions of suitable habitat are unlikely to result in occupancy across all of the suitable areas, as areas must be accessible and stay suitable for long enough for birds to find them. Hence, to incorporate our second criteria on access to alternative suitable habitat, all cells further than 17 km from the closest cell centroid, were considered too isolated and reclassified as 'negligible'. We also downgraded 'core' cells farther than 16 km from another 'core' cell centroid to 'occasional',

for not providing consistent access to alternative suitable areas. The distances were chosen according to the maximum dispersal distance recorded for BTFS (17 km), and the longest movement recorded for BTFS moving between habitat patches in a span of time suitable for our monthly temporal scale, approximately 16 km in 49 days (Rechetelo et al., 2016).

As a last step, we calculated an additional suitability metric exclusively for ‘core’ cells using the positive average deviation between monthly suitability value and our minimum suitability threshold, as:

$$\text{Positive Average Deviation} = \frac{\sum(X_{\geq t} - t)}{N_{X_{\geq t}}}$$

Where  $t$  is the threshold used to establish the binary suitability classification,  $X_{\geq t}$  is any monthly score greater or equal to  $t$ , and  $N_{X_{\geq t}}$  is the count of  $X_{\geq t}$ . The purpose of this metric was to provide a more nuanced measure of habitat suitability to support prioritization in areas already identified as high value. By using positive difference, a relative measure of average and dispersal we also wanted to overcome some of the aforementioned shortfalls of simple suitability score averaging.

## Results

Our habitat suitability model showed a strong predictive capacity (10-fold replicate average AUC = 0.967; SD = 0.008). The minimum suitability score used to create the binary transformation was 0.1987, based on the model’s maximum test sensitivity plus specificity threshold. After binary transformation, 647 cells were removed for not qualifying as suitable at any given month in our time series, resulting in a mapped area of 87 050.08 km<sup>2</sup>, which we used for further analyses.

### Seasonality and trend effects

We identified major fluctuations in the extent of suitable BTFS habitat. Maximum area reached 63 573.14 km<sup>2</sup> in the best month of the series, 20.13 times more than the 3158.70 km<sup>2</sup> predicted for the most unsuitable month.

The analysis of the seasonal component showed a significant effect of month over the extent of suitable area ( $p < 0.001$ ), revealing a predictable monthly pattern regardless of the year. Suitable BTFS habitat is most extensive at the onset of the year, declining towards the colder, drier months of the austral winter (Fig. 4.2). There were no significant differences in average suitable area among consecutive months before the transition between May and June, coinciding with the early months of the dry season ( $p = 0.002$ , Bonferroni adjusted). Average area tends to reach its lowest extent in July,



when it is reduced to approximately a 40% of the maximum yearly values, typically occurring in January (Fig. 4.2). This extent increases progressively towards the end of the year, with a small, non-significant decline in November followed by a significant increase in December ( $p = 0.004$ , Bonferroni adjusted).

The magnitude of monthly fluctuations differed dramatically across years. While in years such as 2010, the amount of monthly suitable extent varied as much as 15 493 km<sup>2</sup>, in 2000 we found a dramatic decline from 38 452.08 km<sup>2</sup> of suitable habitat in May to just 3761 km<sup>2</sup> in June, a total 93% reduction from the annual peak close to 55 000 km<sup>2</sup> in January. The deseasonalized trend component supported this large interannual variability, showing rapid transitions when suitable area can contract by a half or a third within the span of 1 to 3 years, and recover in a similar amount of time (Fig. 4.2).

The overall trend revealed a significant reduction in suitable area occurring over the period of our study ( $r_s = 0.14$ ,  $p = 0.03$ ). This reduction was most evident after a substantial decline in suitable area from 2010 to 2011 reaching the lowest value for the series with no subsequent recovery to the extent of 2010. Due to the large seasonal variability, annual average extent comparisons did not show significant differences among most consecutive years, even when looking at lags of 2 or 3 years. The only exception was in the transition between 2010 and 2011 ( $p = 0.005$ , Bonferroni adjusted), which highlights the unpredictability of dramatic suitability changes.

#### Habitat mapping

We identified 22 037.5 km<sup>2</sup> of core BTFS habitat with high conservation value, a 29.91% of the extent of potentially suitable habitat within our time series (Table 4.2).

Core habitat was almost exclusively confined to the BTFS's two remaining population strongholds (Fig. 4.3). The central subregion of the Desert Uplands known as the Alice Tableland, contained the largest cluster of high-quality BTFS habitat, representing on its own more than 70% of the total core area and covering 54.21% of the extent of the subregion. While most recent BTFS occurrences in the Alice Tableland concentrate in the southeastern edge, core areas also extended throughout the western border of subregion making them a potential target to find relict populations, since survey efforts in these locations have been scarce.

In comparison, the smaller Townsville Plains had less than 10.23% of the total core habitat, covering almost 30% of the subregion (Fig. 4.3). Nonetheless, the high average positive deviation of suitability

in peripheral areas west and southwest of Townsville city highlight the importance of this region as a reservoir for BTFS.

Occasional cells concentrated near the main core clusters, occupying areas around the Alice Tableland and the space between the Townsville Plains cluster and the sea. The rest of the projected habitat extended towards the Rockhampton area in the southeast, but predominantly classified as poor value.

## **Discussion**

Effective conservation management demands that planners account for the dynamic processes influencing species and communities. Examining spatiotemporal changes in species habitat suitability can help quantify the recurrence of periods with unsuitable conditions to inform management and find areas that are less exposed to negative events such as resource bottlenecks. This information is key to protect species reliant on ephemeral resources, as is often the case in habitats experiencing irregular weather patterns such as deserts and some savannas, which occupy large areas of the Australian continent (Reside et al., 2019a). In this paper, we show how the extent of suitable habitat available for the endangered black-throated finch southern subspecies can shift dramatically over time, and propose a spatial classification of BTFS habitat according to the recurrence of unsuitable periods.

The variability found across years creates uncertainty about the absolute extent of suitable BTFS habitat at any given time. While in years such as 2010, the minimum monthly extent was over 38 000 km<sup>2</sup>, less than a 30% reduction from the maximum for the same year; years such as 2000, 2007 and 2011 stand out for their abrupt changes or consistently unsuitable conditions, as suitable area declined up to a 93%, reaching between 6000 and 3000 km<sup>2</sup>. During the study period, suitable area in the most suitable month was over 20 times more extensive than in the least suitable month. This ratio doubles the threshold for IUCN Red List criteria B (IUCN, 2019), which defines temporal range fluctuations as 'extreme'. These fluctuations are similar in magnitude to those of wide-ranging nomadic granivores in Australia (Runge et al., 2015a). Yet, the lower mobility of BTFS may render them poorly equipped for the combined threats of habitat loss and climate change (Franklin et al., 2017).

A climate-driven decline may already be reflected in our results. The particularly unfavorable conditions of 2011, coinciding with Category 5 Tropical Cyclone Yasi (Bureau of Meteorology, 2011), seem to have influenced an overall trend of decline in BTFS habitat, either caused by a slower recovery due to the magnitude of this event, or a permanent range reduction. Although the evidence is not

definitive, this might reflect the early impacts of a change in the climatic conditions, aligning with general forecasts for the region (Reside et al., 2012). The rise in recurrence and severity of extreme weather events is a phenomenon that is already creating long-term impacts for species and communities in Australia and worldwide (Bateman et al., 2015; Dowdy et al., 2019; Saunders et al., 2011; Smale Dan A. and Wernberg Thomas, 2013). An expected increase in the frequency of resource bottlenecks (Maron et al., 2015; Williams and Middleton, 2008), might force BTFS to move more often to find food, which added to the lack of access to alternative habitat due to habitat loss and fragmentation, will increase the likelihood of local extinctions (Piessens et al., 2009).

Despite this climate-driven variability, we found a consistent monthly pattern in suitable BTFS area relative to the year, aligning with processes influencing seed availability. Suitable habitat becomes scarcer between May and July due to the cold, dry conditions, and increases again as temperatures rise in August, even though rainfall remains low (Fig. 4.4). This pattern suggests a prevalent role of temperature over rainfall as a driver for habitat suitability, which can be also seen in the high contribution of temperature variables to our model (Table 4.1). Biologically, this effect can be linked to the high optimal growth temperatures typical from tropical and subtropical grasses, which tend to decrease their yields substantially under colder conditions (Bade et al., 1985; Moore et al., 2006).

We identified a second decline in suitable area between October and November. This phenomenon can be also linked to field observations of BTFS and other granivorous birds (Mitchell, 1996; Wyndham, 1980). As water becomes more available, it triggers the germination of the depleted seed bank, creating food shortages (Crowley and Garnett, 1999). These shortages tend to be brief, since most grass species used by BTFS tend to have rapid growth rates and can set seed in five or six weeks, although the cumulative effect of the late dry season, may aggravate them enough to elicit resource-tracking responses (Mitchell, 1996).

Information on the recurrence of these seasonal patterns can help conservation managers to implement mitigation actions during periods prone to resource shortages. However, the occurrence and severity of these events is ultimately dependent on the unpredictable year conditions. Therefore, the safest strategy to protect the BTFS, as well as other species exposed to unpredictable resource bottlenecks, is to allow natural adaptability by securing sites that can act as temporal refuges (Verboom et al., 2010).

Given the major contraction in the BTFS's historic range, preventing further loss of habitat where known populations occur is the main priority for conservation (Laguna et al., 2019). However, these areas are still subject to multiple development project proposals, many of which have already received approval to clear BTFS habitat (Reside et al., 2019b). This context opens up challenges for decision-makers who need to specify areas for protection and management. Due to their higher environmental resilience, targeting areas that remain consistently suitable and provide access to alternative suitable habitat is likely to increase the impact and security of conservation action. The high representation and spatial continuity of core areas in the Alice Tableland makes this subregion a priority for the protection of BTFS habitat. The combination of stable environmental conditions and low clearing rates, in contrast to the surrounding regions within the BTFS's historic range such as the Brigalow Belt to the southwest (Accad et al., 2019), could have preserved the region as a refuge for BTFS. While more than 90% of the vegetation in the Alice Tableland is classified as remnant (either not cleared or largely undisturbed), only 40% is classified as such in the Brigalow Belt (Accad et al., 2019). Likewise, the prevalence of high quality core areas in the eastern edge of the Townsville Plains, where the impact of Townsville's urban development has been smaller, highlights the higher resilience of areas that have remained unmodified.

The methods outlined here are constrained by the limitations of broad modelling approaches based on imperfect data and projected at a coarse resolution. This consideration makes these methods more suited to understand overarching trends rather than accurately defining local conditions. Furthermore, our model disregards variables that might be crucial to determine fine-scale suitability, such as land use or presence of invasive non-palatable grasses. Therefore, our results do not aim to be an accurate representation of BTFS range or remaining habitat, and should be complemented with on-site measures of habitat community and composition to determine site-scale suitability (Rechetelo et al., 2016).

Nevertheless, our model can help to partially define BTFS suitability within the complex environmental space in which they occur, which can prove essential to orient conservation. The parallels found between known grass productivity patterns in our study region and our model projections, support the robustness of this method and its potential as a tool to identify periods prone to shortages of ephemeral, climate-driven resources. Identifying the regularity, or lack thereof, of these bottlenecks can help in the design of seasonal habitat management strategies that can ensure species' access to critical resources.

Recent work has highlighted the importance of refuge areas for species with dynamic responses to irregular spatial and temporal conditions (Keppel et al., 2015; Reside et al., 2019a). Protecting these areas is particularly important in the face of an expected increase in extreme events such as large fires and severe droughts. A focus on climate change has brought attention to the idea that areas designed for conservation action may need to change according to dynamic ecological processes (Reside et al., 2018), for example, creating temporary reserves that shift according to species' use (Pressey et al., 2007; Rayfield et al., 2008). The methods presented here offer a detailed way to incorporate unpredictable variation in habitat suitability in the identification of priority areas for conservation. This dynamic perspective allows a more comprehensive evaluation of the long-term value of investing in protecting essential habitat, since consistently suitable areas are less exposed to extreme weather events that can lead to local extinctions. This information is best used as a base for planning and surveying, and should be complemented by on-site assessments. We recommend the use of similar methods to incorporate irregular spatiotemporal dynamics in conservation planning, with particular emphasis for species and systems with unpredictable or poorly-known responses. Building upon this work, it could be possible to predict where suitable habitat is likely to be found in the future, but in more species-relevant timeframes than often used.

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## Tables

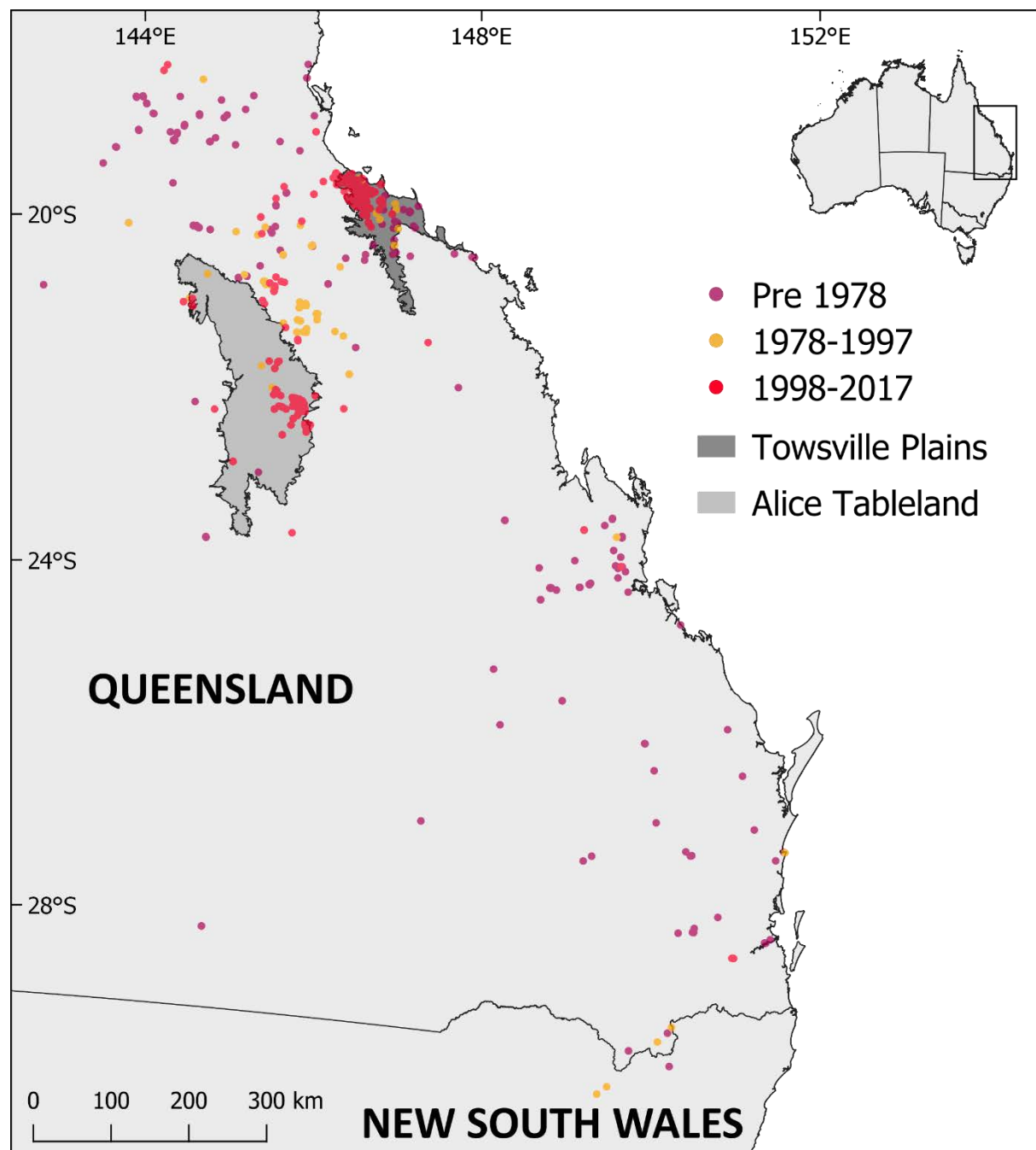
**Table 4.1.** Percent contribution and permutation importance of the 12 variables included in the final MAXENT model.

<b>Variable</b>	<b>Percent contribution</b>	<b>Permutation importance</b>
Temperature maxima, mean past 12 months	24.8	52.6
Lithology	20.3	10.6
Broad Vegetation Group	14.7	4.8
Temperature minima, mean past 12 months	14.2	5.5
Rainfall, seasonality past 12 months	12	1.1
NDVI	3.7	8.4
Temperature maxima, seasonality past 6 months	2.5	5.4
Rainfall, mean past 6 months	2.1	4
Temperature maxima, mean present month	1.9	1.8
Rainfall, mean past 3 months	1.4	4.3
Rainfall, mean present month	1.3	0.3
Rainfall, mean past 12 months	1.1	1.3

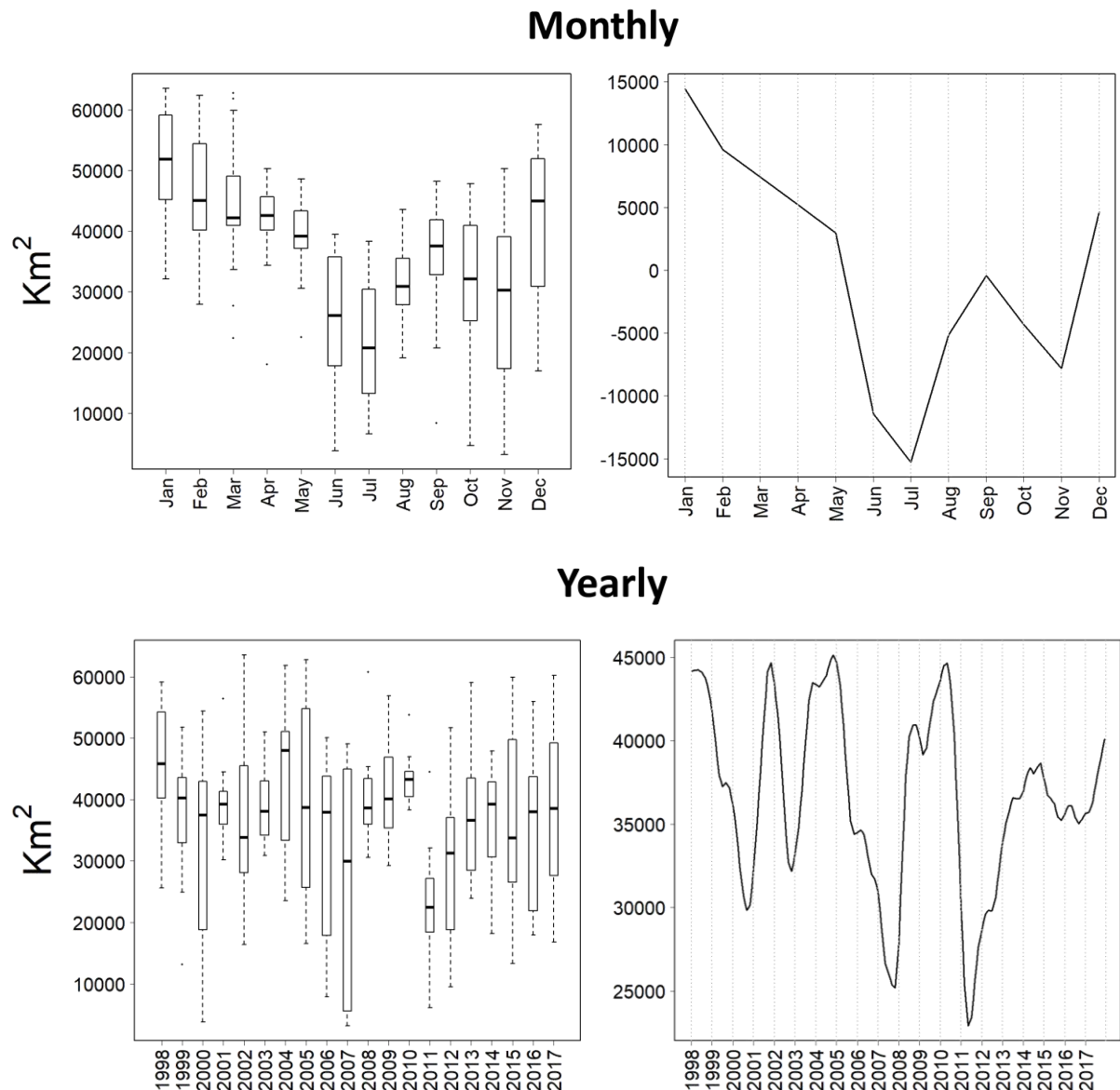
**Table 4.2.** Suitability consistency classes by area and percentage.

<b>Class</b>	<b>Area (km2)</b>	<b>%</b>
<b>Core</b>	22 037.50	29.91
<b>Occasional</b>	20 430.87	27.73
<b>Marginal</b>	3484.00	4.73
<b>Negligible</b>	27 735.47	37.64
<b>TOTAL</b>	73 687.83	

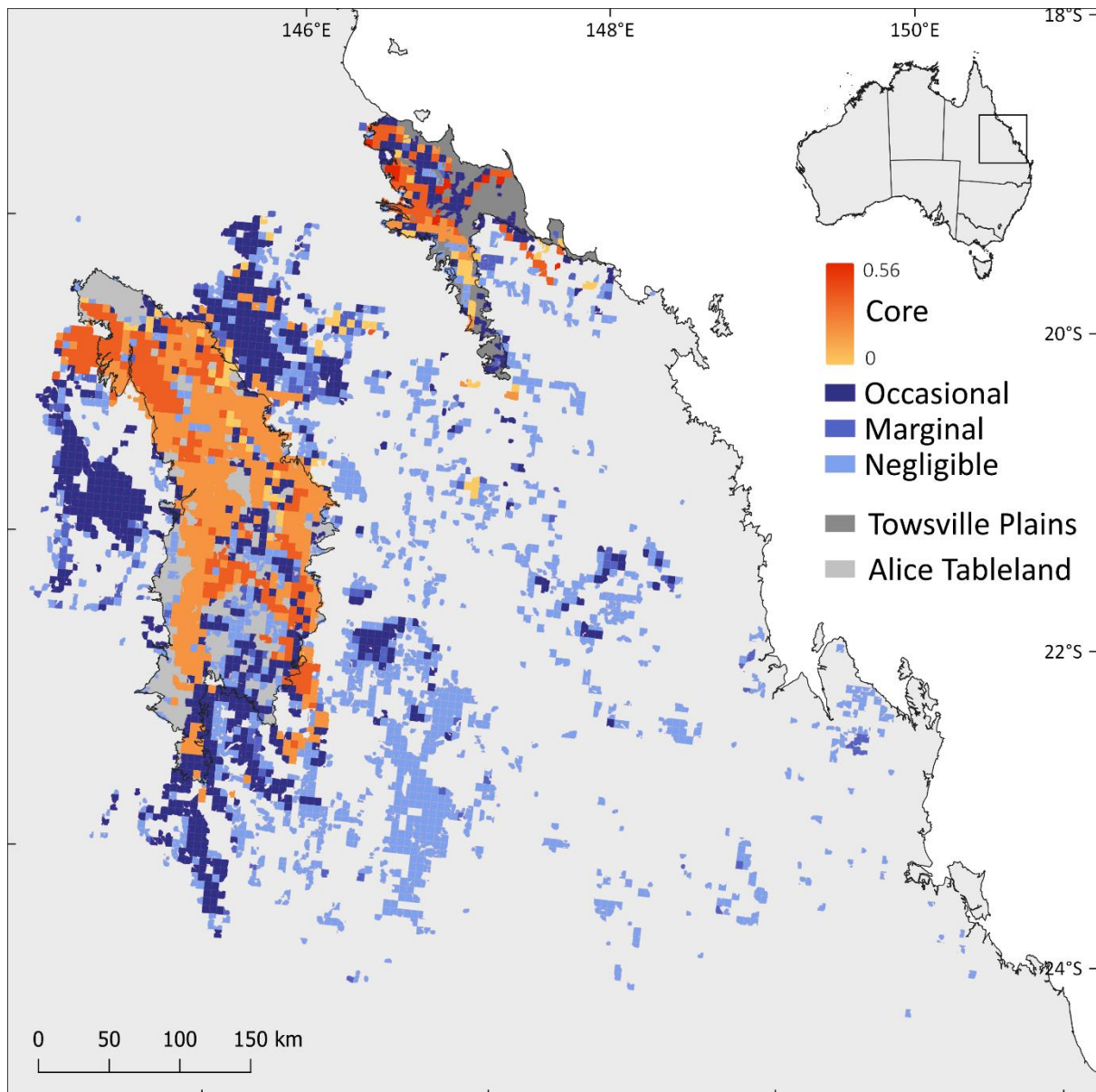
## Figures



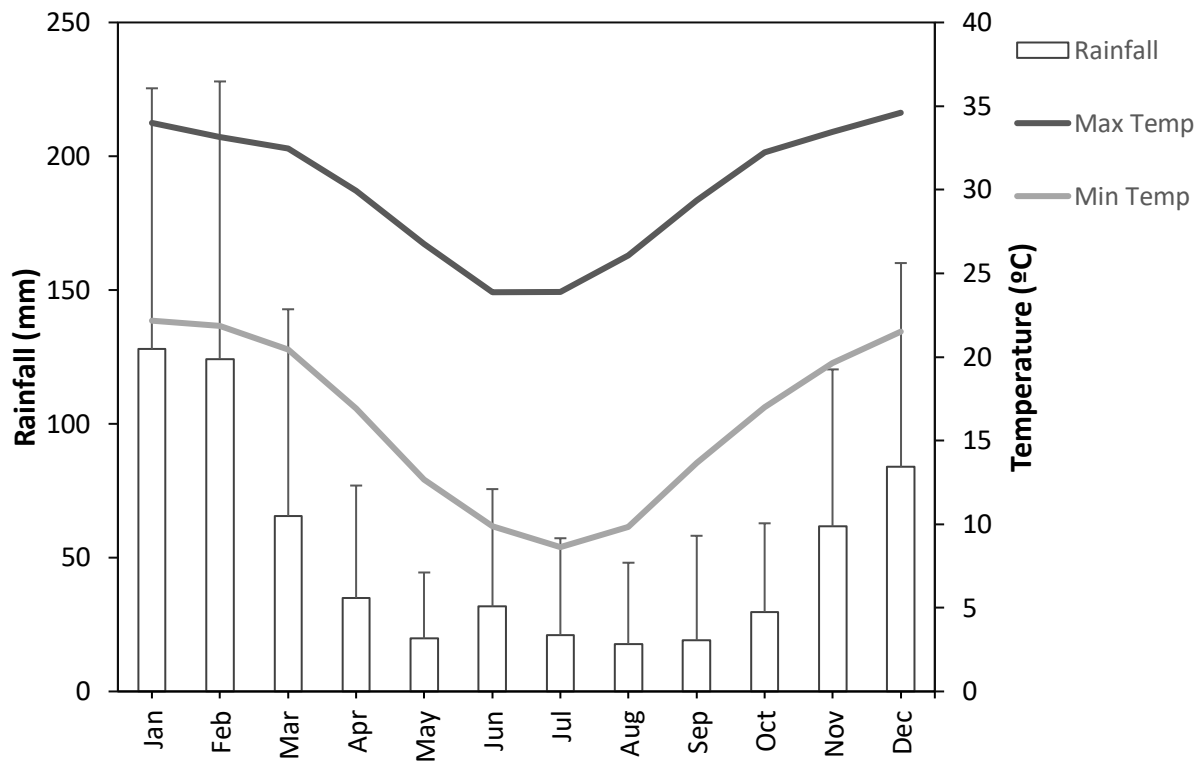
**Figure 4.1.** Southern black-throated finch records color-coded by time period. The mapped area contains all the historic distribution of the subspecies. Dark grey areas represent the two subregions where most BTFS currently occur.



**Figure 4.2.** Extent of projected suitable southern black-throated finch habitat. Boxplots show the average suitable area ( $\pm 25^{\text{th}}$  and  $\pm 75^{\text{th}}$  percentiles) by month (top left), or year (bottom left). Line plots show the isolated components after time series decomposition. The detrended monthly component (top right) was calculated using the centered moving average by month after removing the trend component. The deseasonalized trend component (bottom right) used a moving average smoothing function to remove seasonal volatility.



**Figure 4.3.** Southern black throated finch habitat suitability consistency based on dynamic habitat suitability projections (see methods). Categories are defined by the number of months a cell classified as suitable in a 20 year period (1998-2017): Negligible (less than 60 months), marginal (between 60 and 120 months), occasional (between 120 and 180 months), core (more than 180 months). Core cells also show the positive average deviation as an additional measure of suitability. Dark grey areas delimit the two subregions where most BTFS currently occur.



**Figure 4.4.** Average monthly rainfall, temperature maxima and temperature minima between 1998 and 2017. The data presented here is restricted to the area used in our projections.

# Chapter 5

## Picky finches? Ruling out dietary specialisation as a driver of the decline of the endangered southern black-throated finch (*Poephila cincta cincta*)

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### Abstract

Specialised dietary behaviours can limit species' adaptability to environmental changes. Biological invasions and widespread habitat modifications have caused substantial shifts in the type and availability of dietary resources in Australian savannas, leading to the decline of multiple endemic species. Among them, the endangered black-throated finch southern subspecies (*Poephila cincta cincta*) has lost 88% of their extent of occurrence in the last 40 years. Habitat clearing is recognised as the leading cause for their decline, however, it has been hypothesized that southern black-throated finches' particularly acute contraction, might have been accentuated by a lack of adaptability to changes in access to suitable seeds on which to forage. To assess the magnitude of diet-related threats, we compared foraging selectivity and willingness to explore novel seed types between southern black-throated finches and three other non-threatened granivorous Estrildid finches with different degrees of taxonomic relatedness: the northern black-throated finch (*Poephila cincta atropigyalis*), the long-tailed finch (*Poephila acuticauda*), and the zebra finch (*Taeniopygia guttata*). Our results showed that southern black-throated finches were not substantially more selective than the other taxa, and were generally willing to explore novel seed types. Contrary to our expectations, zebra finches, the most widespread Estrildid finch species in Australia, were also the most selective and reluctant to try novel seeds. Southern black-throated finches were the only taxon in the study that substantially changed their preferences depending on the presentation of the seeds, becoming more selective when seeds types were presented in separately. Overall, we found no evidence suggesting that southern-black throated finch's diet may make them particularly vulnerable to changes in seed availability. However, some of the behaviours identified could still have significant implications for conservation. This study reveals novel aspects of the ecology of Estrildids and southern black-throated finches, which can help to guide urgent conservation effort. Additionally, we provide further insight into the assumptions



around dietary specialists, whose susceptibility to resource changes may depend on a plethora of behavioural and environmental factors.

## **Introduction**

Dietary specialization is often cited as one of the main ecological characteristics linked to species' rarity and risk of extinction (Harcourt, Coppeto, & Parks, 2002; Purvis et al., 2000; Walker, 2006). An exclusive dependence on a small range of food types, and strategies to access them, can make dietary specialists particularly vulnerable to processes affecting the availability of their main resources. (Clavel, Julliard, & Devictor, 2011; Laurance, 1991; Wolf & Ripple, 2016). While this link seems evident, determining the degree of specialisation of a species, and its susceptibility to threatening processes, is a complex task that requires a detailed understanding of multiple behavioural and ecological traits.

Dietary specialisation is a relative trait that can change according to the availability of resources. Many species that are classified as specialists based on their observed diets, often have a wider fundamental niche, and can shift their dietary composition and foraging behaviour to incorporate previously unused or novel food resources (Shipley, Forbey, & Moore, 2009). Thus, determining the degree of plasticity in species' diets is key to understanding their vulnerability to rapid environmental changes (Renton et al., 2015; Varner & Dearing, 2014). To do so, particular behaviours, such as the lack of strong dietary preferences, or a willingness to explore and consume novel food types, can indicate a higher adaptive capacity (Greenberg, 1983; Marples & Kelly, 1999), and can be used as proxies to estimate the impacts of widespread threats such as climate change, habitat loss, or the introduction of invasive species.

Habitat modification and biological invasions are recognised as two of the most prominent threats for species in the tropical and subtropical savannas of northern Australia (Cook & Grice, 2013; Grice et al., 2013; Hobbs, 2005; Whitehead, Russell-Smith, & Woinarski, 2005). These regions are dominated by pastoral land uses (Australian Bureau of Agricultural and Resource Economics and Sciences, 2019), which are typically associated with transformative processes such as vegetation clearing, changes in grazing and fire regimes, and the spread of exotic vegetation. As a consequence, native plant communities have experienced substantial structural and compositional modifications, resulting in changes in the abundance, access and type of foraging resources available.

Granivorous birds have been one of the main groups affected by changes in Australian savannas, with one species declared extinct, and many others experiencing substantial declines (Franklin, 1999;

Franklin et al., 2005). Among them, the southern subspecies of the black-throated finch (*Poephila cincta cincta*) is one of four taxa of Estrildid finches that are listed as threatened under Australian legislation (Commonwealth Environment Protection and Biodiversity Conservation Act 1999). Southern black-throated finches (hereafter BTFS) once occupied a large range in the north-eastern portion of the continent (Laguna et al., 2019), but have since lost 88% of their former distribution. This decline is primarily associated with the high rate of habitat clearing within their historic range (Reside et al., 2019), although stock grazing, modified fire regimes, and invasive vegetation are likely to have contributed *via* mechanisms that are still uncertain.

A recent study using Value of Information Analysis to identify the main conservation priorities for the BTFS, highlighted research on the impact and management of diet-related threats, as one of the key actions to inform effective management (Mula-Laguna et al., 2020, Chapter 3, manuscript submitted for publication). However, knowledge of BTFS' diet is still sparse, and their rarity is a limiting factor in the collection of field data, creating uncertainty about the magnitude of potential threats. Among the factors influencing a possible diet-driven decline, it has been hypothesized that behavioural traits associated with a specialised diet could have limited BTFS' ability to adapt to changes in abundance and access to seed across its range.

BTFS exhibit strong signs of specialisation, as they normally require areas of sparse vegetation and small patches of bare ground, where they can easily detect and forage on the fallen seeds of grasses (Rechetelo, 2015). Nevertheless, BTFS have shown the ability to adapt to periods of seed shortage by varying their foraging techniques or consuming insects and seeds of other plant families (Mitchell, 1996; Rechetelo, 2015). Similarly, although BTFS associate with habitats dominated by native vegetation, some flocks have been observed feeding on the seeds of exotic grasses on a regular basis (Mitchell, 1996; Rechetelo, 2015). This information suggests a certain degree of dietary plasticity, but their vulnerability to environmental changes remains unknown.

Here we investigated the dietary plasticity of BTFS and three other taxa of non-threatened Australian Estrildid finches. Our aim was to identify behavioural aspects of BTFS' diet that could make them particularly susceptible to the historic and ongoing threats in Australian savannas. To do so, we focused on two traits: the display of strong dietary preferences, or selectivity; and a willingness to explore and consume novel food types, or boldness. We hypothesized that species that present both higher selectivity and a lower boldness are less likely to adapt to community changes reducing the availability of favoured resources. Our findings clarify the importance of these traits in relation to the decline of

the BTFS, and offer critical information that can be applied in threat prioritisation for conservation planning. Additionally, we provide an interesting perspective on the assumptions made about specialised dietary behaviours, which are often associated with rare or geographically constrained species, although this link might depend on a plethora of other ecological traits.

## **Materials and methods**

### **Ethics statement**

This study was approved by the Macquarie University Animal Ethics Committee (2018/028), in accordance with the Australian code of practice for the care and use of animals for scientific purposes (8th edition, 2013). Finches were provided with food and water at all times, and were only handled when necessary to ensure minimal disturbance. We had access to trained personnel, who performed regular health checks on the finches.

### **Study species**

To obtain a relative measure of BTFS' susceptibility to changes in dietary resources, we compared their behaviours to those of three other Estrildid finches occurring in savanna habitats in northern Queensland, which have not experienced substantial declines. All taxa shared similar foraging strategies with the BTFS, primarily feeding on the fallen seeds of grasses. The comparison was done at three taxonomic levels: using a different subspecies, the northern black-throated finch (*Poephila cincta atropygialis*); a species in the same genus, the long-tailed finch (*Poephila acuticauda*); and a species of the same family, the zebra finch (*Taeniopygia guttata*).

Northern black-throated finches (BTFN) are the only other subspecies of black-throated finch that is currently recognised (Tang, 2017). The two taxa are parapatric, with BTFN restricted to Cape York Peninsula, north of the range of BTFS. Not much is known about the niche differences between the two subspecies, as the information on BTFN is even more limited than for BTFS. However, while BTFS have suffered an evident decline, there have been no signs of a reduction in numbers or range of BTFN (Franklin, 1999).

Long-tailed finches (LTF), occur across the northern edge of the continent with the exception of Cape York. Although information is also scarce, there is evidence suggesting slight behavioural differences between the two species, as for example, LTF home ranges might be larger than those of BTFS (Evans et al., 1985; Franklin et al., 2017; Rechetelo et al., 2016).

Zebra finches (ZBF), are a classic model for research on captive birds, and there is a vast amount of information on multiple aspects of their biology. The species is also the most widespread Estrildid finch in Australia, occupying most of the continent, with the exception of coastal regions in the north and south (Higgins et al., 2006). Their habitat ranges from tropical and subtropical woodlands to drier inland grasslands and shrublands, and unlike the other taxa in the study, they are a fully nomadic species with high dispersal capabilities (Franklin, 2017; Zann & Runciman, 1994).

## Husbandry

The study consisted of four experiments carried out between October and December 2018. In each experiment we observed the behaviour of 40 adult captive-bred finches of unknown sex, 10 of each taxa. Finches were obtained from Macquarie University's Fauna Park in Sydney, where the study was also conducted. All experiments shared a similar cafeteria-style design in which finches had free choice to feed uninterrupted on four different seed types. However, the specific seed types, food presentation and trial length were changed according to the objective of the experiment and other operational limitations.

Finches were housed indoors, in three rows of modular wire enclosures divided into cages by removable separators. To observe individual behaviour, finches were kept alone in each cage. However, to minimise stress and potential behavioural anomalies caused by isolation, we paired each finch with a conspecific (same subspecies in the case of black-throated finches) and put them in adjacent cages divided by wire separators, rather than the solid separators used between different taxa. The relative position of each cage pair was assigned at random.

Every cage was fitted with two horizontal perches at different heights (in the same position in each cage), a drinker, and a removable tray placed under the cage. The tray was used to collect husks and discarded seeds, and was inaccessible to the finches. Both during the experimental trials, and between them, seeds were provided in flat, round, white dishes of ~8 cm diameter. Seeds were presented with husks after removing them from their florets. Between trials, finches were fed *ad libitum* a commercial seed mix containing four seed types used to feed them prior to the study (Avigrain™ Blue).

Finches were moved into the enclosures seven days before the first experiment. On days three, four and five we conducted pilot observations on a subset of eight individuals (two of each taxon) to measure the average hourly feeding rate. For these observations, we placed 5 g of each seed type in the commercial seed mix in a single dish, placed in a central position at the bottom of the cage. Finches

were left to feed undisturbed for seven hours before the dish and tray were inspected and any remaining seeds and husks were collected. Seeds were reweighed and the results were used to decide the amount of seed to be provided during the experimental trials.

### Seed types

For our four different experimental designs, we used two sets of seeds. The first, which we will refer to as ‘familiar’, contained the same commercial seed types used to feed the finches prior to the study. This set consisted of canaryseed (*Phalaris canariensis*), Japanese millet (*Echinochloa frumentaceae* L.), red panicum (*Setaria italica*) and white French millet (*Panicum milliaceum* L.). The four seeds provided a conveniently wide range of morphometrically distinct items to observe preferences in the usual diet of these birds (Table 5.1).

The second or ‘novel’ set, consisted of four types of seed to which the captive finches had not previously been exposed. We chose kangaroo grass (*Themeda triandra*) and black speargrass (*Heteropogon contortus*) as common native plants with palatable seeds occurring throughout the distribution of the species in the study. We chose the other two seed types because they were closely related to exotic fodder grasses that have become invasive in the region. The first one, Gatton panicum (*Panicum maximum*) is a naturalised grass that occurs across the Australian tropics, and is part of the broader category of widespread invasive species known as Guinea grasses. The second, Bahia grass (*Paspalum notatum*) is a less widespread naturalised plant, similar to other seeds palatable to BTFS. All novel seeds were obtained from commercial distributors. Native seeds were obtained from Nindenthana Australian Seeds, while the two exotic seeds were purchased from Australian Wildlife Supplies.

### Studied behaviours

Before conducting the experiments, we first had to establish a clear definition and metrics for the studied behaviours in the context of the study.

### Foraging selectivity

We defined foraging selectivity as the display of distinct dietary preferences when presented with multiple choices. Preference was measured using the Manly’s alpha feeding preference index (Chesson, 1983), as implemented in the ‘selectapref’ package in R (Richardson, 2020). This index calculates the proportion of a food item consumed over all items available, while incorporating additional control variables for a more accurate description of preference than a simple percentage.

For example, although we always provided an equal amount of each seed type at the beginning of every trial, we found that during the foraging process, finches often discarded or involuntarily tossed a significant number of seeds out of the dishes. These seeds were collected in the tray under the cage, but became unavailable for the rest of the trial. If enough seed was discarded, this factor could have had a substantial effect on consumption, as selection can be influenced by the availability of each resource. While we could not know the specific amount of seed available after the start of the trial, Manly's alpha can be calculated when the amounts of each food item are unequal. We decided that subtracting the amount of seed found in the tray from the initial amount provided was a more accurate estimate of the total seed available during the trial. Manly's alpha also incorporates a factor for depletion, which can approximate the progressive reduction of food available based on the amount consumed at the end of the trial. The result of this index is a proportional value between 0 and 1 for each item in the trial, where the values for all items add up to 1, and higher indices represent higher preference.

Selectivity was estimated upon statistical analysis of the differences between preference values for all seed types in the experiment. As a reference, due to the proportional character of the index, when all index values were close to  $1/\text{number of items}$  (in our case  $1/4 = 0.25$ ), it was clear that preferences were very similar, indicating lower selectivity.

#### *Foraging boldness*

Foraging boldness was defined as the willingness of an individual to use novel food items when not forced to do so. We measured this by counting the number of seed types explored during a trial (out of four novel types presented) where we also provided a sufficient amount of familiar seeds. Thus, a bold finch was one that explored or consumed every novel seed type available, while a shy one only approached the familiar seeds.

#### Experimental designs

##### *Experiment 1: Foraging selectivity using a set of familiar mixed seeds*

Experiment 1 consisted of five trials. Our objective was to measure the degree of foraging selectivity displayed by finches in their regular diet. To do so, at the beginning of each trial, we replaced the dish used to feed the finches outside of the experimental trials by an identical dish with a known number of seeds equivalent to 0.2 g of each of the four familiar seed types. The figure was determined by doubling the average hourly consumption rate for all taxa, which was measured in our pilot observations. This quantity was enough to ensure that choice was entirely based on preference, as

finches were provided with sufficient seeds of each type to be satiated. The dish was placed at the centre of the cage's floor and finches were left to feed undisturbed for 60 minutes. At the end of the trial, the dish and tray were inspected and any remaining seeds and husks were collected. Seeds were recounted and used to calculate the total number of seed of each type consumed by the individual.

#### *Experiment 2: Foraging selectivity using a set of familiar seeds separated by type*

Experiment 2 consisted of ten trials. In this experiment, we tested for possible changes in foraging selectivity and seed preference when the selection process was made easier by presenting them separately. We used a similar design to experiment 1, in which we presented 0.2 g of each seed type in the familiar set. This time however, each seed type was put in an identical, yet separate dish. The dishes were placed in the centre of the cage's floor, leaving ~2 cm between them, randomising the relative position of each seed type in every trial. Finches were left to feed undisturbed for 60 minutes before the dish and tray were inspected, and any remaining seeds and husks were collected. Seeds were reweighed and used to calculate the total mass of each seed type that was consumed.

#### *Experiment 3: Foraging selectivity using a set of novel seeds*

Experiment 3 consisted of six trials. This experiment was designed to observe if selectivity patterns in finches differed substantially when foraging on seeds that were not part of their regular diet. Here we replicated the design for experiment 2 in which we presented each seed type in a separate dish, but replaced the familiar seed types by the novel set. Due to logistic constraints, we could not obtain sufficient Kangaroo grass and black speargrass seeds, so instead of presenting 0.2 g of each seed type, we used 0.043 g, the equivalent average mass of 10 Kangaroo grass seeds, and reduced trial time to 30 min. As in previous trials, finches were left to feed undisturbed before the dish and tray were inspected, and any remaining seeds and husks were collected separately. Seeds were reweighed to calculate the total mass of each seed type that was consumed. This experiment occurred chronologically after experiment 4, which means that finches had already been briefly exposed to the novel seed types.

#### *Experiment 4: Foraging boldness*

Experiment 4, consisted of six trials. In this experiment we wanted to measure foraging boldness using the novel seed types. In each trial we presented finches with four dishes containing ten seeds of a unique type in the novel seed set, to which they had never been exposed, while also leaving a fifth dish containing a more-than-sufficient quantity of familiar seed mix. The dishes were placed on the cage's floor with the familiar seed in the centre and the novel seeds around it, randomising the relative

position of the novel seed types in every trial. Finches were left to feed undisturbed for 60 minutes, before the dish and tray were inspected looking for seeds and husks. The outcomes for number of novel seed types consumed were recorded *in situ* using a binary classification: when all ten seeds were found in the dish or tray without clear signs of manipulation, we classified the response as ‘no interest’; if seeds were consumed or presented clear signs of manipulation (e.g. broken or partially consumed), we classified the response as ‘interest’.

## Data analysis

### *Foraging selectivity*

We analysed the foraging selectivity results by fitting separate Bayesian generalised multivariate mixed models for experiments 1, 2 and 3. The reason we separated the analysis by experiment was two-fold. First, the operational limitations (e.g., different number of trials or trial length per experiment) resulted in an unbalanced design when data were pooled. Most importantly however, the initial exploration of the models revealed an effect of repeated measures (trial number) on the response that varied according to the experiment. Given the considerable span of time passed between the first and last experiment, we considered that this effect could introduce significant bias in our comparisons, and decided to analyse experiments separately. Although we discuss the differences found among experiments, comparisons were made based on patterns found within the same experiment.

To fit the models, we used Manly’s alpha index values as the dependent variable, specified as a multivariate response with one value per seed type. Finch species was included as a fixed effect, as well as trial number and their interactions. Trial number was transformed to a categorical variable to avoid model misspecifications, since not all trials were conducted with an equal period of time between them. Finally, to control for individual variation and non-independence in the response of repeated observations on the same finch, we added a random effect for finch identity. Models were created in Stan computational framework (<http://mc-stan.org/>) through the ‘brms’ package in R (Bürkner, 2020). We selected this package for its implementation of mixed effects models with the option of using a Dirichlet distribution, a multivariate generalization of the beta distribution family appropriate for the analysis of compositional data (Douma & Weedon, 2019). Each model was fitted using 3000 iterations and four Markov chain Monte Carlo (MCMC) chains, allowing ‘brms’ to automatically specify mildly informative priors according to the chosen model structure and distribution.



### *Foraging boldness*

To test for differences in foraging boldness, we fit a binomial Generalized Linear Mixed Model (GLMM), using an Item Response Tree (IRTree). IRTrees are a specific type of linear model designed for the correct analysis of multi-level behavioural data (Boeck & Partchev, 2012). Building an IRTree model requires the specification of categorical behavioural responses as a sequence of binary decisions called ‘nodes’. Since the objective of this experiment was to quantify the exploratory behaviour of finches regardless of the specific type of seed consumed, we first established a categorical response with five levels: ignore all seeds, try 1, 2, 3, or 4 seeds. Each of these categories can then be seen as a series of binary decisions to explore more seed types. Thus, we built an IRTree in which each of the five categorical responses for number of seeds tried, was encoded as four binary values (Fig. 5.1). For example, the response of a finch that tried two novel seed types was specified with a 1 for nodes n1 and n2, a 0 for node n3, and no value for node n4. The resulting model’s response can be interpreted as the probability of escalation for each decision node (i.e., a high estimate for node n1 implies a high likelihood of trying 1 seed or more, while node n2 determines the probability of trying 1 seed, compared to trying more than 1). For more details and guided examples on IRTree GLMM, see López-Sepulcre et al., 2015.

The final IRTree model was fitted in R using the ‘glmer’ function in the ‘lme4’ package (Bates et al., 2020). We used the binary node values as the dependent variable and specified a binary distribution family. Similar to our selectivity models, we included fixed effects for finch species and trial number as a category, as well as their interactions. Additionally, we added the effect of node and its interaction with finch species to compare probability of escalation by node. Finch identity was included as a random effect, as well as observation, a unique identifier of trial per finch identity used to control for the fact that multiple nodes shared variability across the same observation.

## **Results**

### *Experiment 1: Foraging selectivity using a familiar set of mixed seeds*

When familiar seeds were presented mixed, we found a general tendency to select two of the seed types over the other two (Fig. 5.2a). The only exception was BTFS, which had similar preferences for three of the four seed types. Overall, white French millet was more likely to be ignored, while red panicum and Japanese millet were preferred by all taxa, although BTFN did not show interest for the latter. Canaryseed was the seed type that elicited the most diverse range of responses, as it was generally avoided by LTF and ZBF, while BTFN showed a strong preference for it, milder in the case of BTFS.

The close preference values among three of the four seed types suggest that BTFS were the least selective taxon in the experiment. These results however, are somewhat unclear, as the large credible intervals of our model's posterior probabilities for all taxa reveal substantial overlap both among seeds, as well with the 0.25 threshold. Despite this, ZBF's more extreme values and clear aversion to canaryseed, indicate a higher selectivity relative to the rest of finches.

#### *Experiment 2: Foraging selectivity using a familiar set of seeds separated by type*

When seeds were presented separately, finches maintained consistent preferences with the previous experiment, although differences became clearer (Fig. 5.2b). Again, BTFS was the main exception, since their preference for canaryseed declined substantially, indicating an increase in selectivity when seeds were presented separately.

Overall, BTFN's similar preference values for all seed types, suggest that this taxon was the least selective among the four, although it was closely followed by LTF. In contrast, ZBF displayed substantial differences among three of the four seed types, confirming the patterns found in the first experiment, and establishing it as the most selective species. ZBF also had the most different from the other taxa, displaying a substantially higher dislike for canaryseed than the rest of finches, and a greater preference for Japanese millet.

#### *Experiment 3: Foraging selectivity using a set of novel seeds*

In general, selectivity patterns with novel seed types were consistent with our findings on familiar seeds. Again, ZBF were the most selective taxon, showing the largest differences in preference among the four seed types (Fig. 5.3). Meanwhile, except for small differences in their preference for Bahia grass, BTFN, BTFS and LTF were extremely similar, all sharing a low degree of selectivity.

ZBF also displayed substantial preference differences with the other taxa, as they were the only one with a clear preference for black speargrass, which was disliked by the rest, and the only taxon with a substantial disinterest for Bahia grass. Gatton panicum was liked by all taxa, while kangaroo grass was generally avoided, although this dislike was less evident in LTF.

#### *Experiment 4: Foraging boldness*

Our boldness trials (Fig. 5.4) revealed that BTFN, BTFS and LTF were highly exploratory, all showing a very high likelihood of trying at least three of the four seed types (BTFN: 91.4% [67.6, 98.2]; BTFS:

85.65% [55.73, 96.6]; LTF: 79.92% [47.86, 94.5]). In contrast, ZBF had less than a 70% probability of trying even one seed type (67.38 [32.07, 90]), and less than 20% (17.05% [2.74, 60]) of trying three or more. Due to the wide confidence intervals, particularly large in the case of ZBF, the magnitude of these differences is somewhat uncertain, although given the considerably lower estimates for ZBF in all nodes, it is clear that ZBF was the only taxon of the four with a disinterest or reluctance to consume the novel seeds presented.

Additionally, we searched for a potential effect of trial number on the probability of escalating from one node to another, but we did not find significant differences for any of the species (Table S5.1), suggesting that familiarisation with the novel seed types did not influence the likelihood of trying them, at least for the duration of the experiment.

## Discussion

Dietary specialisation is a risk factor that can contribute to the decline and extinction of threatened species. Behavioural traits associated with a lack of dietary plasticity can limit species' ability to adapt to processes that influence the availability of their preferred foraging resources. Understanding these behaviours is a fundamental step in determining the magnitude of diet-related threats, which can prove essential to the design of conservation plans and the implementation of effective management actions.

Although it has been speculated that factors linked to a specialised diet might have contributed to the decline of the endangered southern black-throated finch, we found no evidence to support these claims. BTFS were not particularly more selective nor were they more unwilling to explore new seed types than the closely related BTFN and LTF. Furthermore, all our experiments indicated that despite being the most widespread Estrildid finch in Australia, ZBF's dietary plasticity was substantially lower than the more geographically restricted *Poephila* taxa (BTFS, BTFN and LTF).

While disproving our initial hypothesis, our findings may highlight the importance of dietary plasticity as an adaptation in BTFS and many granivorous birds in Australian savannas. These habitats are characterised by their irregular weather patterns, which drive the abundance of water and seed in the landscape (Garnett & Williamson, 2010). As a consequence, species such as the BTFS are exposed to extreme variability in the condition of their habitat, which can lead to unpredictable periods of resource shortages (Mula-Laguna et al., 2020, Chapter 4, manuscript submitted for publication). BTFS respond to these shortages in two ways: either by broadening their diets and foraging strategies to

make use of the remaining resources (Mitchell, 1996), or by undertaking movements to find suitable areas (Laguna, 2019; Rechetelo, 2016). In both cases, the capacity to make use of a diverse spectrum of seed types, reinforced by a higher willingness to explore novel resources, are fundamental to maintain these strategies.

General macroecological theory suggests that common, widespread species are more likely to present generalist behaviours (Gaston, Blackburn, & Lawton, 1997). We expected that, because of their broader geographic and habitat type distribution, ZBF would display an equal or lesser degree of foraging selectivity than the other taxa, as well as a higher willingness to consume novel seed types. ZBF's lower dietary plasticity may be explained by their nomadic lifestyle. In some cases, dietary specialists need to move further and more often to find their preferred food items (Clutton-Brock, 1975; Terraube et al., 2011). We suspect that, while the more sedentary *Poephila* species might have adapted to use a broader spectrum of food types within their habitats, ZBF's higher mobility may allow them to have a more specialised diet.

The generally consistent preferences (or lack thereof) of each taxa, regardless of the way seeds were presented, indicates that preference is a major factor determining their dietary composition. BTFS was the only exception to this trend, as they partially changed their preferences when seeds were separated, and became more selective. This shift is consistent with optimal foraging theory (Krebs, Stephens, & Sutherland, 1983), which explains changes in food selection as a response to factors determining the total energetic budget (e.g., food availability or handling time, versus nutritional or caloric value). When seeds are mixed, they require more energy and time to separate and consume, which can lead to a decrease in selectivity to avoid caloric expenditure or higher predation risk (Brown & Mitchell, 1989; Charalabidis et al., 2017). By comparison, this behaviour suggests that BTFS dietary choices may be less based on preference and instead vary depending on factors such as abundance and access.

Although the behaviours studied here offer certain advantages to cope with changes in the abundance and diversity of food (Corrigan et al., 2011; Robinson et al., 2019; Varner, 2014), they could also pose risks for conservation that should be considered. For example, species with a low foraging selectivity may feed on a higher diversity of food types, and have higher tolerance for nutritional imbalances derived from temporal shifts in their diet (Raubenheimer & Simpson, 2003; Wehi, Raubenheimer, & Morgan-Richards, 2013). Yet, an inability to select higher quality resources might make them particularly vulnerable to long-term changes where poor quality foods become prevalent (Drummond,

2005; Kennish, 1996). BTFS may overcome this problem by becoming more selective. However, the fact that mixing could already decrease selectivity by a significant margin, makes us think that BTFS are not willing to spend a substantial effort to find and consume high quality food types. Furthermore, this effect could be aggravated by additional threats to species with a generalist diet, such as an increase in competition, and a decrease in foraging success as resources become rarer (Abrams, 1990; Petrov et al., 2020).

A more comprehensive explanation for diet-driven impacts on BTFS is likely to be linked to a decrease in access to seed due to structural habitat changes (Black-throated Finch Recovery Team, 2007). BTFS are strongly associated with areas of short grass with small patches of bare ground on which to forage (Rechetelo, 2015). Exotic, high-biomass grasses, such as grader grass (*Themeda quadrivalvis*), and gamba grass (*Andropogon gayanus*), can dominate the communities where they are introduced (Grice, 2013; N. Rossiter et al., 2004), creating a dense vegetation layer which limits access to fallen seed. Additionally, exotic grasses can generate other synergistic effects, affecting nutrient cycling (Grice, 2013; N. Rossiter-Rachor et al., 2009), or increasing the fuel load, which in turn increases the recurrence and intensity of fires (Miller et al., 2010; N. A. Rossiter et al., 2003; N. A. Rossiter-Rachor et al., 2008). By comparison, the habitats of BTFN and LTF have experienced far less modification than those of BTFS (Bradshaw, 2012; Franklin, 2005; Reside, 2019), which could help to explain the particularly acute decline of the latter.

The results of this study offer a novel insight into the dietary behaviour and threats to BTFS and Estrildid finches in Australia. However, generalisations should be made with caution, as foraging behaviours in wild birds might be influenced by factors that were not present in captivity. For example, while we tried to minimise the effect of isolation, all of the taxa used in the study are group foragers (Higgins et al., 2006), a trait that could have affected individual responses during the experiments. Coleman and Mellgren (1994) revealed that ZBF exhibit a higher degree of neophobia when feeding alone. Although said study only tested neophobia on non-food items (i.e., unfamiliar objects around the feeder), this effect could potentially extend to novel seed types. Furthermore, prior to our experiment, finches had been only exposed to a small variety of seeds, which could both increase neophobia due to a lack of experience with new food types, or reduce it as a result of naivety (Eccles, 2018; Marples et al., 2007). Wild ZBF are also more likely to experience higher stress during postnatal and adolescent stages than captive-bred individuals, which has been correlated with neophobia in non-food objects and wariness to enter new environments (Emmerson & Spencer, 2017; Spencer & Verhulst, 2007). While we do not discard a possible effect of these confounding factors in our results,

we expect that the fact that all individuals were raised in similar conditions may allow us to measure general behavioural differences among all taxa.

Future work on dietary behaviour should evaluate the effect of low selectivity as a threat for BTFS and other Estrildid finches. Measuring giving-up densities might help to understand the drivers behind the identified shifts in BTFS foraging selectivity. Meanwhile, studies on health condition can help to determine the consequences of processes leading to a dominance of poor quality foraging resources. If possible, findings should be confirmed through field experiments or observations, which should be paired with additional research on the impacts of changes in habitat structure. This information however, might be difficult to obtain due to BTFS' rarity, and additional ethical considerations.

Our findings add to the body of evidence indicating that, although traits linked to dietary specialisation can increase risk of extinction, there are multiple other variables that condition the role of dietary behaviour in species' decline. Species with substantial dietary plasticity, such as the BTFS, could still be impacted by local changes in food quality or habitat structure, while more selective species can become widespread and maintain their diet thanks to their nomadic habits. Understanding the complex mechanisms behind a species' decline is key to identifying relevant threats and improving the efficiency of conservation management. While the results of this study need to be complemented with additional research to draw more detailed conclusions in this regard, this is a first look into the role of diet in the decline of a flagship species for conservation in Australia. Halting clearing remains the number one priority for the conservation of the BTFS, yet our results provide additional information to guide future conservation research and support management within their remaining habitat.

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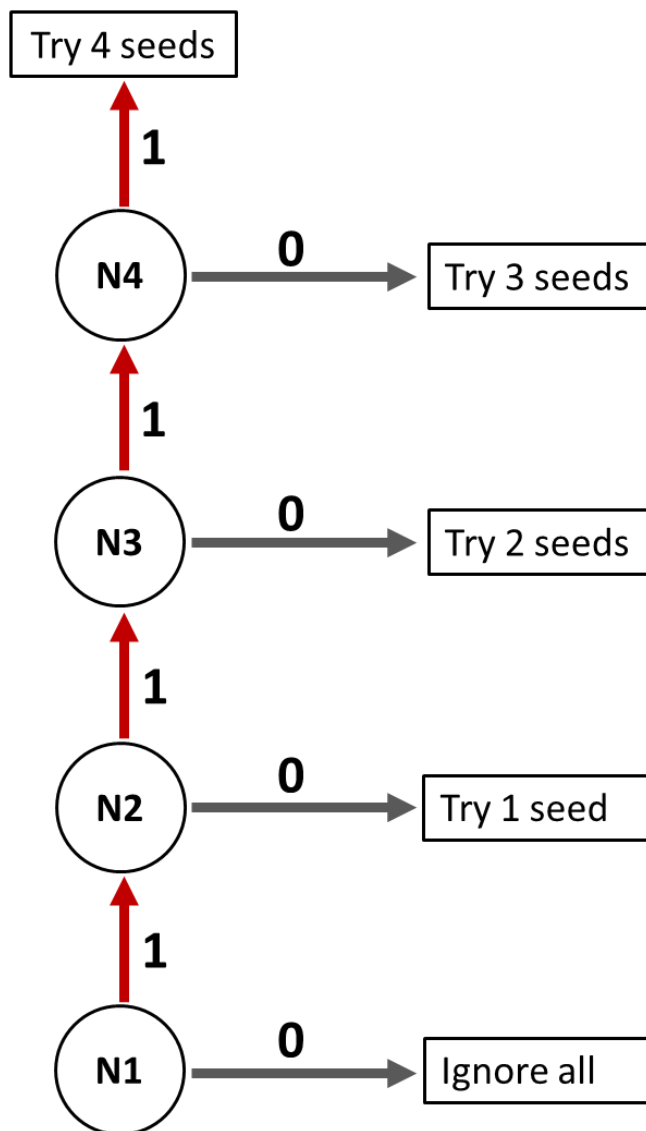
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## Tables

**Table 5.1.** Average and standard deviation of length, width and weight of all seed types used in the study. Measurements are based on 10 samples obtained from the same sources that were used in the experiment. Length and width were taken at the longest and widest point respectively.

		Code	Length (mm)		Width (mm)		Weight (mg)	
Aviary								
Canaryseed	<i>Phalaris canariensis</i>	CAN	5.16	±0.35	1.91	±0.10	6.74	±0.11
Japanese Millet	<i>Echinochloa frumentaceae</i> L.	JAP	3.46	±0.48	1.94	±0.11	3.17	±0.06
Red Panicum	<i>Setaria italica</i>	RED	2.69	±0.14	1.64	±0.06	2.55	±0.05
French White Millet	<i>Panicum miliaceum</i> L.	WHT	2.98	±0.23	2.02	±0.24	4.35	±0.08
Novel								
Bahia Grass	<i>Paspalum notatum</i>	BHG	2.85	±0.23	1.64	±0.04	1.51	±0.09
Gatton Panicum	<i>Panicum maximum</i>	GTP	2.90	±0.07	0.89	±0.04	0.99	±0.09
Kangaroo Grass	<i>Themeda triandra</i>	KGR	8.91	±0.52	1.06	±0.18	4.04	±0.06
Black Speargrass	<i>Heteropogon contortus</i>	SPG	8.14	±0.15	0.60	±0.06	1.35	±0.06

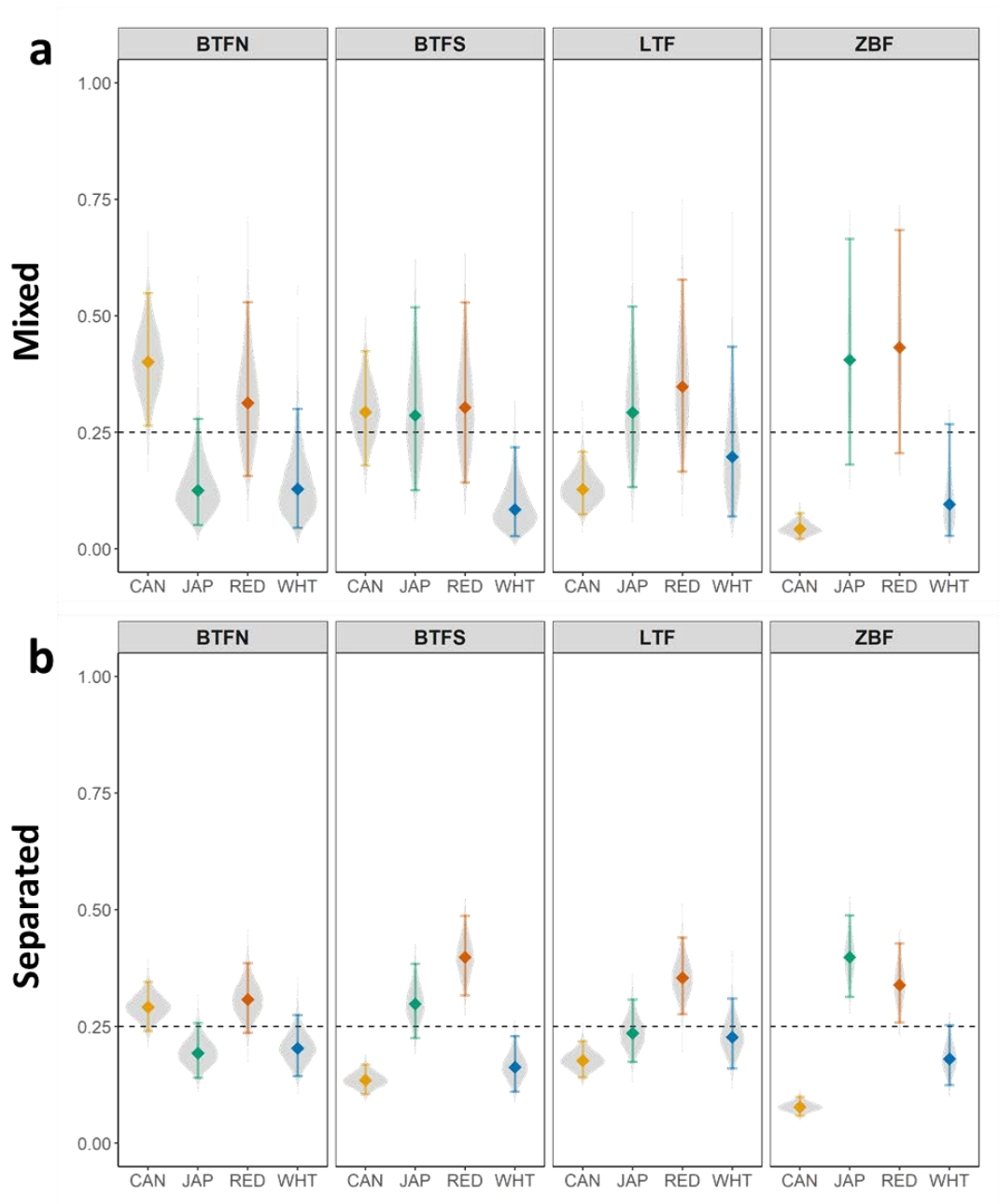
## Figures



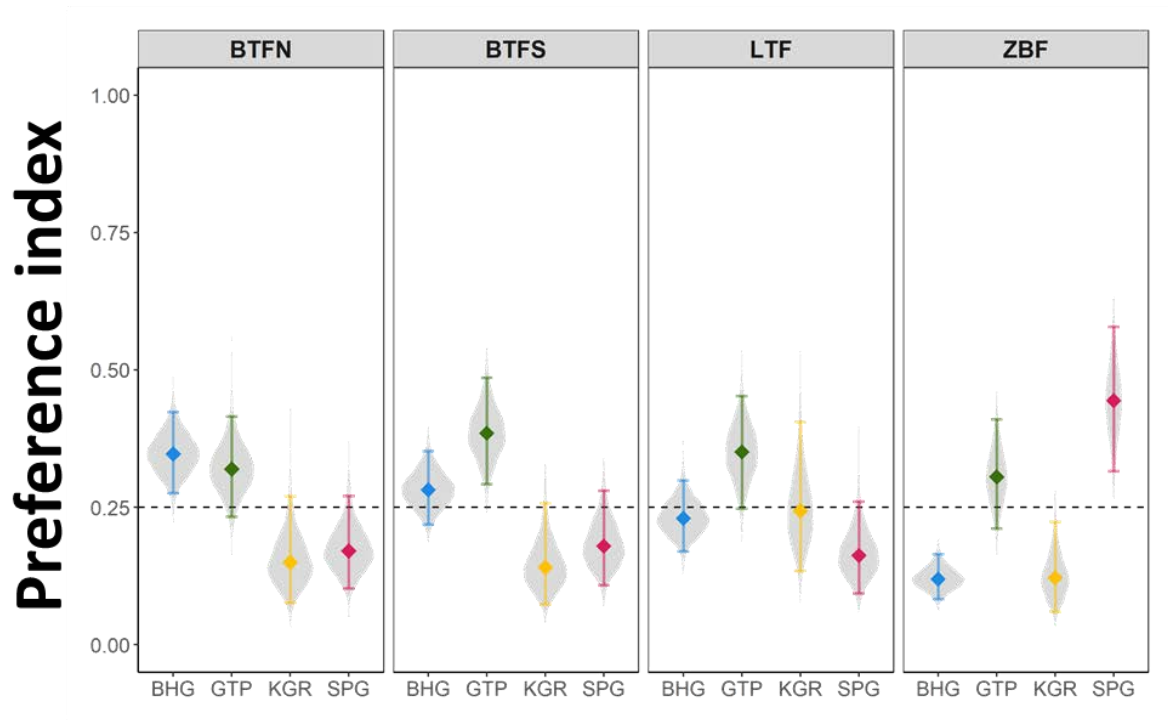
**Figure 5.1.** Item Response Tree diagram used to model the response of our foraging boldness experiment. Each node of the tree (N1-N4) represents a binary decision in which finches decide to show interest for a higher number of seed types (1) or not (0).



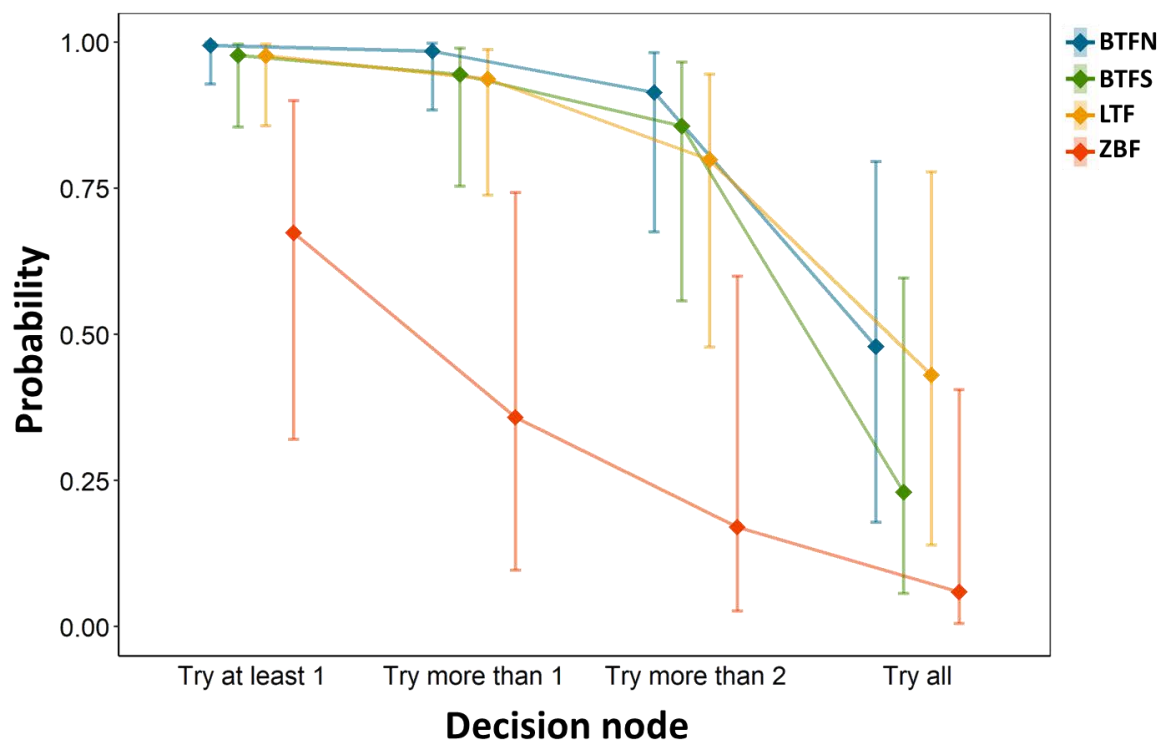
## Preference index



**Figure 5.2.** Seed preferences of four taxa of Estrildid finches using a set of four familiar seed types, when seeds were presented mixed (experiment 1; a) and separated (experiment 2, b). The title of each box corresponds to each finch taxa: northern black-throated finch (BTFN), southern black-throated finch (BTFS), long-tailed finch (LTF), and zebra finch (ZBF). The x axis includes the codes for each seed type: canaryseed (CAN), Japanese millet (JAP), red panicum (RED) and white French millet (WHT). Seed preference measured as the Manly's alpha preference index is displayed on the y axis. Grey areas show the posterior distribution of our Bayesian model, while points and error bars were used to indicate the mean of the distribution and 95% credible intervals. When the four preference values are clustered around the 0.25 threshold (marked with a dotted line) the taxon can be considered less selective.



**Figure 5.3.** Seed preferences of four taxa of Estrildid finches using a set of four novel seed types. The title of each box corresponds to each finch taxa: northern black-throated finch (BTFN), southern black throated finch (BTFS), long-tailed finch (LTF), and zebra finch (ZBF). The x axis includes the codes for each seed type: Bahia grass (BHG), Gatton panicum (GTP), kangaroo grass seed (KGR) and black speargrass seed (SPG). Seed preference measured as the Manly's alpha preference index is displayed on the y axis. Grey areas show the posterior distribution of our Bayesian model, while points and error bars were used to indicate the mean of the distribution and 95% credible intervals. When the four preference values are clustered around the 0.25 threshold (marked with a dotted line) the taxon can be considered less selective.



**Figure 5.4.** Responses of four taxa of Estrildid finches when presented with four types of novel seed. Each decision node represents the binary probability (mean and 95% confidence intervals, back-transformed from log-odds probability estimates of a binary model), of taking the specified decision; in this case consume more seed types (1) or not (0).

# Chapter 6

## Synthesis and conclusion

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The protection of threatened species demands a judicious use of the time and resources available. Information is an important foundation for the success of conservation decisions, yet declining species often become rare and hard to study, resulting in a poor understanding of their ecology and threats, and an increased cost of research. The combination of urgency and lack of information creates a dilemma between investing in research to improve the outcomes of management, and acting to prevent further declines. The act of prioritising information with a higher value for management is a crucial step in conservation planning, and methods that can make the most of the data and resources available can prove to be the decisive factor in the persistence of species at risk of extinction.

Australia has one of the highest number of endemic species of any country, yet a high percentage of them have declined or gone extinct (Chapman, 2009; Woinarski et al. 2019). Among these, the endangered southern subspecies of the black-throated finch has lost 88% of its historic range, due to habitat clearing and other threats associated with pastoral land uses. Protecting the southern black-throated finch requires urgent conservation action, but our knowledge about some of their fundamental requirements is still incomplete, which has been an obstacle for the design and implementation of management strategies.

This thesis is a multidisciplinary approach to the conservation case of the southern black-throated finch (hereafter BTFS). My primary goal was to create useful outputs that can be applied to the immediate protection of the BTFS. I have also used this opportunity to explore the use of tools to support conservation in complex cases where information is scarce and hard to obtain. I followed these two aims to complete: 1) a review of knowledge on BTFS ecology and threats with a list of eight research and monitoring priorities to support conservation; 2) a quantitative assessment of the conservation value of novel information to aid in the prioritisation of investment choices; 3) a description of the spatiotemporal patterns affecting BTFS habitat and a map of high value, secure areas for conservation; and 4) an examination of the role of dietary behaviour traits in the decline of the BTFS.

### **Conservation decisions under uncertainty**

By definition, the decision-making process is an uncertain one. Information is always incomplete, and the number of variables affecting possible outcomes is too high for them all to be considered. These limitations apply particularly well in the case of conservation decisions, which are stymied by the complexities of ecological systems and the difficulties derived from studying threatened species. Decision-making tools, such as Value of Information analysis, offer a structured method to evaluate uncertainty, and guide decisions after assessing the risks and rewards of implementing specific actions. Value of Information (Vol), measures the benefits that can be obtained from collecting information prior to taking a decision, which can help decide in the choice between investing in research, and managing with limited information.

I applied Vol analysis to the case of the BTFS (chapter 3), and found that the effectiveness of conservation decisions would not necessarily be improved by the collection of additional data. In line with previous work (Reside et al. 2019; Vanderduys et al. 2016), the results agreed that land clearing is the leading driver in the decline of the BTFS, and investing in preventive actions to halt habitat destruction is likely to outweigh the benefits of alternative management options. Sparing land from clearing where BTFS occur, and dedicating these areas to conservation, was considered the most effective action to avoid further declines. This is unsurprising given the nature of sparing, as it acts both as a preventive measure against clearing, while also minimising the impacts derived from pastoral land uses, which are still poorly understood. Thus, land sparing is particularly efficient, as it eliminates the need to investigate how to manage threats, by preventing them.

Despite the benefits of sparing, it is unlikely that this action can be implemented as a general solution everywhere where BTFS occur. Remaining BTFS populations are predominantly restricted to privately managed properties dedicated to cattle grazing (Reside et al. 2019). The costs of purchasing land are high, and competing socioeconomic interests over the land and its resources can be an obstacle to securing important areas. A more realistic situation is likely to combine the protection of priority areas with additional management to maintain BTFS populations in pastoral land. In a scenario where sparing is not an option, I found that further ecological research could substantially increase the effectiveness of conservation decisions, as there still is significant uncertainty on the impacts of threats other than clearing. Most of this uncertainty concentrated on the effects of a potential decline in the abundance of suitable seeds for foraging, their availability through the year, as well as changes in the configuration of habitat that affect the spatial distribution of resources in the landscape. Understanding the interactions between these threats and BTFS ecological requirements, as well as

their causes, can help to determine which actions need to be implemented first, resulting in a more efficient use of resources and greater benefits for BTFS conservation.

It is worth emphasising that although the proposed research actions could improve the effectiveness of management decisions in the absence of sparing, the expected outcomes were lower than sparing without collecting further information. This result exemplifies the compromises made between optimal, yet hard-to-implement solutions, and suboptimal alternatives chosen due to factors beyond their conservation goals. Considering the feasibility of management actions is fundamental to find practical solutions to real problems (Knight et al. 2008; Mills et al. 2013). Yet, the systematic prioritisation of actions based on their lower cost, or a lack of conflicting interests, can lead to an inefficient investment of resources and residual benefits for conservation (McCreless et al. 2013). This problem has been widely discussed in the context of the selection of areas for protection, as many of these areas tend to be established in sites with a marginal interest for conservation (Devillers et al. 2015; Vieira, Pressey, and Loyola 2019). My work offers a first insight into the risks of excluding effective, yet seemingly unfeasible actions from Vol and the recovery planning process, which could ultimately lead to suboptimal recommendations.

The example of the BTFS is a perfect illustration of how Vol can help inform the recovery planning process. Vol analysis is still limited by biases inherent to the decision-making process, and ultimately is an oversimplification of the case study that requires careful interpretation. Nevertheless, Recovery Plans or similar key conservation-planning documents can benefit from the structured framework of these tools, which provide a quantitative basis on which to make critical recommendations.

### **Protecting habitat in a variable environment**

Sparing BTFS habitat for conservation is the most effective and efficient action to stop further declines. Yet, the opportunities to implement this action are limited, demanding a critical evaluation of areas that offer a better value for conservation. When making these decisions, BTFS habitats can pose particular challenges, as Australian savannas are characterised by irregular weather patterns that influence the condition of habitat (Garnett and Williamson 2010). Due to this variability, savanna species are often exposed to unpredictable periods of resource shortages, to which many of them have adapted by moving and tracking resources in the landscape.

BTFS are predominantly sedentary. The limited data available suggest that they prefer to keep small home ranges, shifting their diet according to changes in the availability of seed (Mitchell 1996).

However, extreme weather events can trigger resource-tracking responses, forcing BTFS to move several kilometres on the look for suitable habitat patches (Laguna et al. 2019; Mitchell 1996; Rechetelo 2015). Habitat loss and fragmentation limit the access to and availability of patches that can act as a safeguard during shortage periods, increasing the likelihood of local extinctions. Furthermore, the sedentary predisposition of BTFS may make them particularly vulnerable to these changes, since their ability to disperse in a fragmented landscape is likely to be more limited by physiological adaptations, when compared to nomads (Franklin et al. 2017).

Areas that are less exposed to extreme suitability shifts, while maintaining connectivity between stable habitat patches, offer a higher resilience against stochastic environmental factors, and should be prioritised for their protection. Long-term assessments that can incorporate a dynamic perspective on habitat suitability can help in the recognition of spatiotemporal patterns and the identification of stable, high value areas for conservation. Dynamic Species Distribution Models (DSDM) have proven particularly effective at predicting the distribution of highly mobile species (Mordecai et al. 2011; Reside et al. 2010; Runge et al. 2015), but their conservation applications are still novel (Webb et al. 2017). These methods are an extension of species distribution models that replace static climate variables based on long-term data, with short-term conditions in the month of an observation. I used a DSDM to create BTFS habitat suitability maps for every month in the 20-year period between 1998 and 2017 and examine spatiotemporal patterns in the availability of suitable BTFS habitat (chapter 4).

As hypothesized, I found that BTFS are exposed to extreme fluctuations in the extent of suitable habitat. While I was able to identify a consistent seasonal pattern, the interannual variability created significant differences in the condition of habitat even among consecutive years. These results confirmed my initial expectations around the unpredictability of shortage events, supporting the need to identify low risk areas for conservation. Based on my projections, I proposed a classification of habitat according to its stability and distance to alternative, stable areas. Unsurprisingly, the areas with the highest value, which I named 'core', predominantly overlapped the two main strongholds where remaining BTFS occur, representing 30% of the total extent of habitat projected as suitable at some point in the time series. Nevertheless, I was also able to identify extensive areas of 'core habitat' in remote and poorly surveyed locations, which warrants further investigation to confirm the presence of populations that may be currently unknown.

Core areas can serve as a rough guide in the design of a coordinated plan for the protection of BTFS habitat. However, due to the resolution of the data available, my models do not take incorporate

small-scale variables with a strong influence on the local habitat condition, such as land use, or topography. Thus, the identification of specific sites for conservation should be complemented with additional on-site assessments. Further analyses incorporating socioeconomic factors are also a key addition to spatial planning and prioritisation, as there are external conditionals that can be important for the long-term success of these plans.

### **The role of dietary plasticity**

One of the research priorities to improve BTFS conservation management decisions is to resolve the current uncertainty around diet-related threats. There is a general assumption that widespread modification of BTFS habitat derived from changes in grazing and fire regimes, as well as the introduction of invasive grasses, might have affected the abundance and steady access to suitable seeds throughout the year. However, the real impact of these threats on the decline of the BTFS and how to best manage them, remains unsure.

As previously discussed, BTFS can shift their diet and foraging habits according to unpredictable changes in the availability of seed (Mitchell 1996). Yet, much of this information is based on a small number of observations within specific populations, and not much is known about their behavioural responses to the seeds of exotic plants. A lesser degree of dietary plasticity, such as the display of strong preferences, or an unwillingness to explore and make use of novel food types can result in poorer adaptations to these changes (Renton et al. 2015; Varner and Dearing 2014), which could have accelerated the decline of BTFS when compared to other granivorous finches.

As the final chapter to my thesis (chapter 5) I observed dietary selectivity and exploratory behaviour in BTFS, and three other non-endangered Estrildid finches with different degrees of taxonomic relatedness. My objective was to identify dietary traits in BTFS that could indicate a particularly high susceptibility to changes in the type of dietary resources available. The results showed no evidence linking the decline of the BTFS with the studied behaviours. In fact, zebra finches (*Taeniopygia guttata*), another species used in the experiment, and the most common and widespread finch in Australia, proved to be substantially more selective and reluctant to try new seeds. This behaviour could be explained by differences in mobility between the two taxa, as previously highlighted for other species (Clutton-Brock 1975; Terraube et al. 2011). Due to their predominantly sedentary strategy, BTFS might rely on a higher dietary plasticity to adapt to local changes in their habitat. Zebra finches on the other hand, could maintain a more specialised diet as a result of their fully nomadic adaptations, which enable them to successfully track their favoured seeds in the landscape.



The only trait that distinguished BTFS from the other three taxa in the study, was a substantial shift in foraging behaviour depending on the way the seeds were presented. While the other finches kept consistent behaviours regardless of presentation, BTFS changed their preference for one of the seed types and became significantly more selective when seeds were separated into different dishes by type, rather than mixed. This behaviour suggests that BTFS diet might be strongly affected by factors influencing the foraging energy budget, such as seed availability, handling time or caloric content.

Experiments with captive animals suffer from multiple limitations for the study of complex behavioural traits. However, based in the comparison with other taxa under the same experimental conditions, I am confident that lack of dietary plasticity is unlikely to have played a significant role in the decline of the BTFS. Although this conclusion contradicted the initial hypothesis, there are still certain considerations for conservation that should be taken into account. BTFS adaptability might be an effective strategy allowing them to cope with temporary changes in the availability and abundance of seed (Drummond 2005; Kennish 1996). However, low selectivity could also lead to a reduction in fitness if grasses with low quality seeds dominate the community. Furthermore, a relatively generalist diet, particularly when still associated with a specific resource type such as seed, can result in lower foraging success and increased competition when resources become scarce (Petrov et al. 2020).

### **Conclusions, recommendations and future research**

The search for solutions to reconcile anthropogenic uses of the land and biodiversity conservation is a key aspect in the future persistence of species worldwide. However, a failure to recognise and address the original causes for species' declines in expectation of a convenient answer can only lead to further losses and the eventual extinction of threatened species. Despite the efforts made in this thesis to identify efficient and feasible ways to protect the BTFS, I came to the conclusion that the simplest, yet most effective action that need to be taken to stop further declines is to halt clearing of habitat where BTFS occur.

Through this thesis I have put a strong emphasis on the notion that effective conservation action requires a judicious allocation of resources. Investing in targeted research and management can help to mitigate the impacts resulting from pastoralism and other extractive uses of the land. Yet, removing any extent of habitat from a taxon that has lost 88% of its former range will inevitably result in a net loss for conservation, outweighing the benefits that can be obtained from conservation investment.

Stopping habitat clearing is the first step in the right direction, but additional threats that are less well understood still need to be addressed. As discussed in chapters 4 and 5, BTFS rely on multiple adaptations to cope with extreme changes in their habitats. Dietary plasticity allows BTFS to adapt to seasonal shifts in the type and overall availability of resources, while resource-tracking movements might only be triggered as a response to extreme shortages caused by drought periods or tropical cyclones. Given the magnitude and unpredictability of such events, the best way to ensure the persistence of BTFS is to enable their natural adaptations by minimising threats that limit access to alternative resources and habitat patches.

Securing land for protection through the enactment of policies or private purchase is the best option to achieve all BTFS conservation objectives at once. Based on their conservation value, I encourage using the core areas identified in chapter 4 as a foundation for the design of a coordinated spatial management plan with the objective of protecting a network of secure, high-quality sites. To ensure their effectiveness, modelling results should be complemented by on-site population and habitat surveys, as well as additional planning to account for strategic and socioeconomic factors.

Additional population monitoring, especially within the two stronghold regions harbouring substantial BTFS populations, is essential to make sure that impacts derived from threats or management choices do not go unnoticed. The long-standing monitoring effort in the Townsville region (Laguna et al. 2019) should be continued, improved, and extended to the Desert Uplands population. The proposed core areas also offer a prime guide for surveying in the search of unknown populations in poorly-studied locations. The remoteness of these areas presents a limitation for surveying in itself, but novel methods developed for the identification of cryptic species, such as the night parrot (*Pezoporus occidentalis*), can be adapted to serve as a cheap and effective alternative to detect the presence of BTFS and follow up with more exhaustive surveys (Menkhorst et al. 2020).

Future research should prioritise obtaining a more detailed understanding of the relation between BTFS and their access to resources in the landscape. I suspect that any potential diet-related threats to BTFS are most likely associated with structural habitat factors. Invasive grasses can often dominate the community where they are introduced, changing the vegetation structure from hummocking to sward-forming grasses, and reducing the extent of patches of bare ground on which to forage. Further experimental trials to study foraging success based on structural factors such as physical obstruction or visibility might prove useful to understand the magnitude of this phenomenon, while research on the ecological processes leading to changes in vegetation structure may help managing it.

Studies on BTFS movement ecology are also likely to be a valuable source of information to address current conservation concerns. Understanding the effects of a potential change in the distribution of resources in the landscape demands a better grasp on BTFS habitat and resource use. Moreover, long-term tracking data may help to clarify some uncertainty around the triggers and extent of resource-tracking movements. So far, this type of research has been hampered by BTFS' small size, rarity, and technological constraints (Rechetelo et al. 2016). However, novel techniques currently being developed and applied to the Gouldian finch, a closely-related species, could be used in the future to bypass some of these issues (Griffin et al. 2020).

I recommend taking a continued critical stance on the need for further information. The results of my work provide evidence to support that the collection of data is not always the best choice for conservation, and the research proposed here should only occur while the known threats are being addressed. I hope that the example portrayed here can help conservationists and decision-makers to acknowledge and resolve common shortfalls in the protection of rare and hard-to-study species. The outcomes of this thesis can be directly incorporated in the update of the Black-throated Finch Recovery Plan due in the upcoming months, contributing to the persistence of this iconic Australian finch.

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# Appendices

## Appendix S2. Tables listing the main sources of information for each of the four main aspects of the BTF's biology and ecology.

**Table S2.1.** Major original sources and key findings describing BTF habitat.

Source	Area	Methods	Key findings
Morris <i>et al.</i> , 1981	New South Wales	Compilation of records.	<ul style="list-style-type: none"> <li>Recorded in dense shrubbery bordering watercourses in savanna woodlands.</li> </ul>
Immelman, 1982	Distribution-wide	Personal observations and literature review.	<ul style="list-style-type: none"> <li>Habitat described as woodland with a dense understory of grass and scrub.</li> </ul>
Baldwin, 1976	New South Wales	Compilation of records.	<ul style="list-style-type: none"> <li>Recorded in dense riparian vegetation.</li> </ul>
NRA, 2005	TCP	2 observational studies at nesting sites: First study: Site 1 visited on 32 occasions March 2004 to May 2005. Site 2 visited on 10 occasions April 2003 to May 2005. Second study: Both sites visited monthly October 2004 to May 2005.	<ul style="list-style-type: none"> <li>Observed foraging in Eucalypt woodlands, exotic and native grasslands and exotic shrublands. Apparent preference for foraging in disturbed areas next to areas of intact habitat.</li> <li>Nests primarily found in areas of <i>Eucalyptus platyphylla</i> and <i>Corymbia clarksoniana</i> woodland on alluvial plains. Also recorded in non-remnant vegetation.</li> </ul>

Isles, 2007	TCP	Habitat surveys and systematic observations conducted at 2 sites. Sites visited every second week March to August 2006.	<ul style="list-style-type: none"> <li>Recorded breeding in areas of <i>Eucalyptus platyphylla</i> and <i>Corymbia clarksoniana</i> woodland on alluvial plains.</li> </ul>
Maute, 2011	TCP and Cape York	Blood sampling at 2 sites visited November and December of 2007 and 2008 as well as June of 2008 and 2009. 228 BTFs sampled.	<ul style="list-style-type: none"> <li>BTFs in grazed areas showed higher variation in health indices than <i>P. cincta atropygialis</i> in protected areas.</li> </ul>
NRA, 2009	TCP	Desk based analysis using nest locations and environmental layers. Nest data obtained from previous surveys 2003-2009.	<ul style="list-style-type: none"> <li>Nests predominantly found in woodlands and open woodlands in alluvial plains, pediplains or rises dominated by <i>Eucalyptus platyphylla</i>, <i>Eucalyptus drepanophylla</i>, <i>Corymbia clarksoniana</i>, <i>Corymbia dallachiana</i>, <i>Corymbia erythrophloia</i>, and <i>Casuarina cunninghamiana</i>.</li> <li>During the dry season, predicted nesting habitat contracts by 44% in the Brigalow Belt North bioregion and 17% in the Wet Tropics bioregion.</li> <li>Average distance of nests to water was 167m.</li> </ul>
GHD, 2012	DEU	Study comprising 4 survey methods (water source watches, 2 ha bird searches, remote fauna cameras and habitat assessment) conducted 21-26 May 2012.	<ul style="list-style-type: none"> <li>Mostly recorded in <i>Eucalyptus melanophloia</i> open-woodland, with a mosaic of <i>Eucalyptus brownii</i> open woodland to woodland and <i>Eucalyptus melanophloia</i> woodland, with occasional <i>Corymbia dallachiana</i>, on sandy alluvial plains. Also recorded in non-remnant vegetation.</li> </ul>



			<ul style="list-style-type: none"> <li>Grass species <i>Digitaria divaricatissima</i>, <i>Paspalidium rarum</i>, <i>Schizachyrium fragile</i> and <i>Themeda triandra</i> significantly more abundant at sites where BTFs were present.</li> </ul>
GHD, 2013	DEU	Study comprising 4 survey methods (water source watches, 2 ha bird searches, remote fauna cameras and habitat assessment) conducted 23-31 May 2013.	<ul style="list-style-type: none"> <li>Most abundant in areas dominated by <i>Eucalyptus melanophloia</i> woodlands and the associated <i>Eucalyptus similis</i> and <i>Eucalyptus populnea/brownii</i> woodlands.</li> <li>Presence associated with higher percentages of hummock grass cover and particular species such as <i>Triodia pungens</i>, <i>Cymbopogon obtectus</i>, <i>Panicum effusum</i>, and <i>Tripogon loliformis</i>.</li> <li>Recorded using smaller and ephemeral water sources (troughs, scrapes, puddles in drainage lines).</li> </ul>
Rechetelo, 2016	TCP	<p>Multiple studies:</p> <p>Bird surveys conducted weekly or monthly November 2011 to January 2014 at 10 sites.</p> <p>Habitat surveys conducted July to December 2013 at the same sites.</p> <p>Vegetation and ground cover surveys conducted June 2013 to January 2014 at 33 foraging patches.</p>	<ul style="list-style-type: none"> <li>General BTF habitat characterized by a prevalence of native grass species, low shrub cover and abundance, high density of dead standing trees and presence of grasses <i>Eragrostis spp.</i> and <i>Setaria surgens</i>.</li> <li>Foraging habitat characterized by medium cover of woody vegetation, maintaining a low abundance of shrubs and dead standing trees used as a medium strata.</li> </ul>

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Tree characteristics measured for 50 nesting trees. Habitat surveys carried out around a subset of 20 nests.

- Foraging patches (as small as 2 m<sup>2</sup>) characterized by lower habitat complexity, ground cover and diversity than adjoining areas. Most of them <400m away from water.
  - Nesting habitat characterized by lower tree density and shrub density than surrounding areas, ground cover parameters did not play an important role in nesting site selection.
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**Table S2.2.** Major original sources and key findings describing the movement ecology of the BTF.

Source	Area	Methods	Key findings
Baldwin, 1976	New South Wales	Compilation of records.	<ul style="list-style-type: none"> <li>• BTFs not found in their regular areas of occurrence after a drought period in 1976.</li> </ul>
McCutcheon, 1976	New South Wales	Compilation of records.	<ul style="list-style-type: none"> <li>• BTFs recorded in 1968 in an area where they were not observed before, as a severe drought took place in surrounding areas.</li> </ul>
Longmore, 1978	Rockhampton area (Queensland)	Field observations from February 1973 to October 1974.	<ul style="list-style-type: none"> <li>• BTFs reported to move locally.</li> <li>• Mostly recorded in pairs and flocks of up to 20 individuals.</li> </ul>
Passmore, 1982	South Queensland	Compilation of records.	<ul style="list-style-type: none"> <li>• Recorded in 1979 but reported to leave after a drought in 1980. Later recorded in close areas but not same site as it was mined.</li> <li>• Dispersion to breeding sites occurred early in the year.</li> </ul>
Mitchell, 1996	TCP	Observational study around 5 general areas visited monthly January to December 1995.	<ul style="list-style-type: none"> <li>• Pairs returned to non-breeding sites late in the year, after the onset of the wet season.</li> <li>• Daily foraging movements of up to 1.5km, depending on foraging habitat availability.</li> </ul>
NRA, 2005	TCP	2 observational studies at nesting sites:	<ul style="list-style-type: none"> <li>• Predominantly seen in pairs, foraging in small groups (2 to 8 individuals) although less often in larger groups of &gt;20.</li> </ul>

		<p>First study: Site 1 visited on 32 occasions March 2004 to May 2005. Site 2 visited on 10 occasions April 2003 to May 2005.</p> <p>Second study: Both sites visited monthly October 2004 to May 2005.</p>	<ul style="list-style-type: none"> <li>• Early in the breeding season, pairs intensively used the same small area (12ha) to forage, breed and roost.</li> <li>• Distance from nest sites to foraging sites increased as conditions became drier.</li> <li>• In the dry season, BTFs infrequently found during the day around nests, although they would return to roost overnight.</li> </ul>
Isles, 2007	TCP	Habitat surveys and systematic observations conducted at 2 sites. Sites visited every second week March to August 2006.	<ul style="list-style-type: none"> <li>• Main portion of the day spent foraging close to the nest in short bouts, rarely traveling more than 350m.</li> <li>• Foraging occurred more often at particular locations that were visited repeatedly.</li> </ul>
GHD, 2012	DEU	Study comprising 4 survey methods (water source watches, 2 ha bird searches, remote fauna cameras and habitat assessment) conducted 21-26 May 2012.	<ul style="list-style-type: none"> <li>• BTFs moving or foraging in mixed flocks on 33% of occasions they were recorded. Most predominantly with <i>Artamus cinereus</i>, <i>Tanaetopygia bichenovii</i>, <i>Oreoica gutturalis</i>, <i>Myiagra inquieta</i>, and <i>Microeca fascinans</i>.</li> </ul>
Vanderduys <i>et al.</i> , 2012	Northern Queensland	Multiple bird surveys between 2004-2010.	<ul style="list-style-type: none"> <li>• BTFs commonly found in mixed flocks with other species such as <i>Artamus cinereus</i>.</li> </ul>
GHD, 2013	DEU	Study comprising 4 survey methods (water source watches, 2 ha bird searches,	<ul style="list-style-type: none"> <li>• Found foraging in mixed flocks, especially with <i>Artamus cinereus</i> and <i>Rhipidura leucophrys</i>.</li> </ul>

		remote fauna cameras and habitat assessment) conducted 23-31 May 2013.	
Rechetelo, 2016	TCP	<p>Studies conducted in 8 sites 2012 to 2014.</p> <p>Banding study: 102 BTFs banded in a total of 1088.5 mist-netting hours.</p> <p>Radio-tracking study: 15 BTFs radio-tracked individually at different times in the dry season. Average tracking time for each individual was 11.6 days, with active tracking 5-12 hours a day. Number of fixes varied from 1-11 per day and a total of 2-111 per individual.</p>	<ul style="list-style-type: none"> <li>• &gt;50% of resightings within first 100 days and 200 m of banding site.</li> <li>• 5 resightings in the same site 400 days after banding, and 1 &gt;600 days.</li> <li>• 3 resightings &gt;15 km from banding site (49 and 132 days after last sighting).</li> <li>• Home ranges from 25.15 to 120.88 ha (95% KDE) and increased later in the dry season.</li> <li>• Seen in small flocks (2-3 individuals) early in the morning and aggregating at foraging areas into bigger flocks (20-40 individuals) by mid-morning.</li> </ul>
Tang, 2017	TCP	<p>Sampled blood from 86 BTFs at 7 sites between 2011 and 2013. 48 samples additional samples obtained in 2009 from a previous study (Maute, 2011).</p>	<ul style="list-style-type: none"> <li>• Distinct spatial population structuring occurs at a scale of 10-20km.</li> <li>• Large bodies of water are a barrier reducing gene flow, while other landscape structural variables are potential drivers limiting dispersal.</li> </ul>

**Table S2.3.** Major original sources and key findings describing the diet and foraging ecology of the BTF.

Source	Area	Methods	Key findings
Mitchell, 1996	TCP	Systematic observations around 5 general areas visited monthly January to December 1995.	<ul style="list-style-type: none"> <li>• 13 seed types explicitly recorded as consumed out of 21 seed types potentially used, 6 from non-native grasses and most of them perennial.</li> <li>• Introduced grass <i>Urochloa mosambicensis</i> dominated diet in January and early February. After that, birds moved to breeding areas and actively selected for patches of native <i>Digitaria ciliaris</i>.</li> <li>• Diet breadth largely increased after September until the end of the year.</li> <li>• Predominantly foraged from the ground, although diversity of foraging techniques increased in September and remained high until November.</li> </ul>
NRA, 2005	TCP	Opportunistic observations between 2003 and 2005.	<ul style="list-style-type: none"> <li>• 12 seed types recorded as consumed, 3 from non-native grasses.</li> </ul>
Isles, 2007	TCP	Habitat surveys and systematic observations conducted at 2 sites. Sites visited every second week March to August 2006.	<ul style="list-style-type: none"> <li>• 9 grass species identified as significantly more abundant within foraging areas compared to habitat matrix, predominantly natives.</li> <li>• 5 other grass species were found to be significantly less abundant.</li> </ul>
GHD, 2012	DEU	Opportunistic observations in May 2012.	<ul style="list-style-type: none"> <li>• Recorded foraging on 5 seed types, all native.</li> </ul>

Meyer & Agnew, 2012	DEU	Opportunistic observation.	<ul style="list-style-type: none"> <li>Recorded likely foraging on eucalypt seeds.</li> </ul>
Rechetelo, 2016	TCP	Opportunistic observations between 2011 and 2014.	<ul style="list-style-type: none"> <li>Foraging on seeds of <i>Melinis repens</i>, <i>Gomphrena celosioides</i> and flying termites.</li> </ul>

**Table S2.4.** Major original sources and key findings describing the nesting and breeding ecology of the BTF.

Source	Area	Methods	Key findings
North, 1901-14	Queensland and New South Wales	Compilation of records.	<ul style="list-style-type: none"> <li>• Multiple records of breeding behaviour as early as March and as late as December.</li> <li>• Nests recorded in tree branches, hollows, under raptor nests or sugar-cane leaves.</li> <li>• Number of eggs recorded ranged from 1 to 7, 5 or 6 being the most common clutch size recorded.</li> </ul>
Roberts, 1955	Queensland	Compilation of records since 1954.	<ul style="list-style-type: none"> <li>• BTFs recorded using old nests of babblers.</li> </ul>
Campbell, 1974	Australia	Compilation of records.	<ul style="list-style-type: none"> <li>• Bottle-shaped nests constructed out of grass in hollows or the foliage of tree branches.</li> <li>• Clutch size average is 5-6 eggs.</li> </ul>
Morris <i>et al.</i> , 1981	New South Wales	Compilation of records.	<ul style="list-style-type: none"> <li>• Eggs mainly found August-December.</li> </ul>
Shephard, 1989	Captivity	Compilation of records.	<ul style="list-style-type: none"> <li>• Captive BTFs reach sexual maturity is reached after 6 months</li> <li>• Life expectancy is 4-6 years</li> </ul>



Mitchell, 1996	TCP	Observational study around 5 general areas visited monthly January to December 1995.	<ul style="list-style-type: none"> <li>• Breeding activity began in March, 2 months after substantial rain, when seed was most abundant.</li> </ul>
			<ul style="list-style-type: none"> <li>• BTFs form communal nesting sites, including both breeding and non-breeding dormitory nests.</li> <li>• Most nests recorded in <i>Eucalyptus platyphylla</i> and <i>Melaleuca viridiflora</i>. Other hosts included <i>Corymbia tessellaris</i>, <i>Corymbia dallachiana</i> and <i>Ziziphus mauritiana</i>.</li> </ul>
NRA, 2005	TCP	<p>2 observational studies at nesting sites:</p> <p>First study: Site 1 visited on 32 occasions March 2004 to May 2005. Site 2 visited on 10 occasions April 2003 to May 2005.</p> <p>Second study: Both sites visited monthly October 2004 to May 2005.</p>	<ul style="list-style-type: none"> <li>• Most nests constructed &gt;4 m above the ground in branches and less often tree hollows, mistletoes or the base of raptor nests.</li> <li>• Average distance of nests to water was 280 m. Up to 400 m for permanent water.</li> <li>• Nests often used &gt;200 days.</li> <li>• First breeding evidence recorded late January and last in mid July.</li> <li>• Apparent return to same breeding area in consecutive years.</li> </ul>

NRA, 2009	TCP	Desk based analysis using nest locations and environmental layers. Nest data obtained from previous surveys 2003-2009.	<ul style="list-style-type: none"> <li>• Average distance of nests to water was 167m.</li> </ul>
GHD, 2013	DEU	Study comprising 4 survey methods (water source watches, 2 ha bird searches, remote fauna cameras and habitat assessment) conducted 23-31 May 2013.	<ul style="list-style-type: none"> <li>• Nests found in <i>Eucalyptus melanophloia</i> and <i>Acacia coriacea</i>.</li> </ul>
Rechetelo, 2016	TCP	Surveys conducted during 2011-2014. Tree characteristics were measured for 50 nesting trees. Habitat surveys carried out around a subset of 20 nests.	<ul style="list-style-type: none"> <li>• Preferred nesting tree species were <i>Eucalyptus platyphylla</i> and <i>Melaleuca viridiflora</i>.</li> <li>• Nests most often built within foliage in the top quarter of trees.</li> <li>• Nests predominantly located within 400 m of a water source.</li> </ul>

**Table S2.5.** List of identified species used as seed sources by the BTF. ‘Record’ column categories include: O = Observed. BTFs directly observed consuming the seed of the species; P = Potential. Species found to be significantly more present in foraging patches used by BTF (results only based on quantitative studies).

Species	Phenology	Origin	Region	Record	Reference
<i>Alloteropsis cimicina</i>	Annual	Native	TCP	P	Isles, 2007
<i>Alloteropsis semialata</i>	Perennial	Native	TCP	O, P	Mitchell, 1996 NRA, 2005
<i>Bothriochloa decipiens</i>	Perennial	Native	TCP	O, P	Isles, 2007 Mitchell, 1996
<i>Chloris inflata</i>	Annual/Perennial	Introduced	TCP	O, P	Mitchell, 1996 NRA, 2005
<i>Chloris spp.</i>	-	-	TCP	P	Isles, 2007
<i>Dactyloctenium spp.</i>	-	-	TCP	O, P	Mitchell, 1996
<i>Dicanthium sericeum</i>	Annual/Perennial	Native	TCP	O	NRA, 2005
<i>Digitaria brownii</i>	Perennial	Native	DEU	O	GHD, 2012
<i>Digitaria ciliaris</i>	Annual	Introduced	TCP	O, P	Mitchell, 1996
<i>Digitaria divaricatissima</i>	Perennial	Native	TCP	P	Mitchell, 1996
<i>Echinochloa colona</i>	Annual	Introduced	TCP	O, P	Mitchell, 1996
<i>Echinopogon spp.</i>	-	-	TCP	O, P	Mitchell, 1996
<i>Eleusine indica</i>	Annual/Perennial	Introduced	TCP	O, P	Mitchell, 1996
<i>Enteropogon acicularis</i>	Perennial	Native	TCP	O, P	Mitchell, 1996

<i>Enteropogon ramosus</i>	Perennial	Native	DEU	O	GHD, 2012
<i>Eragrostis basedowii</i>	Annual	Native	TCP	O	NRA, 2005
<i>Eragrostis sororia</i>	Perennial	Native	TCP	O	NRA, 2005
<i>Eragrostis spp.</i>	-	-	TCP	O, P	Isles, 2007 Mitchell, 1996
<i>Eriachne mucronata</i>	Perennial	Native	TCP	O	NRA, 2005
<i>Eulalia aurea</i>	Perennial	Native	TCP	P	Mitchell, 1996
<i>Gomphrena celosioides</i>	Other	Introduced	TCP	O	Rechetelo, 2016
<i>Heteropogon contortus</i>	Perennial	Native	TCP	P	Mitchell, 1996
<i>Melinis repens</i>	Annual/Perennial	Introduced	TCP	O, P	Mitchell, 1996 NRA, 2005 Rechetelo, 2016
<i>Oxychloris scariosa</i>	Annual/Perennial	Native	TCP	P	Mitchell, 1996
<i>Panicum decompositum</i>	Perennial	Native	TCP	O	NRA, 2005
<i>Panicum effusum</i>	Perennial	Native	TCP	O	NRA, 2005
<i>Panicum spp.</i>	-	-	TCP	P	Isles, 2007 Mitchell, 1996
<i>Paspalidium rarum</i>	Annual	Native	DEU	O	GHD, 2012
<i>Paspalum spp.</i>	-	-	TCP	O, P	Mitchell, 1996
<i>Schizachyrium fragile</i>	Annual	Native	DEU	O	GHD, 2012
<i>Setaria apiculata</i>	Annual	Native	TCP	P	Isles, 2007

<i>Setaria surgens</i>	Annual	Native	TCP	O	NRA, 2005
<i>Sorghum spp.</i>	-	-	TCP	O	Mitchell, 1996
<i>Sporobolus caroli</i>	Annual/Perennial/Ephemeral		TCP	P	Isles, 2007
<i>Sporobolus diander (type)</i>	-	-	TCP	P	Mitchell, 1996
<i>Sporobolus indicus (type)</i>	-	-	TCP	P	Mitchell, 1996
<i>Stylosanthes spp.</i>	-	-	TCP	P	Isles, 2007
<i>Themeda triandria</i>	Perennial	Native	TCP	O, P	Mitchell, 1996 NRA, 2005
					Isles, 2007
<i>Urochloa mosambicensis</i>	Perennial	Introduced	TCP	O, P	Mitchell, 1996 NRA, 2005

### Appendix S3. Expert estimates summaries by objective

**Table S3.1.** Expert estimates summary including average hypothesis weights and average outcome estimated as area of occupancy in 10 years for the top ten hypotheses and actions. The best action for each hypothesis is shown in bold with a grey background. Greyed out values not in bold correspond to the best action when land sparing (A1) is not considered. The last row shows the average of the action weighted by hypothesis.

O1	Area of occupancy	Weight (%)	A0 No action	A1 Land sparing	A2 Clearing restrictions	A3 Deter pastoralism	A4 Cattle removal	A5 Grazing management	A6 Fire management	A7 Structure management	A8 Exotic grass	A9 Exotic shrubs	A10 Native grass
H1	Urban encroachment	14.37	61.15	<b>74.92</b>	68.19	61.14	61.13	61.15	61.12	61.09	61.13	61.14	61.12
H2	Large-scale mining	16.21	55.90	<b>73.03</b>	65.74	55.91	55.92	55.89	55.92	55.93	55.92	55.89	55.89
H3	Small-scale clearing	14.94	66.29	<b>78.72</b>	75.91	66.28	66.28	66.28	66.28	66.28	66.27	66.30	66.27
H4	Connectivity loss	8.44	71.88	<b>81.55</b>	77.17	71.90	71.92	71.92	71.92	71.91	71.91	71.89	71.90
H5	Seed productivity	11.60	66.90	<b>79.34</b>	66.91	77.18	76.79	75.84	74.04	71.67	74.34	69.81	72.85
H6	Seed continuity	9.53	66.12	<b>77.69</b>	66.15	73.81	75.43	72.05	70.63	71.22	69.49	68.27	70.56
H7	Seed quality	3.38	72.79	<b>81.41</b>	72.79	80.22	81.41	80.23	80.87	77.07	75.79	74.66	75.82
H8	Vegetation structure	5.34	67.57	<b>81.63</b>	67.56	77.04	77.77	76.03	77.68	74.58	73.06	71.45	72.10
H9	Landscape configuration	12.91	66.54	<b>82.12</b>	66.52	76.73	79.08	76.15	74.85	74.27	74.62	70.69	72.47
H10	Nesting resources	3.27	78.00	<b>84.91</b>	78.04	78.90	80.92	81.06	84.02	81.19	78.03	76.98	78.03
	Weighted average		65.10	<b>78.35</b>	69.59	69.13	69.68	68.74	68.44	67.76	67.72	66.41	67.31

**Table S3.2.** Expert estimates summary including average hypothesis weights and average outcome estimated as extent of occurrence in 10 years for the top ten hypotheses and actions. The best action for each hypothesis is shown in bold with a grey background. Greyed out values not in bold correspond to the best action when land sparing (A1) is not considered. The last row shows the average of the action weighted by hypothesis.

O2	Extent of occurrence	Weight (%)	A0 No action	A1 Land sparing	A2 Clearing restrictions	A3 Deter pastoralism	A4 Cattle removal	A5 Grazing management	A6 Fire management	A7 Structure management	A8 Exotic grass	A9 Exotic shrubs	A10 Native grass
H1	Urban encroachment	14.37	61.81	<b>76.26</b>	70.23	61.82	61.83	61.80	61.83	61.83	61.82	61.83	61.83
H2	Large-scale mining	16.21	57.10	<b>73.89</b>	65.73	57.10	57.10	57.12	57.12	57.13	57.11	57.10	57.11
H3	Small-scale clearing	14.94	66.74	<b>80.00</b>	76.59	66.75	66.75	66.75	66.73	66.73	66.74	66.76	66.73
H4	Connectivity loss	8.44	72.86	<b>82.40</b>	78.14	72.88	72.89	72.89	72.87	72.88	72.89	72.90	72.87
H5	Seed productivity	11.60	67.32	<b>78.58</b>	67.33	75.70	<b>76.65</b>	75.54	75.02	72.76	73.77	70.29	73.75
H6	Seed continuity	9.53	66.61	<b>76.92</b>	66.57	73.48	<b>75.71</b>	72.93	71.23	71.63	70.36	68.73	70.89
H7	Seed quality	3.38	73.10	<b>81.88</b>	73.07	79.91	<b>81.41</b>	80.24	80.75	77.81	76.86	75.10	76.45
H8	Vegetation structure	5.34	70.89	<b>82.06</b>	70.92	77.47	<b>78.22</b>	76.47	<b>78.29</b>	75.48	75.18	72.52	73.54
H9	Landscape configuration	12.91	70.01	<b>82.12</b>	69.99	75.83	<b>79.15</b>	76.74	75.57	75.11	75.69	71.31	73.06
H10	Nesting spots	3.27	79.02	<b>85.30</b>	79.00	79.19	81.44	81.80	<b>84.21</b>	82.20	79.00	79.64	79.00
	Weighted average		66.30	<b>78.84</b>	70.82	69.27	70.19	69.36	69.18	68.58	68.50	67.20	68.11

**Table S3.3.** Expert estimates summary including average hypothesis weights and average outcome estimated as local population trend in 10 years for the top ten hypotheses and actions. Original values have been normalized to percentages. The best action for each hypothesis is shown in bold with a grey background. Greyed out values not in bold correspond to the best action when land sparing (A1) is not considered. The last row shows the average of the action weighted by hypothesis.

O3	Local population	Weight (%)	A0 No action	A1 Land sparing	A2 Clearing restrictions	A3 Deter pastoralism	A4 Cattle removal	A5 Grazing management	A6 Fire management	A7 Structure management	A8 Exotic grass	A9 Exotic shrubs	A10 Native grass
H1	Urban encroachment	14.37	47.61	61.72	<b>63.66</b>	47.62	47.66	47.62	47.64	47.59	47.60	47.62	47.64
H2	Large-scale mining	16.21	49.14	62.64	<b>63.40</b>	49.11	49.11	49.09	49.09	49.11	49.11	49.12	49.12
H3	Small-scale clearing	14.94	51.14	<b>65.20</b>	63.32	51.18	51.17	51.16	51.15	51.17	51.13	51.14	51.15
H4	Connectivity loss	8.44	60.82	<b>67.21</b>	65.32	60.81	60.83	60.82	60.82	60.84	60.83	60.84	60.81
H5	Seed productivity	11.60	54.75	<b>65.54</b>	54.75	62.04	<b>62.53</b>	62.22	61.21	61.67	62.00	59.46	60.81
H6	Seed continuity	9.53	56.09	<b>65.48</b>	56.09	62.95	62.93	62.78	62.15	62.46	<b>62.97</b>	60.16	61.67
H7	Seed quality	3.38	61.28	66.23	61.27	66.98	<b>67.22</b>	66.88	65.72	66.56	66.94	64.07	65.44
H8	Vegetation structure	5.34	59.62	66.25	59.62	65.84	65.75	65.85	66.58	<b>66.69</b>	66.67	63.75	65.12
H9	Landscape configuration	12.91	59.33	<b>66.59</b>	59.36	65.39	65.77	65.21	65.65	66.09	65.77	63.42	64.62
H10	Nesting spots	3.27	60.16	<b>69.66</b>	60.17	64.17	64.16	63.28	64.60	<b>65.02</b>	60.67	61.99	60.72
	Weighted average		54.16	<b>64.94</b>	60.98	57.10	57.22	57.05	56.97	57.16	57.07	56.00	56.54



**Table S3.4.** Expert estimates summary including average hypothesis weights and average outcome of all objectives for the top ten hypotheses and actions. The best action for each hypothesis is shown in bold with a grey background. Greyed out values not in bold correspond to the best action when land sparing (A1) is not considered. The last row shows the average of the action weighted by hypothesis.

AVERAGE		Weight (%)	A0 No action	A1 Land sparing	A2 Clearing restrictions	A3 Deter pastoralism	A4 Cattle removal	A5 Grazing management	A6 Fire management	A7 Structure management	A8 Exotic grass	A9 Exotic shrubs	A10 Native grass
H1	Urban encroachment	14.37	61.85	<b>74.04</b>	67.13	65.17	65.70	65.05	64.86	64.50	64.43	63.20	63.99
H2	Large-scale mining	16.21	54.05	<b>69.86</b>	64.96	54.04	54.04	54.03	54.04	54.06	54.05	54.04	54.04
H3	Small-scale clearing	14.94	61.39	<b>74.64</b>	71.94	61.40	61.40	61.40	61.39	61.39	61.38	61.40	61.38
H4	Connectivity loss	8.44	68.52	<b>77.05</b>	73.55	68.53	68.55	68.54	68.54	68.54	68.54	68.54	68.53
H5	Seed productivity	11.60	62.99	<b>74.49</b>	63.00	71.64	<b>71.99</b>	71.20	70.09	68.70	70.03	66.52	69.14
H6	Seed continuity	9.53	62.94	<b>73.36</b>	62.93	70.08	<b>71.36</b>	69.25	68.00	68.44	67.60	65.72	67.71
H7	Seed quality	3.38	69.06	76.51	69.04	75.70	<b>76.68</b>	75.79	75.78	73.81	73.19	71.28	72.57
H8	Vegetation structure	5.34	66.03	<b>76.65</b>	66.03	73.45	73.91	72.78	<b>74.18</b>	72.25	71.64	69.24	70.25
H9	Landscape configuration	12.91	65.29	<b>76.94</b>	65.29	72.65	<b>74.67</b>	72.70	72.02	71.83	72.03	68.47	70.05
H10	Nesting spots	3.27	72.39	<b>79.95</b>	72.41	74.09	75.50	75.38	<b>77.61</b>	76.13	72.57	72.87	72.58
Weighted average			62.57	<b>74.48</b>	67.10	66.36	66.96	66.23	66.01	65.60	65.52	64.11	65.01

## Appendix S4 – MAXENT variables

**Table S4.1.** List of all variables considered for our MAXENT model. The 12 variables included in the final model are marked in bold.

Variable name	Period
<b>Broad Vegetation Group</b>	-
<b>Lithology</b>	-
<b>NDVI</b>	-
<b>Rainfall, mean</b>	<b>present month</b>
Rainfall, mean	past month
<b>Rainfall, mean</b>	<b>past 3 months</b>
<b>Rainfall, mean</b>	<b>past 6 months</b>
Rainfall, mean	past 9 months
Rainfall, mean	past 12 months
Rainfall, seasonality	past 3 month
Rainfall, seasonality	past 6 month
Rainfall, seasonality	past 9 month
<b>Rainfall, seasonality</b>	<b>past 12 month</b>
<b>Temperature maxima, mean</b>	<b>present month</b>
Temperature maxima, mean	past month
Temperature maxima, mean	past 3 months
Temperature maxima, mean	past 6 months
Temperature maxima, mean	past 9 months
<b>Temperature maxima, mean</b>	<b>past 12 months</b>
Temperature maxima, seasonality	past 3 months
<b>Temperature maxima, seasonality</b>	<b>past 6 months</b>
Temperature maxima, seasonality	past 9 months
Temperature maxima, seasonality	past 12 months
Temperature minima, mean	present month
Temperature minima, mean	past month
Temperature minima, mean	past 3 months
Temperature minima, mean	past 6 months
Temperature minima, mean	past 9 months

<b>Temperature minima, mean</b>	<b>past 12 months</b>
Temperature minima, seasonality	past 3 months
Temperature minima, seasonality	past 6 months
Temperature minima, seasonality	past 9 months
Temperature minima, seasonality	past 12 months

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## Appendix S5 – Foraging boldness GLMM Item Response Tree coefficients

**Table S5.1.** Estimated regression parameters, standard errors, z values and p values for the binomial Item Response Tree model testing foraging boldness: response ~ node \* taxon + trial \* species + (1|birdID) + (1|observation). Estimates are given in the log-odds scale.

	Estimate	Std. Error	z value	Pr(> z )	
<b>Intercept</b>	4.13318	1.30914	3.157	0.00159	**
<b>node2</b>	-1.02931	1.09957	-0.936	0.34922	
<b>node3</b>	-2.81803	1.13083	-2.492	0.0127	*
<b>node4</b>	-5.26388	1.33331	-3.948	7.88E-05	***
<b>BTFS</b>	-1.94436	1.57572	-1.234	0.21722	
<b>LTF</b>	0.60181	1.65196	0.364	0.71564	
<b>ZBF</b>	-3.90426	1.59198	-2.452	0.01419	*
<b>trial</b>	0.28379	0.17068	1.663	0.09637	.
<b>node2:BTFS</b>	0.0708	1.32583	0.053	0.95741	
<b>node3:BTFS</b>	0.81083	1.28662	0.63	0.52856	
<b>node4:BTFS</b>	0.26156	1.39797	0.187	0.85158	
<b>node2:LTF</b>	-0.02922	1.33949	-0.022	0.98259	
<b>node3:LTF</b>	0.44213	1.29435	0.342	0.73267	
<b>node4:LTF</b>	1.22735	1.37849	0.89	0.37328	
<b>node2:ZBF</b>	-0.27977	1.27115	-0.22	0.8258	
<b>node3:ZBF</b>	0.5105	1.31426	0.388	0.6977	
<b>node4:ZBF</b>	1.78101	1.41265	1.261	0.2074	
<b>BTFS:trial</b>	0.15059	0.23489	0.641	0.52145	
<b>LTF:trial</b>	-0.54845	0.23892	-2.296	0.0217	*
<b>ZBF:trial</b>	-0.14936	0.22225	-0.672	0.50156	