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Population Assessment and Conservation Implications for the Mahogany Glider in the Fragmented Lowlands of Australian Wet Tropics

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Degree of Doctor of Philosophy
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Front cover: A Mahogany Glider (*Petaurus gracilis*) spotlighted and photographed at Jourama Fall, Paluma National Park, in 2020

Thesis Declaration

I, Yiyin Eryn Chang, hereby declare the following:

This thesis has been substantially completed during my enrolment in the degree.

No part of this thesis has been previously submitted for the award of any other degree or diploma in my name or in any other institution.

In the future, I will not use any portion of this thesis in a submission for any other degree or diploma in my name, at any university or tertiary institution, without prior approval from James Cook University and, where applicable, any partner institution responsible for the joint-award of this degree.

This thesis is devoid of any material that has been previously published or authored by any other individual, except where appropriate references have been meticulously incorporated into the text and, as relevant, in the Authorship Declaration that ensues.

This thesis is devoid of any violation or infringement of copyright, trademark, patent, or any other rights of any person or entity.

The research involving animal data reported in this thesis was evaluated and approved by the James Cook University Animal Ethics Committee (Approval number: A2699).

Prior to commencing the work described in this thesis, all necessary approvals were obtained, including the Protected Area Permit (PTUKI-100021853) and Non-Protected Area Permit (WA0025939) from the Queensland Government.

This thesis encompasses work that has been published or prepared for publication, some of which has been co-authored.

Abstract

Habitat loss and subsequent fragmentation are major threats for approximately 70% of species at risk of extinction. In addition to habitat loss and fragmentation, a multitude of other threats also contribute to the current extinction crisis. These threats include, but are not limited to, climate change, invasive species, overexploitation, pollution, and disease. Species conservation requires an understanding of their biological boundaries, including detailed distribution, population sizes and trends monitoring, and genetic structure and diversity investigation to estimate the long-term survival of the species. This comprehensive approach allows for the development of targeted conservation strategies, ensuring the preservation of biodiversity and the continued survival of threatened species. This project applied conservation science to assess the population status of the Endangered Mahogany Gliders (*Petaurus gracilis*). In collaboration with conservation practitioners and stakeholders, our objective was to optimize the practical application of science in the conservation efforts, therefore effectively addressing the needs of the species while aligning with real-world practices in conservation science.

The Mahogany Glider is a medium-sized gliding marsupial and is endemic to a specific range of lowland sclerophyll forests within the Wet Tropics Bioregion of Australia. The species survival is under threat due to extensive deforestation caused by cattle, pine, and sugar cane farming. Its naturally limited distribution coupled with ongoing habitat loss and fragmentation have led to concerns about its genetic health, such as the accumulation of deleterious genes, loss of genetic diversity and adaptivity, and inbreeding depression. These factors have contributed to the Mahogany Glider classification as an Endangered species. In response to this pressing conservation concern, a National Recovery Plan and the Mahogany Glider Recovery Team have been established to guide conservation efforts to protect the gliders, restore habitat connectivity using gliding poles, and revegetate their habitats.

Despite these measures, substantial knowledge gaps remain. These gaps include the lack of a comprehensive habitat suitability map, insufficient survey efforts, uncertainty about the current population size and status, limited understanding of population connectivity, and the potential for inbreeding in small, isolated populations. My thesis addresses these gaps by employing species distribution models, cage and camera trapping surveys, and occupancy models to estimate current densities and population sizes. Furthermore, I utilized genetic data (Single Nucleotide Polymorphism - SNPs) to examine population structures across the distribution and assess genetic diversity of the species and the sampled localities.

The ongoing clearing of habitat and subsequent fragmentation, particularly in areas with Mahogany Glider records, underscore the need for detailed identification of suitable habitats. In Chapter 2, I employed species distribution modelling to delineate suitable habitat for the species. By integrating spatial data with known occurrence records, species distribution models predicted suitable habitat at a fine scale, thereby guiding targeted survey efforts. The models also predicted unknown populations both within and beyond the established distributions, including on Hinchinbrook Island. Further, the findings highlighted that the current suitable habitat is extensively fragmented, thus underscoring the urgency of conservation initiatives to bolster habitat connectivity and limit further fragmentation.

The habitat suitability map also directed Chapter 3, in which I combined field surveys with a Bayesian integrated distribution model to estimate the abundance of Mahogany Gliders across the known range. The survey results indicated low glider densities at most sampling sites, although higher density patches were detected in the southern area of the range. Based on the integrated model, which combines presence-only and presence-absence data, we estimated median abundance at 6,030, 4,834, and 2,820 individuals for home ranges of 9, 16, and 25 ha, respectively. These estimates narrow the previously hypothesized range of 1,200 to 20,000 individuals and provide a critical baseline for future conservation planning. The research highlighted density variations across the range and the necessity for long-term monitoring to refine the model and tracking the population trends. Based on these findings, a

long-term monitoring plan was formulated for three populations in collaboration with conservation practitioners and stakeholders.

Chapter 4 involved the use of genome-wide Single Nucleotide Polymorphisms (SNPs) to assess population structure and genetic diversity across the known distribution of Mahogany Glider. Additionally, I conducted a comparative genetic analysis of the Mahogany Glider with its close relative, the Squirrel Glider (*Petaurus norfolcensis*). Pronounced genetic structures were observed between the northern and southern halves of the Mahogany Glider distribution, suggesting potentially limited connectivity between the two clusters. The genetic diversity of the surveyed populations was generally satisfactory, except for the northern-most site, which was deemed poor. Evidence of introgression (genetic admixture) was detected between Mahogany Gliders and Squirrel Gliders in both the north and south of the Mahogany Glider's range. It is difficult to ascertain whether this introgression is current or historic. Regardless, this introgression implies taxonomic uncertainty as to whether the Mahogany Glider should be considered a full species (as currently recognised) or a subspecies of the Squirrel Glider. To resolve this issue, comprehensive sampling is essential at locations where both species are in close proximity.

In summary, this thesis has filled knowledge gaps in the conservation of the Endangered Mahogany Glider. Current suitable habitats have been identified in detail, many of which have no glider records and therefore warrant surveys. Field surveys have estimated sampling densities and a total population size. Genetic analyses have revealed structures between the north and south populations and adequate genetic diversity within most populations at present. These findings will guide ongoing conservation efforts, including population monitoring and on-ground efforts to improve habitat protection and connectivity. This research also uncovered evidence of introgression between Mahogany and Squirrel Gliders and provided a clear path for addressing this taxonomic complexity. More broadly, the integration of various methodologies, as done here for Mahogany Gliders, can be applied to numerous other threatened species worldwide.

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I came here knowing nothing about gliders, but now seeing them gliding through the starry sky just before sunrise has become one of the most treasured experiences of my life.

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Statement of Contribution of Others

Supervision

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Publications and co-author contributions

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- Chapter 2

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  Details of the work

  The study was conceived by Chang and Hoskin. Chang collected data, conducted modelling, created figures, and wrote the initial draft. Hoskin and Bertola provided input and feedback to all aspects of the study, and revised drafts.

- Chapter 3

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  Details of the work

  The study was conceived and designed by Chang and Hoskin. Chang and Lin conducted surveys, collected data, and performed the analyses. Chang created figures and wrote the initial draft. Hoskin and Lin provided input and feedback to all aspects of the study, including revising drafts.

- Chapter 4

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Details of the work

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- Appendix I – A survey report for the stakeholders

  Mahogany Glider (*Petaurus gracilis*) Cage Trapping Survey Report 2021-2022

  DOI: https://doi.org/10.6084/m9.figshare.21987869.v1

- Appendix II – A standardized monitoring guide for the recovery team

  Long-term Camera Trap Monitoring for the Mahogany Glider

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Chapter 1.

Study Background

1.1. Conservation Science

Conservation science has emerged as a comprehensive and multidisciplinary field dedicated to the preservation of species and ecosystems. Its primary objectives include documenting global biological diversity, examining the impacts of human activities on species and ecosystems, and formulating practical strategies to prevent extinction (Primack 2012). Initially recognized as a “crisis discipline” (Soulé 1985), conservation science emphasized the need for taking action even in the face of incomplete knowledge. However, it has also undergone a transformative process, evolving into a "crisis discipline with evidence" (Segan *et al.* 2011; Pressey *et al.* 2017). This evolution signifies a shift towards actions that are increasingly informed by scientific research.

Significant advancements have been made in the development of sophisticated tools that contribute to effective conservation management. These tools aid in understanding the detailed distribution of threatened species, monitoring population sizes and trends, and investigating genetic diversity and connectivity. These three elements form a framework for filling the knowledge gaps necessary for planning and implementing conservation efforts for threatened species. In the following sections, I elaborate on each of these three components.

Firstly, species distribution modelling has become crucial for predicting the detailed distribution of a species and understanding factors that determine its distribution (Elith and Leathwick 2009). Further application of this model can assess the impact of environmental determinants, such as climate change and habitat loss, thereby contributing to decision making (Rodríguez *et al.* 2007; Lawler *et al.* 2011; Booth 2018; Pecchi *et al.* 2019). For example, species distribution models offer a cost-effective approach to determining the habitat suitability for poorly known species. Empirical studies have also shown that, when combined with machine learning algorithms, the models were able to improve their accuracy and successfully predict unknown populations of threatened species with limited sighting records (Pearson *et al.* 2007; Jackson and Robertson 2011; Oleas *et al.* 2014; Bertola *et al.* 2018). These models also enable researchers to project future scenarios and devise conservation measures (Ednie *et al.* 2023). For species that are vulnerable to climate change, future scenarios have been applied to predict their population trend (Barlow *et al.* 2021), range shift (Handayani *et al.* 2019), and potential climatic refuges (Gavin *et al.* 2014).

Being an efficient and feasible method for tracking and understanding target species, species distribution modelling has limitations in data accuracy, particularly since it relies partially or entirely on citizen science. For example, Richmond *et al.* (2010) outlined four key assumptions of SDM: niche stability, equilibrium between species and environmental conditions, representativeness of training samples for environmental conditions, and the analogy between climatic conditions in training and introduced areas. Additionally, Soley-Guardia *et al.* (2024) identified ten common hazards in data processing, model building, evaluation and interpretation that can significantly impact the accuracy of predictions. Consequently, species distribution models should be regarded as scientifically grounded hypotheses rather than definitive solutions (ALee-Yaw *et al.* 2022).

Secondly, long-term monitoring provides invaluable data on changes in species populations, habitat conditions, and ecosystem health over extended periods (Cusser *et al.* 2021). Continuous monitoring allows researchers to detect trends, identify emerging threats, and evaluate the effectiveness of conservation interventions, providing a basis for adaptive management strategies (Lindenmayer *et al.* 2020). Engaging the public in long-term monitoring through citizen science initiatives further amplifies conservation efforts, gathering extensive data and fostering public awareness (Kobori *et al.* 2016; McKinley *et al.* 2017). The Cape Solander Whale (*Megaptera novaeangliae*) Migration Study at Sydney, Australia, demonstrated a great example of long-term monitoring through citizen science. With a 20-year data on whale sightings, the study reveals a recovering trend in the humpback whale population after exploitation (Pirotta *et al.* 2020).

Camera trapping is recognized as an effective tool for detecting animals with relatively less effort and has therefore been widely used in repeated wildlife surveys and monitoring (Wearn and Glover-Kapfer 2019). However, using camera traps to survey species abundance presents challenges, including issues with individual identification, animal movement, and spatial referencing (Gilbert *et al.* 2020). To address these challenges, the concept of occupancy—defined as the percentage of an area occupied by a species—has been developed as a conservative yet more applicable index for comparing population trends over time (MacKenzie and Nichols 2004; MacKenzie and Bailey 2004). Well-designed camera trap surveys, coupled with robust models, are essential for accurately estimating species occupancy and richness (Foster and Harmsen 2012; Burton *et al.* 2015). Various models have thus been developed to account for factors such as imperfect detection, spatial variation, and the inherent detectability associated with camera trapping (e.g., Bailey *et al.* 2007; Hines and MacKenzie 2006; MacKenzie *et al.* 2017; Koshkina *et al.* 2017).

Conservation genetics, the third component of this thesis, plays a vital role in providing more insights into population status with higher accuracy. Conservation genetics developed from population genetics with the purpose to understand the genetic diversity, population structure, and gene flow of threatened species (Frankham *et al.* 2017). For instance, genetic diversity is a crucial metric as it provides insights to the species' adaptability to changing environmental conditions. Gene flow, the transfer of genetic components from one population to another, can have significant implications for the connectivity and survival of a species. These genetic indices define the genetic health of a species. By analysing the genetic makeup of populations, conservationists can make informed decisions about the value of implementing breeding programs, genetic rescue efforts, and habitat restoration strategies to promote genetic diversity and increase species resilience (Frankham *et al.* 2019). The famous example of the Florida Panther (*Puma concolor* coryi) exemplifies the impact of conservation genetics on Endangered species. Genetic analysis revealed that kinked tails and abnormal sperm were outward indications of inbreeding depression (Roelke *et al.* 1993). Genetic rescue was therefore initiated to address the extremely low population size and genetic diversity and resulted in successful recovery of the panthers over 25 years (Pimm *et al.* 2006; Johnson *et al.* 2010).

The value of conservation science lies in its ability to inform decision-makers, enabling them to allocate limited time and resources efficiently. By relying on scientific evidence, such as resolving detailed distribution, monitoring population size and trend, and investigating genetic diversity and connectivity, conservationists can target their actions to the areas where they will have the most significant impact. This evidence-based approach enhances the precision and efficacy of conservation strategies, ensuring that conservation efforts are not only well-intentioned but also well-informed and cost-effective.

In this PhD project, I applied the concepts of conservation science to investigate these three crucial elements for the Endangered Mahogany Glider (*Petaurus gracilis*) in the lowland forest of northeastern Australia. The overall objective was to fill primary knowledge gaps and provide the data required to target conservation actions. The research closely collaborated with stakeholders, ensuring the delivery of scientific information that is interconnected with real-world decision making. A further goal of this project was to demonstrate a transferable research framework that can efficiently and powerfully assist in the conservation and management of any threatened species.

1.2. The Mahogany Glider (*Petaurus gracilis)*

1.2.1. The gliding marsupials of Australia

In all continents except Antarctica and South America, certain arboreal mammals have adapted to forest environments and independently evolved the ability to glide (Jackson and

Schouten 2012). In Australia, these gliding mammals are marsupials. The gliding marsupials consist of three families: two species of Feathertail Gliders (family Acrobatidae), which are the smallest gliding mammal in the world; the Greater Gliders (family Pseudocheiridae), the largest gliding marsupials in Australia; and the remaining gliding possums in the family Petauridae. This last family includes the Yellow-bellied Glider (*Petaurus australis*), Mahogany Glider (*P. gracilis*), Squirrel Glider (*P. norfolcensis*), and Sugar Glider (*P. breviceps*) species complex.

Most glider species in Australia are found across a wide geographical and climatic range along the northern and eastern coast. These extensive distributions have suggested the possible existence of cryptic species. Recent research has suggested that the three subspecies of the Greater Glider (*Petauroides volans volans, P.v.* minor*,* and *P. v.* armillatus) should be elevated to the species level based on morphological and genomic evidence (McGregor *et al.* 2020), although the split of the species was not accepted due to the lack of evidence (AMTC 2024). Similarly, the Sugar Glider in Australia has been proposed to be split into three separate species: *P. breviceps, P. notatus,* and *P. ariel* (Cremona *et al.* 2020). The Yellow-bellied Glider (*P. australis*) was found genetically structured: the widespread south-eastern populations and the isolated populations in the Wet Tropics of North Queensland (Brown *et al.* 2006). However, challenges such as uneven spatial sampling effort, the lack of a comprehensive phylogenomic study, and subtle morphological differences among the proposed species and subspecies have made it difficult to establish clear boundaries between proposed species within each of these groups (Cooper *et al.* 2023).

Mahogany Gliders were first described by Charles De Vis in 1883 (as *Belideus gracilis*), near Cardwell in northeast Queensland (De Vis 1883; Van Dyck 1993). Lacking a type specimen, the glider was later considered to be either a misidentified Squirrel Glider (*Petaurus norfolcensis*) or a subspecies of Squirrel Glider (Thomas 1888; Iredale and Troughton 1934). These rare gliders were then assumed extinct for over a century, until they were rediscovered at Barrett's Lagoon near Tully in 1989 (Van Dyck 1993; Jackson *et al.* 2011). Based on the new specimens, Van Dyck (1993) found that Mahogany Gliders are morphologically distinct from Squirrel Gliders and resurrected it to species rank. Differing from the closely related Squirrel Gliders, Mahogany Gliders have a larger body size (body length: 215–265 mm, weight: 255–500 g cf. body length: 180–244 mm, weight: 173–300 g), and a longer and less fluffy tail (tail length: 300–390 mm cf. 220–300) (Van Dyck 1993; Jackson 2011; Jackson and Schouten 2012). In skull morphology, Mahogany Gliders have significantly narrower interorbital width, despite having larger skull length, rostral height, and zygomatic width (Van Dyck 1993; Jackson 2011).

Despite the distinct morphology, the alloenzyme data is limited and the genetic evidence was not enough to separate Mahogany and Squirrel Gliders (Jackson 2011). The most recent studies on the phylogeny of the two species were about ten years ago, using two mitochondrial genes (ND2 and ND4) and one nuclear marker (ω-globin gene) (Malekian *et al.* 2010; Ferraro 2012). However, the genetic difference between the two species was low and the species complex remained unresolved, thereby indicating the need for further research in this area.

1.2.2. Habitat and Diet

The ecology of Mahogany Gliders, including life history, habitat preference, and foraging ecology, was extensively studied by Van Dyck (1993) and Jackson (1998) in the 1990s. Both studies suggested that Mahogany Gliders were restricted to a small area of about 122 km in length between Ingham and Tully within the Wet Tropics bioregion, preferring habitats of open canopy sclerophyll forest with an understory of sparsely grown grass and shrubs that are possibly maintained by fire (Van Dyck 1993; Jackson 2000). Although favouring relatively drier habitats and avoiding rainforest, Mahogany Gliders still require a minimum rainfall of approximately 100 mm for the driest quarter (Van Dyck 1993; Jackson and Claridge 1999). The characteristics of currently known habitats are sclerophyll forests with high annual and seasonal rainfall, and high diversity of vegetation species and productivity (Van Dyck 1993; Jackson 2000a)

Van Dyck (1993) provided the first observational study of Mahogany Gliders' habitat and diet by radio-tracking and spotlighting. He found that habitat supporting Mahogany Gliders included at least one species of bloodwood/Eucalyptus tree (*Corymbia intermedia, C. clarksoniana* or *E. dolichocarpa*) accompanied by bird-dispersed Acacia tree (e.g., *A. crassicarpa*). The study of Jackson (Jackson 2000a) drew a similar conclusion that the habitats of Mahogany Gliders are significantly correlated with *C. clarksoniana, C. intermedia*, as well as *Eucalyptus platyphylla*, Black Wattle (*Acacia manguim*), and Blue Paperback (*Melaleuca dealbata*). Based on the vegetation species count at four Mahogany Glider nesting sites and direct observation on the foraging gliders, habitat with Large-fruited Red Mahogany (*E. pellita*) and Grass Tree understory (*Xanthorrhoea johnsonii*) was identified as optimal (Van Dyck 1993).

Two years of observation on radio-collared gliders revealed that they spent an average of 72.8% of their active time feeding on nectar and pollen from the plant family Myrtaceae (*Eucalyptus, Corymbia,* and *Melaleuca* spp.) (Jackson 2001). Although the gliders have a strong preference for nectar and pollen, they are opportunistic feeders and will take exudates, saps, lichens, ants, arthropods and arachnids when available (Van Dyck 1993; Jackson 2001). Sap feeding was only observed from White Siris (*Albizia procera*) and Black Wattle (*Acacia manguim*), accounting for about 30% of diet between January and May (Jackson 2001). *Acacia* aril consumption peaked from November to January when the seeds were readily available (average 16.7% of diet) (Jackson 2001). The gliders feed on insects, lerp and honeydew mainly in the warmer wet season, with lerp and honeydew making up 66.3% and insects 6.5% and their diet when nectar was unavailable (Jackson 2001). The only fruit eaten by the glider seemed to be mistletoe fruit, according to observations by both Van Dyck (1993) and Jackson (2001), but the consumption was low (<11% of diet). Van Dyck (1993) observed feeding on the exudates and pollen of Grass Trees (*Xanthorrhoea johnsonii*), suggesting that Grass Trees may be an important food source.

1.2.3. Social Behaviour and Reproduction

The home range of the Mahogany Glider was extensively assessed by Jackson (2000b). Within continuous habitat, males occupied an average area of 19.25 ha, while females covered 20.34 ha. The combined area for male-female pairs was 23.15 ha. In contrast, within fragmented habitat, the average home range for males reduced to 11.05 ha, and for females, it was 6.80 ha. The combined home range for male-female pairs in this habitat was 11.60 ha. Notably, the study found that the home ranges of paired males and females overlapped significantly, with an average of 85.9% overlap. Conversely, the overlap was only around 11% for non-paired individuals.

The mating system of Mahogany Glider is socially monogamous because paired individuals had a highly overlapped home range that was distinct from the adjacent group, shared a den only with each other, and defended aggressively from other individuals (Jackson 2000a). However, direct observation by Van Dyck (1993) found extra-pair behaviour between the radio-collared individuals. The male that shared a den with a lactating female was observed copulating and consorting with the neighbouring lactating female. It is important to note that the mating system of Mahogany Gliders could be influenced by resource distribution and the availability of home ranges, a phenomenon commonly observed in mammals and documented in species such as the mountain brushtail possum *(Trichosurus cunninghami*) (Martin and Martin 2007). The study by Jackson (2000b) on the population at Muller’s creek (continuous habitat) and Porter’s creek (fragmented habitat) showed that Mahogany Gliders had a distinct breeding season between April and October, matching observations in the study by Van Dyck (1993). A litter usually consists of one or two young and the young take 12 to 18 months to reach maturity (Jackson 2000b).

1.2.4. Threats

Almost all Mahogany Glider occurrences are in the lowlands below 200 m in elevation (Jackson 1998). Since 1880, lowland forest in the Wet Tropics has suffered substantial clearing for sugarcane, pine, and cattle farming (Frawley 1983; Jackson *et al.* 2011; The University of Queensland 2018). In 1989, the rediscovery of Mahogany Gliders in remnants of the Herbert and Tully lowlands triggered a rush of logging in this area before the announcement of clearing restrictions (Jackson *et al.* 2011). Jackson *et al.* (2011) quantified the habitat loss across the distribution of Mahogany Gliders. Vegetation suitable for the gliders was broadly classified, and species distribution model was applied to predict the habitats utilised (Jackson and Claridge 1999). The assessment stated that 49% of total suitable habitats for the gliders were lost between the 1930s and 2007. Of the vegetation cleared, 76% occurred on freehold land. The mixed open forests (high diversity and productivity) that were most suitable for the gliders were largely cleared on freehold land, encompassing 73% of the total mixed open forests cleared.

The Australian Wet Tropics, recognized for its significant natural, aesthetic, and cultural value, was granted World Heritage status in 1988 (World Heritage Centre 1988). This area, spanning 8940 km^2 and primarily consisting of rainforest, stretches from Townsville to just south of Cooktown and west to the Atherton Tablelands. It quickly became one of the world's most effectively regulated and managed protected areas (Weber *et al.* 2021). However, the World Heritage area did not extend to the lowland wet sclerophyll forests, which are home to the Mahogany Glider. Adding to the challenge, much of the Mahogany Glider's habitat is on private property, making regulation and protection difficult. As a result, the threat of habitat loss has persisted, posing ongoing challenges to the conservation of the Mahogany Glider.

The remaining habitats of Mahogany Gliders also face threats from sclerophyll thickening and transitioning to rainforests (Jackson *et al.* 2011). Reduced fire frequency from decreasing Aboriginal activities and long-term climate change are thought to be the reasons for the structural change (Kershaw 1986; Bowman *et al.* 2010). Jackson *et al.* (2011) estimated that about 34% of the remaining habitats were decreasing in suitability because of sclerophyll thickening and transitioning to rainforest. The majority (45%) of this structural change occurred in mixed open forests. Subsequent studies provided transitional and comparative evidence of the forest successions (i.e., sclerophyll forest pockets) with and without fires

(Stanton *et al.* 2014). For 25–79% of sclerophyll forest, the transition to rainforest was not reversible due to the high moisture level of closed rainforests and the absence of regular fires.

1.2.5. Conservation efforts and knowledge gaps

The Mahogany Gliders have been classified as Endangered in both national legislation of EPBC Act and IUCN red list (IUCN 2016; Threatened Species Scientific Committee 2023) due to substantial habitat loss and fragmentation within their naturally limited distribution (Jackson *et al.* 2011; Australian Government 2020). The gliders have been a focus of conservation, with numerous recovery plans proposed (Mahogany Glider Recovery Team and Queensland Parks and Wildlife Service 2001; Parson and Latch 2006; Jackson and Diggins 2020). Gliding poles were installed and monitored near Cardwell and Ingham to reduce the impact of habitat fragmentation (Asari *et al.* 2010). Managed burns and weed control have taken place at key sites (Jackson and Diggins 2020). Some owners of freehold land have adopted wildlife-friendly fencing, as many sightings of Mahogany Gliders were road-kills (13 cases) or killed by barbed wire fences (23 cases including injuries) (Jackson *et al.* 2011; Jackson and Diggins 2020). Additionally, a small-scale captive breeding program has been established in Brisbane as a contingency measure should the wild population face unsustainable conditions (Booth *et al.* 2019).

Despite ongoing conservation efforts, there are still significant gaps in taking effective conservation actions for the Mahogany Glider. The most recent species distribution model is over a decade old (Van Dyck 1993; Jackson and Claridge 1999; Jackson *et al.* 2011), and the glider's current suitable habitats have not been reassessed since. With the advent of advanced algorithms, it is now possible to increase accuracy and include categorical predictors in these models. Additionally, the glider populations have not been monitored since the surveys conducted a decade ago (Lyon 1993; Mckay and Hawkes 1997; Queensland Government 2020). Regular monitoring is essential for tracking population trends and establishing baselines for threatened species. Unfortunately, a crucial aspect, the population size estimate, has never been assessed. As a result, the total abundance of Mahogany Gliders is only roughly extrapolated, ranging from as low as 1,200 to as high as 14,000. This wide range indicates a significant uncertainty in our understanding of the species’ current status.

The National Recovery Plans for Mahogany Gliders underscore the necessity of comprehensive population genetic assessments for the species’ long-term survival (Parson and Latch 2006; Jackson and Diggins 2020). However, it remains a knowledge gap. While there has been a phylogenetic study conducted to understand the relationship between the Mahogany Glider and the Squirrel Glider complex (Ferraro 2012), no study has yet been undertaken that focuses specifically on the population genetics of the Mahogany Glider. There has been no estimation on the genetic diversity and the gene flow between different glider populations. The lack of genetic knowledge hampers the ability to make correct decision and design effective conservation strategies. For instance, without understanding the genetic connectivity between populations, it is challenging to design effective wildlife corridors. Similarly, without a clear understanding of the genetic diversity and structure of the population, it is difficult to develop potential assisted gene flow, genetic rescue, relocation, and captive breeding programs (Frankham 2005; Frankham *et al.* 2017; Frankham *et al.* 2019)

1.3. Research Scope and Structure

This PhD project, in collaboration with Conrad Hoskin (JCU) and Terrain Nature Resource Management, aimed to apply cutting-edge conservation science to the Endangered Mahogany Glider (*Petaurus gracilis*) and inform conservation management. The broad aims of the project were to:

1. Better resolve the distribution of the species.
2. Estimate the population size of the species and establish long-term monitoring of key populations.
3. Assess the genetic structuring and genetic health of populations across the range.

Chapter 2 utilized species distribution models with machine learning algorithms to predict fine-scale suitable habitats in the fragmented landscape. These predictions assisted in conducting targeted cage and camera trapping surveys for the following chapters. Chapter 3 provided the pathway for the long-term monitoring for the glider in three key habitats using camera traps, thereby enabling future temporal assessments of these population and stakeholder engagement. Targeted camera trapping surveys enabled the first scientific estimation of the census population size for the species. Chapter 4 assessed the conservation genetics of the species using genome-wide Single Nucleotide Polymorphisms (SNPs). This analysis examined connectivity across the range and the genetic health of populations. The genetic analysis also assessed relationships with the Squirrel Glider (*P. norfolcensis*).

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Chapter 2.

Species distribution modelling of the Endangered Mahogany Glider (*Petaurus gracilis*) reveals key areas for targeted survey and conservation.

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2.1. Abstract

The Mahogany Glider (*Petaurus gracilis*) is one of the most threatened marsupials in Australia. Its known distribution is an approximately 120 km strip of fragmented coastal woodland in north-east Queensland, from north of Townsville to the Tully area. Records are clustered in a number of well-surveyed areas, with significant areas of lowland habitat unsurveyed. Around 30% of historic records fall in areas that were subsequently cleared for farmland, and ongoing clearing and fragmentation of lowland sclerophyll forest continues within the potential distribution. Resolving the distribution is an urgent requirement to guide conservation but Mahogany Gliders are difficult to detect in the field. Species distribution modelling offers a technique for estimating the fine-scale distribution and for targeting further field survey and conservation efforts. We used known occurrence records (N = 481) to predict the distribution of Mahogany Gliders across the Wet Tropics bioregion. We used climatic, topographic, and other environmental predictors to generate distribution models using Maxent and Random Forest algorithms, each with two bias correction methods. The predictions revealed that many unknown populations may exist within the currently defined distribution and in important areas beyond this (e.g., Hinchinbrook Island). There was reasonable congruence between models, and we include syntheses of the models to present the most likely current distribution. The most important predictor variables across the models were precipitation seasonality (high seasonality), elevation (generally < 100 m), soil type (hydrosols), and vegetation type (including Eucalyptus and Melaleuca woodlands). Our results identify core habitat and reveal key areas that require targeted field surveys. Importantly, the predicted suitable habitat is highly fragmented and ongoing conservation efforts need to improve habitat connectivity and limit further fragmentation.

2.2. Keywords

Australian Wet Tropics, Mahogany Glider, Maxent, Random Forest, fragmentation, road bias

2.3. Introduction

Knowing the distribution of a species is fundamental to understanding its ecology, resolving threats, and implementing conservation actions. Species distribution can rarely be described by knowing the whereabouts of every population; instead, it must usually be estimated based on known occurrences and habitat requirements. Species distribution models (SDMs) can be developed to help estimate and define the likely distribution of a species (Cayuela *et al.* 2009; Drew *et al.* 2011; Gobeyn *et al.* 2019; Zhang and Li 2017). Accurate SDMs can be a time- and cost-effective way to provide essential information for species conservation (Drew *et al.* 2011). Empirical studies have used SDMs to search for additional populations and suitable habitats for threatened species, such as the Gulbaru Leaf-tailed Gecko (*Phyllurus gulbaru*) in north-east Australia (Bertola *et al.* 2018) and Juliana's Golden Mole (*Neamblysomus julianae*) in South Africa (Jackson and Robertson 2011). Distribution models are also powerful in assessing threats and distributional change through time; for instance, quantifying the range and population decline of Spotted-tailed Quolls (*Dasyurus maculatus gracilis*) in north-east Australia over the past century (Uzqueda *et al.* 2020), or evaluating the risk of climate change on the threatened Iberian Desman (*Galemys pyrenaicus*) in Europe (Morueta-Holme *et al.* 2010). The predictions from SDMs can also identify areas of high conservation value and improve conservation planning; for instance, systematically selecting reserves with high avian diversity (Moradi *et al.* 2019), or ranking threats and prioritizing management actions (Ricca *et al.* 2018).

A variety of algorithms have been developed for species distribution modelling. By overlaying environmental predictors (spatial data) with known sighting records of one or multiple species, the algorithms compute the probability (likelihood) of a species occurrence given a set of conditions. The distance-based BIOCLIM algorithm (Busby 1991) was the first algorithm widely used to answer a variety of questions in ecology and conservation (Nix and Busby 1986; Busby 1991; Booth *et al.* 2014) but was largely replaced by machine-learning algorithms in the 2000s (Elith and Leathwick 2009; Gobeyn *et al.* 2019; Pecchi *et al.* 2019). Machine-learning algorithms, especially Maxent (which is based on probability density) and Random Forest (which utilizes decision trees), dominate current SDM methodology. They are known for being ecologically interpretable, stable and accurate, and being able to integrate categorical predictors and missing data (Zhang and Li 2017; Pecchi *et al.* 2019). To account for uneven sampling/sightings, bias-correcting methods that manipulate the background selection (pseudo-absence) to reduce sampling bias were also established (Vollering *et al.* 2019a; Phillips *et al.* 2009). Contemporary SDMs with corrected bias and testable accuracy have therefore become a powerful tool to model suitable habitat of a species currently, in the past, or in future scenarios (Zimmermann *et al.* 2010). Examples include managing natural resources (Booth 2018) and predicting distributional change of invasive or threatened species under climate or other human-induced changes (Jaeschke *et al.* 2013; Rodríguez-Rey *et al.* 2019).

The Mahogany Glider (*Petaurus gracilis*) is an Endangered arboreal marsupial endemic to the Australian Wet Tropics of north-eastern Queensland (Goldingay and Jackson 2004) (Fig. 2.1C). The species was originally collected from a few specimens in the 1800s and then not seen for over a century (Van Dyck 1992, 1993). Following rediscovery (Van Dyck 1993), the species has been subject to survey and conservation efforts (Jackson 1998; Mahogany Glider Recovery Team and Queensland Parks and Wildlife Service 2001; Parson and Latch 2006). Mahogany Gliders inhabit open canopy sclerophyll forests in the eastern lowlands of the Wet Tropics, with habitat determined by a complex interplay between rainfall, fire, and possibly other factors (Van Dyck 1993; Jackson 2000; Jackson and Claridge 1999). The species does not occur in rainforests, which cover some of the lowlands and much of the mid and higher elevations of the region. Even within lowland woodland habitats, the glider has a patchy distribution, probably driven by a high diversity of flowering trees as a stable food source (Fig. 2.1B) (Van Dyck 1993; Jackson 2000; Jackson and Claridge 1999).

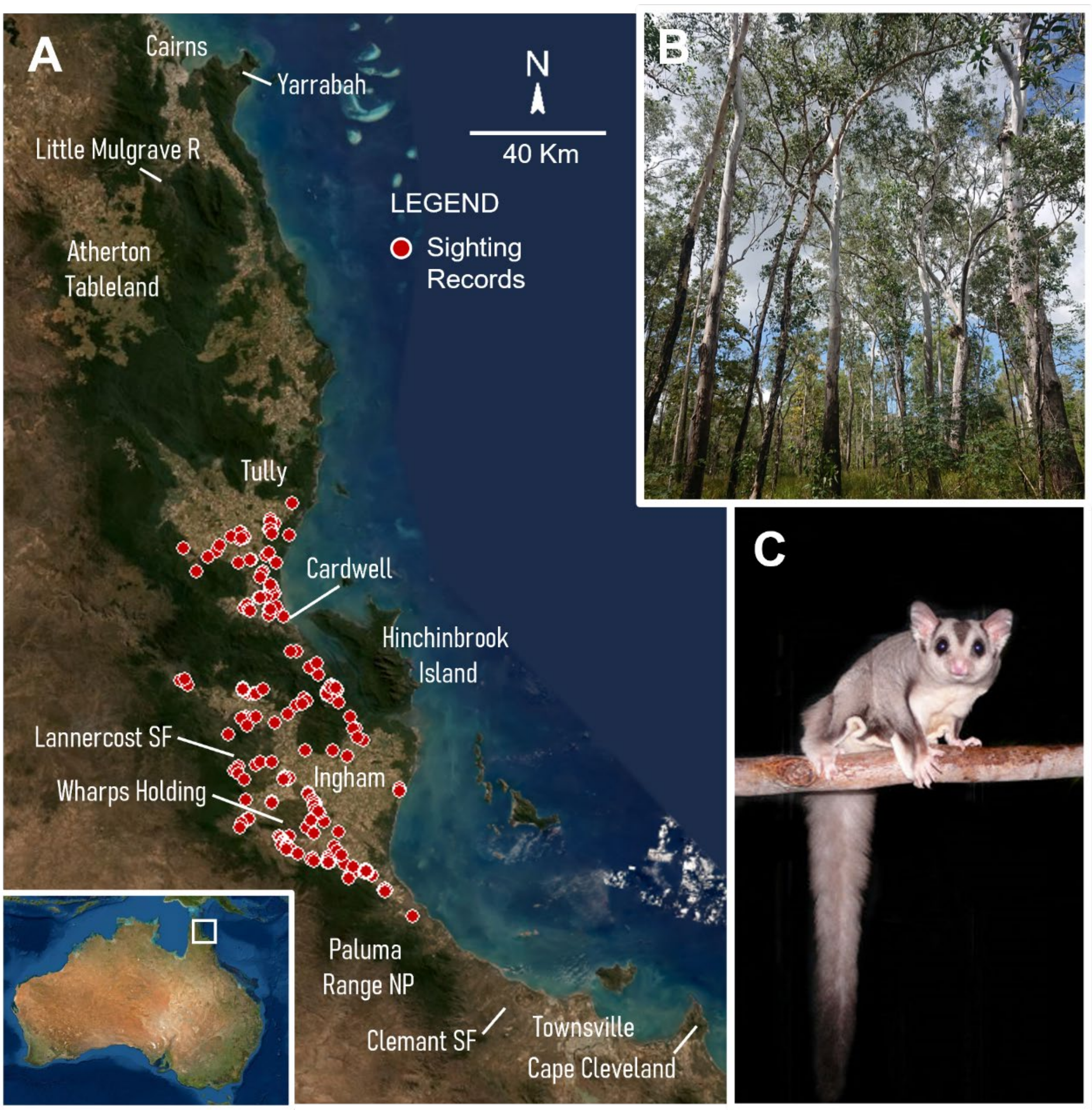

Fig. 2.1 Sighting records and typical habitat of Mahogany Gliders (*Petaurus gracilis*). A Sighting records (red dots) demonstrate the known distribution of the gliders within the Wet Tropics, north-eastern Queensland, Australia. B Mahogany Gliders prefer sclerophyll forests of open structure and with a diversity of flowering plants at the tree- and shrub-level. C Photo of a Mahogany Glider, with characteristic long, tapering tail (Photo credit: Daryl Dickson).

All Mahogany Glider records are located in the southern and central Wet Tropics bioregion, along a coastal strip from Ollera Creek and Crystal Creek at the base of the Paluma Range, near Townsville, to 120 km north near Tully (Fig. 2.1A). The lowland forests in this region have suffered extensive clearing in the last 150 years, due to forestry, cattle grazing, and intensive large-scale sugar cane farming. It is estimated that about 50% of the glider's suitable habitat was lost between 1930 and 2007 (Jackson *et al.* 2011). Habitat loss and accompanying population fragmentation threaten Mahogany Gliders (Parson and Latch 2006b; Jackson and Robertson 2011; Jackson *et al.* 2019; Jackson and Diggins 2020b), and it is therefore essential to understand their current distribution in detail.

The distribution of Mahogany Gliders has been modelled three times using BIOCLIMThe model from Van Dyck (1993) used 16 sighting records and 28 climatic variables, predicting a confined distribution around known points between Ingham and Tully. The second model (Jackson and Claridge 1999) used 144 records and 35 climatic variables, and it extended predicted habitat south to the northern end of the Paluma Range lowlands. The most recent model (Jackson and Robertson 2011) used 310 records, 10 climatic variables, manually incorporated vegetation types, and focussed more on identifying habitat remnants within the known range than assessing the full potential distribution. Two issues have limited the accuracy of modelling efforts to date: (i) bias caused by uneven survey effort has not been adequately accounted for, and (ii) BIOCLIM does not perform as well as subsequent modelling techniques (Phillips *et al.* 2009; Hijmans 2012; (Pecchi *et al.* 2019). Therefore, the modelled distributions to date are likely to misrepresent the Mahogany Glider distribution, and hence populations both within and outside the known range may not be detected and protected. The more advanced modelling methods now available (Hijmans and Elith 2016; Gobeyn *et al.* 2019), enable better correction for sampling bias, identification of important categorical variables (e.g., vegetation type), and quantification of habitat suitability with higher resolution and accuracy.

In this study, we modelled the potential distribution of Mahogany Gliders using two high-accuracy and ecologically interpreAppendix SDM algorithms: Maxent and Random Forest (Elith *et al.* 2011; Zhang and Li 2017). We used a comprehensive, vetted database of known sighting records and modelled all potential habitat in the Wet Tropics region. In the modelling process, we assessed the determinants of the glider's current distribution, including climatic and environmental factors, as well as human land use factors. We expected the new algorithms to provide finer-scale prediction of habitat suitability within the known range, and to better estimate the likelihood of occurrence beyond the known range. We aimed to use species distribution modelling to map all area of potential habitat, identify core and peripheral populations, and assess potential connectivity across the range. The ultimate objective of the modelling was to produce maps to guide on-ground actions such as surveys, replanting and habitat improvement, and inform broad-scale conservation actions such as genetic sampling to assess connectivity among populations.

2.4. Methods

Our broad modelling approach was as follows, with all detail in the sections below. We collated all known sighting records and environmental predictor variables deemed relevant to Mahogany Gliders and modelled their distribution with both Maxent and Random Forest algorithms. We constructed all models in R (R Development Core Team 2008), using three modelling packages (two Maxent packages and one Random Forest package) and two bias-correction methods within each of these, resulting in six models in total (Table 2.1). We then tuned the hyperparameters of the models. For the final distribution maps, we summarised the predictions from Maxent and Random Forest models in two ways: by overlaying a threshold prediction from all six models, and by averaging the predicted probabilities weighted by their accuracy.

Table 2.1 Summary of Species Distribution Models used in this study, including the bias-correction approaches, the modelling algorithm, the R package (shown in italic) in which the model was implemented, and whether variable selection and model tuning were performed.

Model	Bias correction	Algorithm	R package	Variable selection	Model tuning package
1	TGB+spThin	Maxent	MIAmaxent	Yes	No
2	TGB+spThin	Maxent	SDMtune	Yes	SDMtune
3	TGB+spThin	Random Forest	randomForest	Yes	caret
4	BT	Maxent	MIAmaxent	Yes	No
5	BT	Maxent	SDMtune	Yes	SDMtune
6	BT	Random Forest	randomForest	Yes	caret

†Abbreviations used in this table: TGB = Target Group Background, BT = Background Thickening

2.4.1. Sighting records

Sightings of Mahogany Gliders were obtained from Terrain Natural Resource Management (Terrain NRM) (N = 394) and the WildNet Database (Queensland Government 2020) (N = 292). We combined the two datasets, removing duplicate records and records without GPS coordinates (i.e., with only a locality name). We also transformed all Cartesian coordinates (easting, northings) to a standardized datum WGS 84 (EPSG 4326) (Pebesma 2018). The final dataset consisted of 481 records, with 98.5% of these (i.e., 474 records) falling between 1990 and 2010 (Appendix S2-1).

2.4.2. Predictor dataset

We used 19 climatic variables from accuCLIM that were specifically adjusted for the Australian Wet Tropics bioregion, averaged from the time period between 1996 and 2015 (Storlie *et al.* 2013; Appendix S2-2). These climatic predictors have been widely applied to model Wet Tropics species (Bertola *et al.* 2018; Reside *et al.* 2019; Uzqueda *et al.* 2020). We included four topographic variables: elevation, aspect, slope, and distance to major waterways (Queensland Government 2017). These were all continuous numeric values. We also included five environmental variables: vegetation type, soil type, major land use, forest coverage, and fire frequency (Appendix S2-2).

Vegetation type represented pre-clearing vegetation (to ensure the sighting records are not situated on farmland, due to subsequent clearing), and consisted of 41 vegetation types in the Wet Tropics (Department of the Environment 2012). Land use type contained six categories: Conservation and Natural Environments, Relatively Natural Environment, Dryland Agricultural and Plantations, Irrigated Agricultural and Plantations, Intensive Uses, and Water (Department of Environment and Science 2019). Soil type contained 14 major soil groups from the collation of Australian Soil Resource Information System (ACLEP 2014). Land use data were obtained for two years: 1999 (to represent land use for records before the year 2000) and 2010 (to represent land use for records after the year 2000). Forest coverage contained Landsat satellite data that was classified using canopy cover: Non-woody (< 5 %), sparsely covered (5–19%), and densely covered (> 20%) (Department of Industry Science Energy and Resources 2020). Forest coverage was also obtained for two time periods by averaging yearly data from before (1908-1999) and after (2001-2010) the year 2000. Importantly, the two periods represent the time before and after the announcement of new tree-clearing laws (*Vegetation Management Act 1999*), which resulted in a peak in vegetation clearing in the region around the year 1999 (McGrath 2007). Fire frequency was derived from AVHRR (the Advanced Very High Resolution Radiometer), representing the number of fires detected per pixel between 1997 to 2011 (Craig *et al.* 2002).

All 28 variables (19 climatic, 4 topographic, 5 environmental) were standardized to the same geographic extent and resolution as the climatic spatial layers (Pebesma and Bivand 2005; Hijmans and van Etten 2016, cell size = 0.0025 degree) and to the same coordination system matching the sighting records (WGS 84, EPSG 4326). Correlated predictors were removed during model fitting as described below for each of the modelling approaches.

2.4.3. Model prediction

Current suitable habitat for the Mahogany Glider was identified based on the most recent available layers for vegetation type (current post-clearing vegetation, last updated for Queensland in 2006), land use (2019), and forest coverage (2018). All spatial layers used in model training and prediction are presented in Appendix S2-2.

2.4.4. Bias correction

Sighting records can result in bias in the modelling process due to geographically uneven survey effort or detection success, which can affect model performance (Hijmans 2012; Veloz 2009). We addressed sampling bias using two bias-correction methods to identify and correct uneven sampling effort and localised clustering: (1) Target Group Background (TGB) (Phillips *et al.* 2009) in combination with Species Thinning (*spThin*) (Aiello-Lammens, Boria, Radosavljevic, Vilela, Anderson, *et al.* 2015) (demonstrated in Appendix S2-3) and (2) Background Thickening (BT) (Vollering *et al.* 2019a). Bias correction can improve predictions, but trade-offs were also found between correctly identifying known distributions and correctly identifying environmental covariates (Inman *et al.* 2021). Moreover, species with narrow ecological niches pose additional challenges in a biased dataset (Inman *et al.* 2021). By applying these two bias-correction methods, we were able to evaluate the impact of sampling bias on our datasets and explore the potential differences in model predictions based on the correction approach.

(1) Species Thinning in combination with Target Group Background (TGB+spThin)

Target Group Background has been widely used to correct sampling bias in SDM with presence-only data (Phillips *et al.* 2009; Ranc *et al.* 2017). The methodology selects background points using sighting records of similarly surveyed species to assess survey effort across the environment and account for bias. We selected 27 Wet Tropics arboreal mammals that are surveyed in a similar way to Mahogany Gliders (i.e., spotlighting, cage trapping, camera trapping). These included other species of gliders, possums, and tree-dwelling rats (Appendix S2-4). The sighting records of these animals were obtained from the WildNet Wildlife Records spatial dataset (Queensland Government 2020) and were used to create a two-dimensional kernel density estimation, also known as TGB bias grid (Ripley *et al.* 2013) (Appendix S2-5). We thinned the Mahogany Glider sighting records from 481 to 136 for the TGB dataset using a 1 km grid because over-clustered records further bias the prediction (R package *spThin*, (Aiello-Lammens *et al.* 2015) (Appendix S2-3).

(2) Background Thickening (BT)

Background Thickening was proposed as an alternative correction for uneven sampling effort to Species Thinning because, unlike Species Thinning, Background Thickening does not remove sighting records. Instead, it increases the clustering of background points to match the bias in the sighting records (Vollering *et al.* 2019a). The method creates buffers around the sighting records, and then uses the buffers' intersection rate as an indicator of sampling effort. Following the methodology described in Vollering *et al.* (2019a), we created variograms to compute spatial continuity for the environmental variables selected by a pilot model (TGB model) (Gräler *et al.* 2016). Secondly, we created a geodesic buffer using the above continuity distance around the sighting records and calculated the intersection rates of these buffers (Ștefan 2019). The intersection rates served as sampling probability in the bias grid. We then selected the background points to match the sampling bias for sighting records (i.e., more background points being sampled in areas with clustered sighting records).

2.4.5. Model algorithms, variable selection, tuning, and evaluation

We produced species distribution models (SDMs) of Mahogany Gliders with two algorithms: Maximum Entropy (Maxent) and Random Forest. We applied these two broad approaches in R (R Development Core Team 2008), using three modelling packages: *MIAmaxent* (Vollering *et al.* 2019b) and *SDMtune* (Vignali *et al.* 2020) for Maxent modelling, and *randomForest* (Breiman 2018) for Random Forest modelling. We applied the two bias-correction approaches (TGB+*spThin*, BT) as described above in each modelling process, resulting in six SDMs in total (Table 2.1).

We examined and evaluated the models using standard evaluation metrics for SDMs: area under the receiver operating characteristic (ROC) curve (AUC), variable response curves, and Akaike information criterion (AIC). Being widely applied to SDM evaluations, AUC is a simple but important index that discriminates true positives and false positives (Fielding and Bell 1997). However, using one index alone for model evaluation can be misleading (Lobo *et al.* 2008; Jiménez-Valverde 2012; Ruete and Leynaud 2015). Therefore, we also examined the variable response curves to make sure that the predictions were realistic. Lastly, we used AIC to represent model fitting and complexity (Velasco and González-Salazar 2019; Sakamoto *et al.* 1986). In addition, we assessed similarity between predictions by calculating the percentage of overlapping pixels using Schoener's D test (Warren *et al.* 2010).

(1) Maxent (MIAmaxent and SDMtune) models

The algorithm compares probability densities of the predictors between sighting records and bias-corrected background points and estimates the habitat suitability for the target species (Elith *et al.* 2011; Phillips *et al.* 2004). We used two recently published R packages to construct Maxent models: *MIAmaxent* (Vollering *et al.* 2019a) and *SDMtune* (Vignali *et al.* 2020). Both packages adopt the Maxent algorithm and were created to increase ecological interpretability of SDMs. However, the two packages use different methods in variable selection and model selection (Vollering *et al.* 2019a; Vignali *et al.* 2020). Comparing the two procedures allows us to examine the consistency of the resulting predictions.

To select a useful subset of variables, *MIAmaxent* uses forward stepwise selection, which adds variables one by one until the penalty on complexity outweighs the goodness of fit. We withheld 20% of the dataset to test model accuracy (testing data). Instead of demonstrating the presence probability, the predictions of *MIAmaxent* used probability ratio output (PRO; (Halvorsen 2013) as a measure of "relative suitability of one place versus another", where PRO = 1 represents a randomly chosen place with average suitability (Vollering *et al.* 2019b).

In *SDMtune*, variable selection was performed using a built-in function that pairs the correlated variables using Jackknife tests, retaining only the variable with the highest contribution for each pair. We divided the sighting records into training, validation and testing datasets in a 3:1:1 proportion. The validation dataset was used to tune the hyper-parameters: feature class (variable transformation), regularization (penalty on model complexity), and iteration (repetitions) (Vignali *et al.* 2020).

(2) Random Forest models

Random Forest is an algorithm widely applied for species distribution modelling (Evans *et al.* 2011; Mi *et al.* 2017; Zhang and Li 2017). Using thousands of decision trees, Random Forest algorithms find the best determinants to correctly classify a location into presence or absence (Breiman 2001). We constructed Random Forest models in the R package *randomForest* (Breiman 2018). Variables were selected using the varSelRF package (Diaz-Uriarte 2010; Diaz-Uriarte and Diaz-Uriarte 2017) by removing the variables contributing the least but causing the highest classification error. We tuned the number of variables available for classification at each tree node with cross-validation in the *caret* R package (Kuhn 2008). Classification accuracy (ratio of correctly classified samples to total samples) and confusion matrix (expression of true/false positives and negatives) were used to evaluate Random Forest models (Kuhn 2008).

2.4.6. Summarising habitat suitability across models

Choosing the 'best' species distribution model from different modelling approaches and algorithms is not trivial, due to the lack of standardized and universal measures, as well as pros and cons of different models for each species and study area (Araújo and Guisan 2006; Allouche *et al.* 2006; Mouton *et al.* 2010). Thus, to summarise the findings from all six models, we produced two additional outputs: a summary map displaying the number of models in which an area was identified as suitable for the species; and a weighted average map.

For the summary map, we first classified each model output into suitable (1) and unsuitable (0), using a 0.5 probability threshold for *SDMtune* and *randomForest* outputs, and a threshold of 1 for *MIAmaxent* outputs. We overlayed these re-classified outputs, obtaining a map with values ranging from 0 (no model predicted the area as suitable) to 6 (all models predicted the area to be suitable).

The weighted average map was obtained by averaging the prediction probabilities of the *SDMtune* and *randomForest* SDMs, weighted by the model accuracy, using the formula:

$$((AUC^{1}*P^{1}+ AUC^{2}*P^{2}+ AUC^{3}*P^{3}+ AUC^{4}*P^{4})/4$$

AUCs 1 to 4 represent the AUC value from the four models included in the calculations (i.e., the *SDMtune* and *randomForest* models, each with TGB+*spThin* and BT bias correction), and the *P* as predicted probability of occurrence of each pixel from each model. *MIAmaxent* models were not included in the weighted average map because *MIAmaxent* predicted the habitat suitability using the unit of Probability Ration Output (PRO, see Model algorithms section in Methods) rather than probabilities.

We used the weighted averaged map to determine how many habitat patches, of various sizes, contain Mahogany Glider records. To do this we set habitat suitability at a threshold of 0.5 and identified all habitat patches using the R package *terra* (Hijmans *et al.* 2022). We considered all eight neighbours surrounding a central cell as a patch (Queen's adjacency), and each patch is separated from the other with a minimum distance of 60 m (i.e., the maximum gliding distance of Mahogany Gliders (Jackson 1998). We quantified all habitat patches with and without sighting records from the full database (i.e., sightings at any point in time). We assessed this at four patch sizes: < 0.1 km^2, 0.1–1 km^2, 1–10 km^{2}and > 10 km^2. The minimum estimated home range of a Mahogany Glider is about 0.1 km^2 (11 ha) (Jackson 2000), so we consider patch sizes < 0.1 km^2 unlikely to support a population.

2.4.7. Assessing road bias

The Wet Tropics, and particularly lowland areas of the Wet Tropics, are heavily bisected by roads. It is rare to be further than 5 km from a road, or even 2.5 km from a road in these areas. Mahogany Gliders are strictly arboreal and do not use roads but, like many species, observer accessibility likely results in sightings being clustered closer to roads (Kadmon *et al.* 2004). We assessed the Euclidean distance to roads of our species distribution models to assess the degree to which the road bias was removed. We used a map of roads in Queensland (Queensland Government 2017) and created a layer of Euclidean distance to roads in ArcGIS v.10.7, using the Spatial Analyst tool (ESRI 2018). We compared and visualized the distance distributions of the whole Wet Tropics (N = 499,089), chosen background points (BT, N = 4,000; TGB, N = 4,000), predicted suitable habitat from the weighted average map (N = 61,196), and sighting records (N = 481), using an estimator of the empirical Cumulative Distribution Function (ECDF). We then tested whether these five distributions are the same (Kolmogorov-Smirnov test, (Lilliefors 1967), to verify whether our bias correction approaches addressed road bias.

2.5. Results

Species distribution models (SDM) were produced using all known sighting records, a set of biologically relevant environmental and climatic predictors, three modelling approaches, and two bias correction methods. In the sections below, we identify the most important predictor variables, present each of the six models produced (Table 2.1, Fig. 2.2), present two summary models (Fig. 2.3), and assess road bias and whether it was accounted for by the models (Fig. 2.4).

2.5.1. Sighting records and predictor variables

After filtering, 137 and 187 Mahogany Glider sighting records were retained in the Target Group Background (TGB) and Background Thickening (BT) models, respectively. Variable selection resulted in the subsets containing 5 to 13 predictors. The predictors that contributed most and were selected by more than three models were: elevation, precipitation seasonality, soil type, and vegetation type (Table 2.2, Appendix S2-6). To facilitate comparisons between models, we divided the contribution of a single predictor by the total contribution of retained predictors for each model and present the relative contributions. Elevation was selected in all six models and ranked first in contribution in four models. Its relative importance ranged from 11% (randomForest with TGB) to 76% (SDMtune with TGB). All areas predicted as suitable were below 100 m above sea level. Median elevation thresholds in five models fell below 90 meters. Only the *MIAmaxent* model with BT correction predicted higher median elevation (219 m) (Table 2.2).

Precipitation seasonality was selected in all Maxent models but not in *randomForest* models, with a relative importance ranging between 2.8% (*SDMtune* with TGB) and 9.8% (*SDMtune* with BT). Median precipitation seasonality of predicted areas falls between 0.92 and 1 across the four models. The predicted high precipitation seasonality suggests the suitable habitat for Mahogany Glider has a marked seasonal rainfall, with a long dry season (O'Donnell and Ignizio 2012; Walsh and Lawler 1981).

Soil type was selected in five models, with a relative importance between 2.8% (*SDMtune* with TGB) and 26% (*MIAmaxent* with TGB). Among 14 soil types, Hydrosols were consistently predicted with higher suitability (Table 2.2, Appendix S2-7).

Vegetation type was selected in four models. Relative importance of vegetation type ranged between 2% (*SDMtune* with BT) and 17% (*randomForest* with BT). *Eucalyptus* woodlands with a tussock grass understorey and *Melaleuca* open forests and woodlands were identified as the most important vegetation types for Mahogany Gliders in the models (Table 2.2). Details of other less frequently selected vegetation types can be found in Appendix S2-7.

Table 2.2 Details of the four most selected predictors (selected in more than half of the models). Numbers show the median, with 1st and 3rd quantile shown in the brackets. The two vegetation types consistently selected were: (9) *Eucalyptus* woodlands with a tussock grass understory; and (15) *Melaleuca* open forests and woodlands.

R package	**MIAmaxent**		**SDMtune**		**randomForest**	
Bias correction	TGB	BT	TGB	BT	TGB	BT
Elevation (m)	84 (61–112)	219 (148–290)	40 (24–56)	51 (34–67)	30 (13–62)	33 (15–58)
Precipitation seasonality	0.96 (0.92–1)	0.96 (0.91–0.99)	0.92 (0.88–0.97)	1 (0.98–1.01)	-	-
Soil	Chromosols **Hydrosols** Kandosols	**Hydrosols**	**Hydrosols**	**Hydrosols**	**Hydrosols**	-
Vegetation†	-	**9, 15**	**9**, 14, **15**, 44	5, **9**, **15**, 26, 44, 63	-	5, 9, 15

†Abbreviations used in this table: TGB = Target Group Background, BT = Background Thickening

2.5.2. Model evaluation

Area Under the Curve (AUC; Maxent models) and accuracy (*randomForest* models) were high across all six SDMs (Table 2.3). Models corrected with Target Group Background and Species Thinning (TGB+*spThin*) generally had higher AUC than the models corrected by background thickening (BT) (Table 2.3). In Maxent models, the AUC scores differed only slightly (0.92–0.96), while in Random Forest models the accuracy differed by nearly 20% between the two bias-correction methods. The *randomForest* model with BT corrections recorded the lowest AUC among all models, while the *randomForest* model with TGB correction reached the highest AUC of 0.99 (confusion matrix sensitivity = 1, specificity = 0.98).

Table 2.3 Evaluation metrics and tuning parameters for the six tuned models.

R package/ bias correction	**MIAmaxent TGB**	**MIAmaxent BT**	**SDMtune TGB**	**SDMtune BT**	**randomForest TGB**	**randomForest BT**
Algorithm	Maxent	Maxent	Maxent	Maxent	Random Forest	Random Forest
Tuning package	NA	NA	SDMtune	SDMtune	caret	caret
Test data evaluation	AUC = 0.96 AIC = 1380	AUC = 0.92 AIC = 2738	AUC = 0.96 AIC = 2886	AUC = 0.95 AIC = 9534	AUC = 0.99 Accuracy: 0.98 (95% CI = 0.94, 1.00)	AUC = 0.89 Accuracy: 0.79 (95% CI = 0.72, 0.86)
Tuning parameters	NA	NA	fc = lh reg = 1.2 iter = 500	fc = lqp reg = 2.1 iter = 500	mtry = 2	mtry = 2

[†] Abbreviations used in this table: AUC = Area under the curve, AIC = Akaike information criterion, fc = feature classes, reg = regularization, iter = iteration, mtry = number of variables available for splitting at each tree node.

2.5.3. Species distribution models for the Mahogany Glider

Schoener's D similarity tests showed a very wide range of similarity (7-73%) (**Appendix S2-8**). We attribute this to some models predicting heavily around known localities (e.g., Fig. 2.2A), while others predicted much more broadly (e.g., Fig. 2.2B & F). However, three out of six models (Fig. 2.2A, C & D) had moderate to high similarity (range 54-73%). Nevertheless, all models consistently identified suitable habitat around known records between Ingham and Tully (Fig. 2.2), including areas with many sightings and areas with few known sightings (notably, Lannercost State Forest and forest along the Herbert River near Abergowrie in the Ingham area, and the base of the range around Tully). Additionally, all models identified suitable habitat in multiple areas beyond the known distribution (Fig. 2.2), including: lowland areas on the west and north of Hinchinbrook Island (all six models); north of the known distribution in the vicinity of Little Mulgrave River/Gillies Range (all six models); the eastern lowlands of Paluma Range National Park south to Clemant State Forest (three models, Fig. 2.2B–C, F); the Yarrabah region near Cairns (five models, Fig. 2.2B–F); and even further north around Cooktown (four models, Fig. 2.2C–F).

Comparing predictions between bias-correction methods, Target Group Background (TGB) models predicted more conservatively and identified suitable habitat mostly around known sightings (Fig. 2.2A–C), while background thickening (BT) models identified suitable habitat up to ~ 300 km north and ~ 100 km south of known sightings. For instance, three different BT models identified large patches of suitable habitat near Cooktown (Fig. 2.2D–F). Comparing predicted areas between packages, *SDMtune* models produced the most conservative predictions (Fig. 2.2B & E), with most suitable habitat being in close proximity to known records. Random Forest models on the other hand were the least conservative, predicting further from known records, and more often outside the known extent of the species (Fig. 2.2C & F).

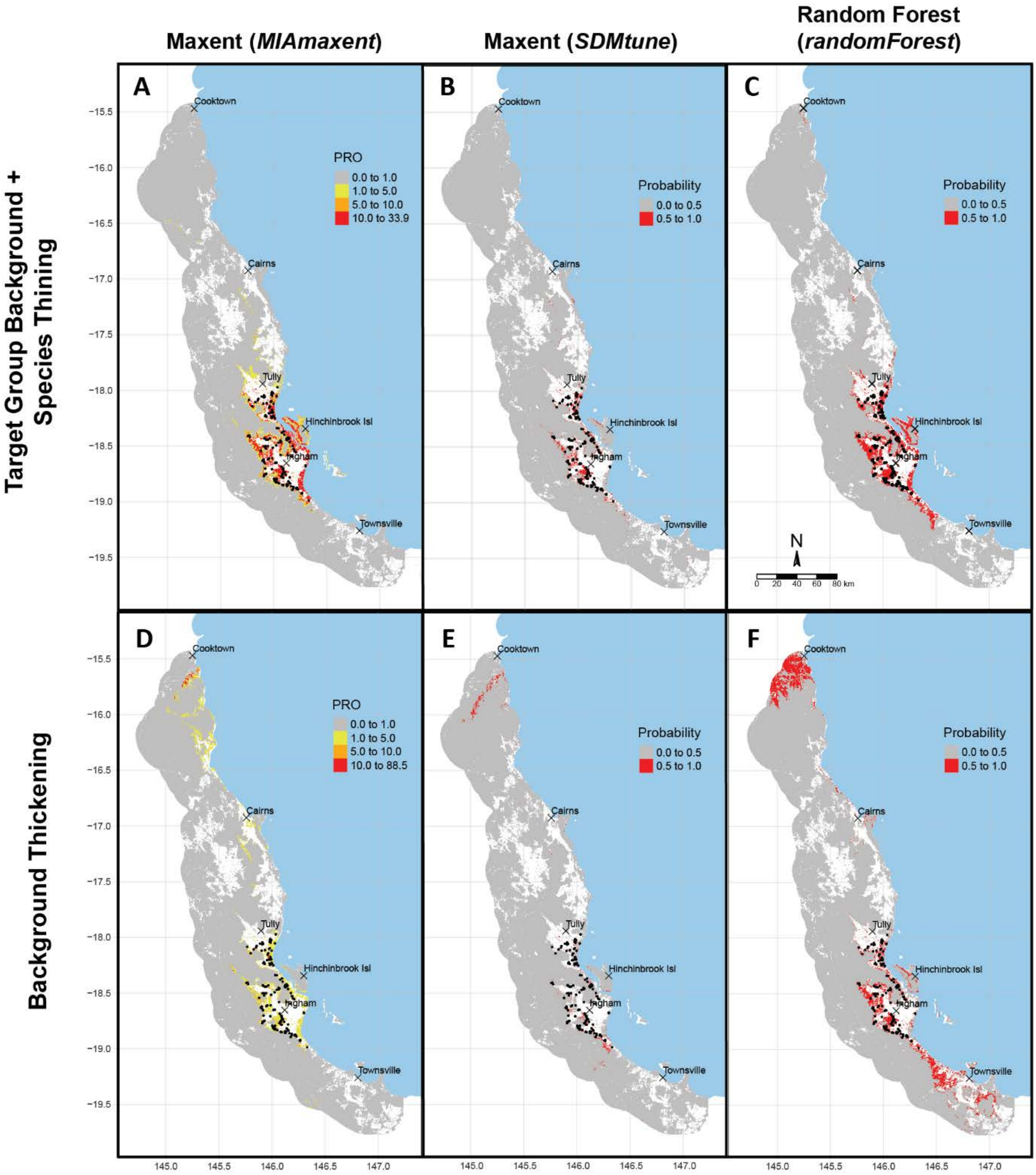

Fig. 2.2 The six models from the combination of three different modelling packages and two bias-correction methods within each. The MIAmaxent models predict suitability via the probability ratio output (PRO), a measure of 'relative suitability of one place versus another' (Vollering *et al.* 2019b). PRO = 1 represents a randomly chosen place with average suitability. In the SDMtune and randomForest models, the habitat suitability is shown as probability of occurrence with a threshold of 0.5 (locations above this threshold are depicted in red). Sighting records are shown as black dots. The white patches represent cleared, non-native vegetation (sugarcane and other crops, cattle grazing land, intensive

pine plantation, and urban areas), or areas outside of the modelled area (the Wet Tropics bioregion). Pale blue shading shows the sea.

2.5.4. Summarising habitat suitability across models

We summarised the findings from the six models to identify areas consistently modelled as suitable regardless of the modelling approach. To achieve this, we produced both a summary map (Fig. 2.3A) and a weighted average map (Fig. 2.3B). Both maps identified similar areas within the core range as suitable habitat for Mahogany Gliders (Fig. 2.3). Additionally, detailed regional summary maps are presented, showing: the suitable habitat supported by four or more of the six models (**Appendix S2-9**), and the weighted average map at a fine scale (**Appendix S2-10**). These detailed maps may be valuable for local stakeholders and conservation managers. The summary map considered all models equally and ignored model accuracy; whereas the weighted average map depicts habitat suitability as a probability, and thus may be particularly useful at a fine scale (**Appendix S2-10**).

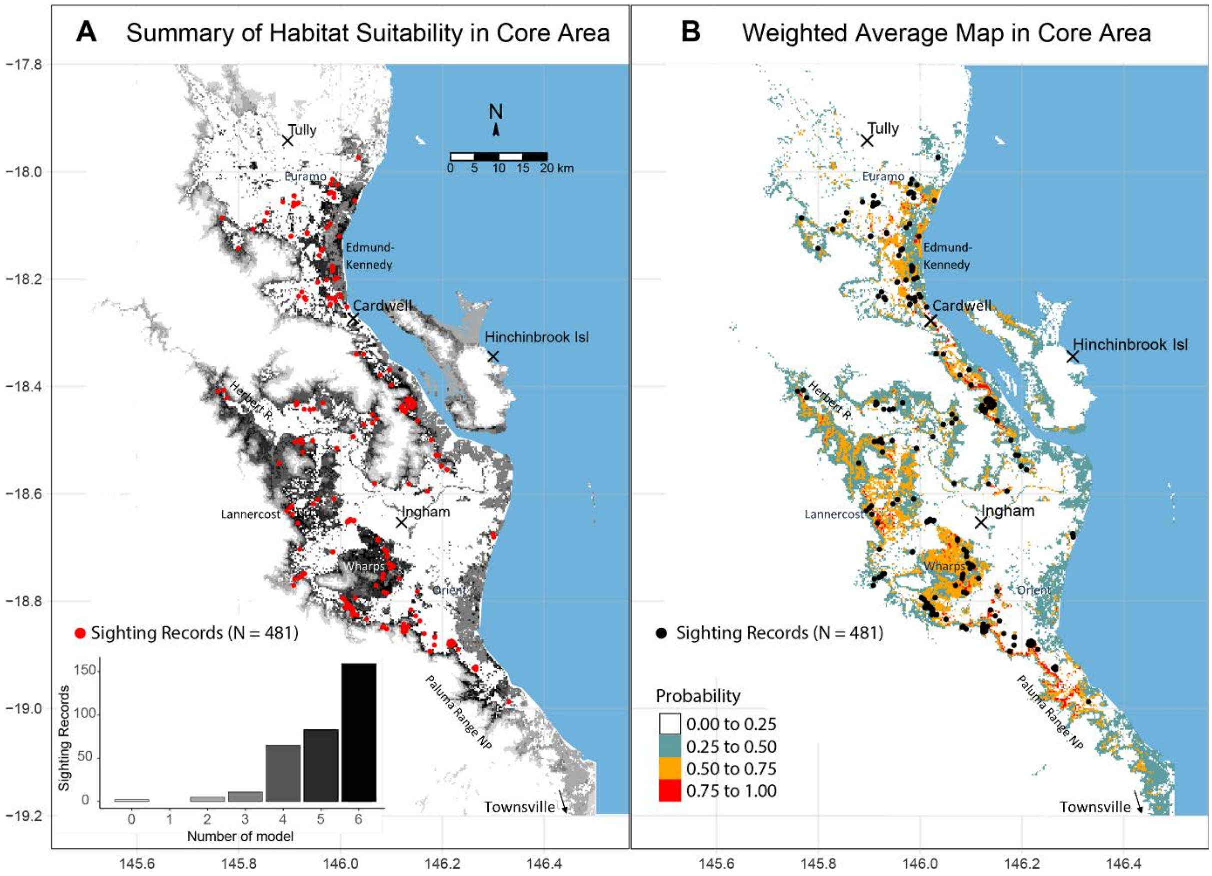

Fig. 2.3 Summary and weighted average maps of predicted habitat suitability from the six models, focused within the known extent of Mahogany Gliders' distribution. **A**Model predictions were classified into suitable (1) or unsuitable (0) habitat using a 0.5 probability threshold for *SDMtune* and *randomForest*, and a PRO of 1 for *MIAmaxent* models. The summary map shows the sum of these values. The grey scale from white (0) to black (6) thus represents the number of models predicting an area as suitable Mahogany Glider habitat. The red dots show all the sighting records, and the bar plot at the bottom left shows the number of sighting records that fall in each of the accumulated model categories. See **Appendix S2-9** for a simplified summary map version that just shows areas predicted by more than three models. **B**For the weighted average map, probability predictions from *MIAmaxent* and *randomForest* models were weighted by AUC, summed and averaged. The weighted average map shows these synthesized probabilities. See **Appendix S2-10** for a more detailed, regional set of weighted average maps for the core distribution of Mahogany Gliders.

2.5.5. Assessing road bias

We examined the effect of road bias on model prediction because the sighting records are clearly biased by observer accessibility (Fig. 2.4). In our exploratory models, Euclidean distance to road was consistently selected as an important variable when included as a predictor. However, when projected, the model prediction with Euclidean distance to road shows very strong, unrealistic, habitat suitability tied to roads (**Appendix S2-11**). Because the road effect is not biologically relevant to the gliders' habitat (i.e., they do not use roads), we removed distance to roads from the set of predictor variables. As shown in the six models we present here (Fig. 2.2 & 3), and explained in detail below, our two bias-correction methods accounted for road bias in observations.

To examine the magnitude of road bias in the sighting records and in our modelling results, we compared the cumulative distributions of distance to roads from sighting records, bias-corrected background points, predicted suitable habitat, and all locations in the Wet Tropics. Figure 4 compares the distributions of Euclidean distance to roads in different datasets, as empirical Cumulative Distribution Function (ECDF). The ECDF shows that sighting records are extremely close to roads compared to the other curves. All except two sighting records are within 2.5 km of a road and their median distance (0 km, quartiles: 0–0.25 km, blue dots) is much smaller than the median distance of all locations in the Wet Tropics to roads (0.94 km, quartiles: 0.31–2.64 km, black dots). The ECDF of the bias-corrected background points we selected to build the SDM models, however, shows less deviation from all locations in the Wet Tropics (Fig. 2.4).

We tested the deviation of sighting records and selected backgrounds to the cumulative distribution of all locations in the Wet Tropics. All deviations are significant ($p < 0.001$), but the magnitude of deviation for the sighting records ($D = 0.49$) is much greater than that of the background points (BT-corrected background points: $D = 0.10$; TGB-corrected background points: $D = 0.16$). The predicted suitable habitats from the models (from the weighted averaged map, with probability > 0.5) also shows significant deviation ($D = 0.13$, $p < 0.001$) (Fig. 2.4), of a magnitude similar to the background points. However, suitable habitat was predicted as far as 12 km from the road and was not constrained to being near roads. These results suggest our bias correction methods sufficiently removed road bias in our modelling.

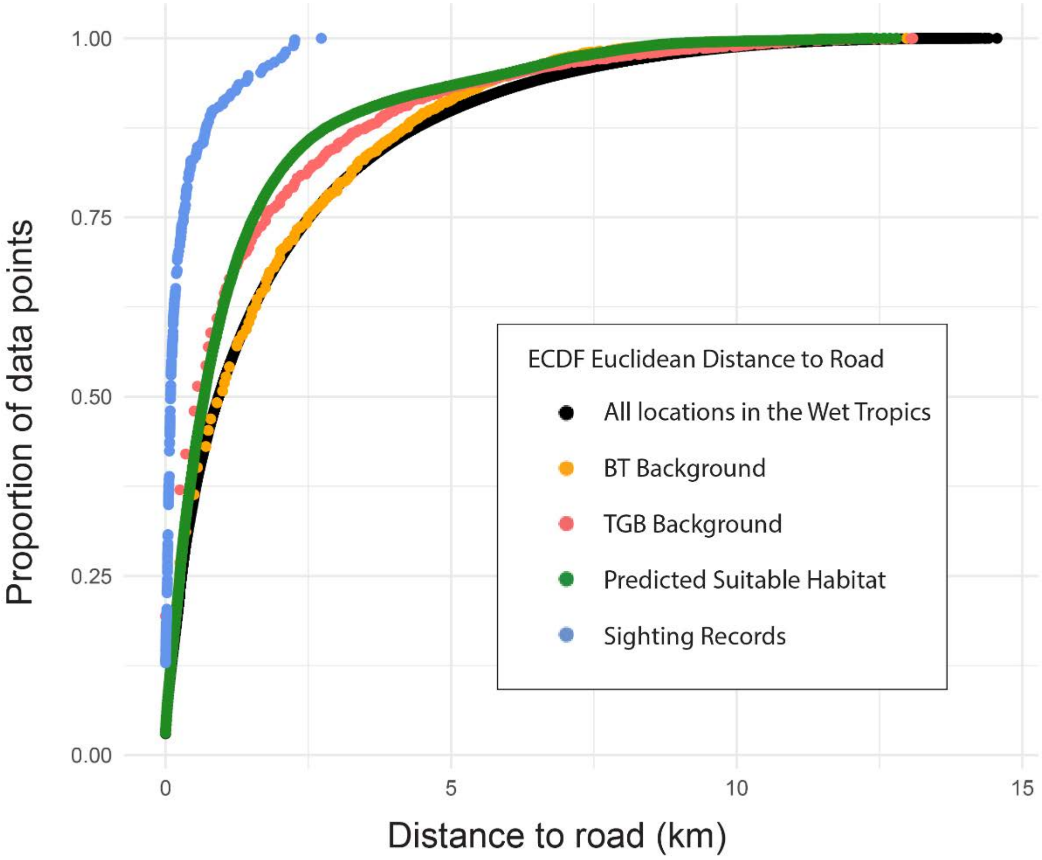

Fig. 2.4 Estimator of empirical Cumulative Distribution Function (ECDF) of the Euclidean distances to roads in five different datasets. Cumulative distribution of distance in BT backgrounds (yellow dots) has the least deviation (D = 0.10) from the control (all locations in the Wet Tropics, black dots). The cumulative distribution of TGB backgrounds (pink dots) and predicted suitable habitats (green dots) are the second (D = 0.13) and third (D = 0.16) most similar to the control, respectively. The cumulative distribution of sighting records (blue dots), in comparison, appears heavily road biased (D = 0.49).

2.6. Discussion

Using all known sighting records and biologically relevant environmental and climatic predictors, we produced species distribution models (SDMs) for the Endangered Mahogany Glider (*Petaurus gracilis*). Elevation, precipitation seasonality, soil, and vegetation type were identified as key predictors of Mahogany Gliders’ distribution (Table 2.2). All models identified suitable habitat in the coastal lowlands in the known extent of Mahogany Gliders, between Paluma and Tully, including many areas of moderate to high suitability habitat with no known sighting records. The models showed that suitable habitat within the known distribution is highly fragmented, and some areas with historical records have since been cleared of native vegetation (Fig. 2.3). Beyond the known distribution, the models also predicted potentially suitable habitat to the south (coastal woodland north of Townsville), east (lowlands of Hinchinbrook Island), and north (particularly several lowland areas in the vicinity of Cairns).

2.6.1. Ecological insights of the selected predictors

The four predictor variables consistently identified as important in the six final models (elevation, precipitation seasonality, soil, and vegetation type) summarise the most suitable habitat for Mahogany Gliders — *Eucalyptus* and *Melaleuca* open woodlands with grassy understory, growing on Hydrosols, in areas below 100 m elevation, and with highly seasonal precipitation. The modelling methodology accounts for correlation between continuous variables (indeed, most of the temperature and precipitation predictors are inter-correlated; **Appendix S2-11**) but is limited in accounting for correlations involving categorical factors. Therefore, the key predictors may not be independent and the biological links between them, and their direct or indirect influence on the species, are worth investigating.

Elevation

The restriction of Mahogany Gliders to low elevations has been discussed in detail previously; for example, Van Dyck *et al.* (1993) noted that all records were found below 90 m in elevation, with most records falling below 20 m. Median elevation thresholds in five of our six models fell below 90 meters. Only the *MIAmaxent* model with BT correction predicted higher median elevation (219 m) (Table 2.2), but it's not clear why this was the case for this one model/correction method combination. It is unlikely that elevation has a direct effect on gliders (e.g., that gliders are physiologically restricted to the hotter lowlands) and the importance of elevation more likely reflects correlations with the other three key predictor variables (distribution of *Eucalyptus* and *Melaleuca* open woodlands with grassy understory; distribution of Hydrosols; highly seasonal precipitation). Diversity in the Wet Tropics bioregion is generally greatest in mid elevation and upland rainforest areas, particularly when considering the endemic species (Uzqueda *et al.* 2020; Leahy *et al.* 2020; Staunton *et al.* 2014), and the Mahogany Glider is an interesting exception.

Precipitation seasonality, soil type, and vegetation type

Precipitation seasonality has been previously identified as an important predictor in BIOCLIM models for Mahogany Gliders (Van Dyck 1993; Jackson and Claridge 1999), with suitable habitat having marked seasonal rainfall and a long dry season (Walsh and Lawler 1981; O'Donnell and Ignizio 2012). Such seasonal variation may limit the growth of unsuitable rainforest habitats, which generally prefer lower precipitation seasonality (Neldner *et al.* 2019). It may also facilitate the formation of Hydrosol soils, which are defined as a group of soils that are seasonally saturated with water for 2–3 months per year (Isbell 2016). Hydrosols *per se* will not be directly impacting arboreal Mahogany Gliders but they promote the development of certain vegetation types, including forests dominated by *Eucalyptus, Corymbia* and *Melaleuca* species in the Wet Tropics (Neldner *et al.* 2019). *Eucalyptus* and *Melaleuca* open woodlands were identified as a key predictor in all models and have been broadly recognised as key habitat for Mahogany Gliders (Jackson 2000; Jackson *et al.* 2011). These vegetation communities provide year-round food sources and den trees (Van Dyck 1993; Jackson 2000). Vegetation type is intuitively thought to be important for habitat suitability of particular arboreal mammals but has not been included as a predictor variable in previous SDMs on gliders or possums (Lindenmayer *et al.* 1991; Jackson and Claridge 1999; Rees *et al.* 2007). Our study shows that it is an important predictor and may reflect the underlying contributions of other less intuitive variables (e.g., precipitation seasonality, soil type).

Fire management

Fire management has been widely recognized as an important factor in maintaining Mahogany Glider habitat, by limiting vegetation thickening (Van Dyck 1993; Jackson 2000; Jackson *et al.* 2011). However, fire frequency (as measured by TERN AusCover 2013) was not selected as an important predictor in our models, possibly because it does not reflect the fine-scale fire patterns of relevance to the gliders. Fire management in Mahogany Glider habitat usually consists of planned burns in the understory, and this fine-scale, below-canopy burning may not be detected by satellite remote sensing that aims to detect wildfire of larger scale and higher intensity. The impact of fire on mammal species has been found to be complicated and dependent on site, context and other factors (Driessen *et al.* 2021). Our modelling did not adequately incorporate the role of fire in habitat suitability, and it requires further investigation.

Removing road bias from models

The sighting records of Mahogany Gliders were strongly biased by observer accessibility — most fall within 100 m of a road and none come from more than 2.5 km from roads (Fig. 2.4). The ECDF curves and the distribution tests showed that road bias was largely accounted for in both the TGB and BT bias correction methods (Fig. 2.4). Predicted suitable habitat occurs up to 12.8 km away from roads, which is as far as any point in Wet Tropics lowland sclerophyll forest is from roads. Although some species, especially some invasive species, use roads to forage and move through the landscape (Brown *et al.* 2006; Rauschert *et al.* 2017; Wysong *et al.* 2020), this is not the case for arboreal Mahogany Gliders, and road bias is driven by observer accessibility. Our results show the importance or testing for road bias in SDM and assessing whether the road is a sensible predictor for the species.

2.6.2. Predicting current suitable habitats for Mahogany Gliders

Our models are an improvement on previous modelling for Mahogany Gliders (Van Dyck 1993; Jackson and Claridge 1999; Jackson *et al.* 2011) because they incorporate more variables, including categorical variables, and have higher spatial resolution (~250 m) and accuracy (AUC of 0.89–0.99). The six models generally predicted similar areas as suitable habitat for Mahogany Gliders within the known distribution area, but the predictions outside the core area varied. Models using the TGB+*spThin* bias correction method were more reflective of the known distribution (but identified many suitable patches that do not contain Mahogany Glider records; see below) and had high prediction accuracy (Fig. 2.2A–C). They would therefore be useful to focus on the fine-scale distribution within the known range limits. In contrast, models using BT bias correction were more likely to identify similar habitats distant from the known distribution; for example, woodlands near Cooktown (Fig. 2.2 D–F). The spatially broader predictions from models with BT bias correction may result from the large geodesic buffer (75.6 km) used in the process (Ștefan 2019; Vollering *et al.* 2019a), potentially resulting in the inclusion of a broader range of backgrounds around the sighting records and thus less conservative models. The positive is that models using BT bias correction could lead to the discovery of unknown populations well outside the currently known range.

The summary map and the weighted average map provide syntheses of our modelling results. There is notable consistency in areas identified as high suitability habitat. These maps, particularly the fine-scale depictions in Appendices 9 and 10, will be useful for identifying the size and connectivity of remnant habitat patches (Jackson and Diggins 2020; Jackson *et al.* 2019), and targeting survey effort to patches with no, or few, records. We found that a large number of predicted suitable habitat patches have no sighting records (Fig. 2.5). Importantly, 266 of these patches (i.e., 55% of all habitat patches without sightings records) are of sufficient size to potentially support a population of Mahogany Gliders (i.e., 0.1–10 Km^2; Fig. 2.5). These patches are a priority for future survey efforts, working from largest to smallest patch size. Our results also showed that 156 out of the total 481 sightings of Mahogany Gliders (i.e., ~30% of all sightings) are now situated in deforested areas; in most cases cleared for sugarcane or cattle grazing. This highlights the need to quantify and monitor habitat loss and ensure high suitability habitat on private land is adequately mapped and protected.

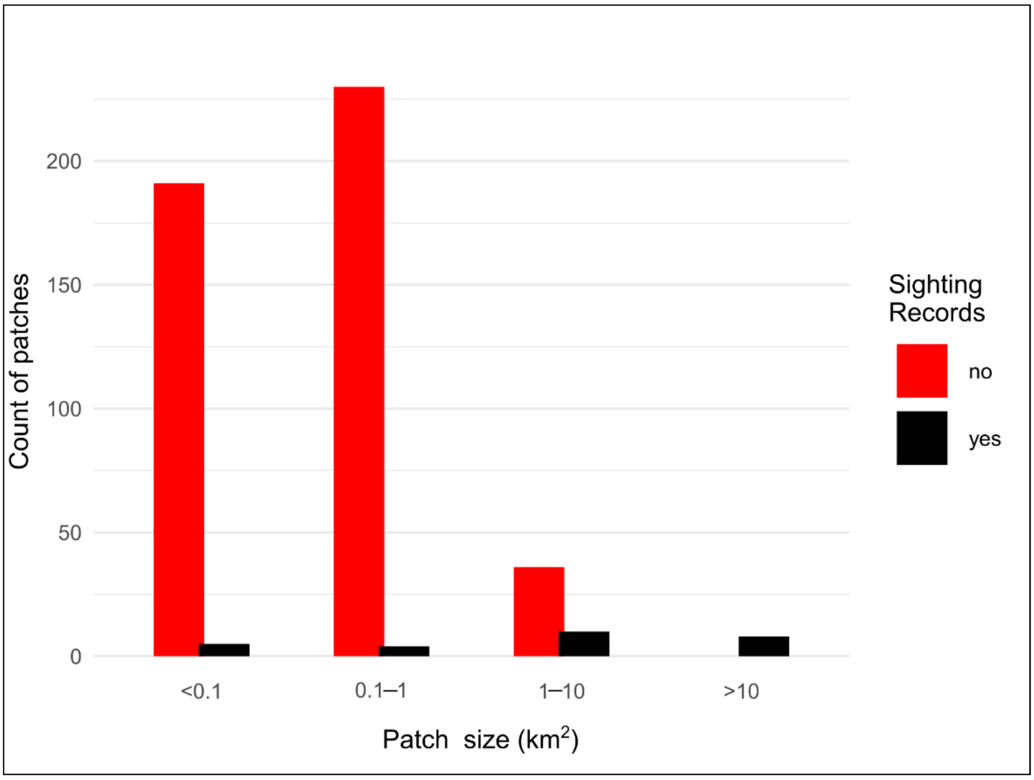

Fig. 2.5 Histogram showing the number of patches within patch size bins, split by patches with Mahogany Glider sighting records (black) and without a record (red). The minimum

estimated home range of a male Mahogany Glider is about 0.1 km^2 (11 ha) (Jackson 2000), so we consider patch sizes < 0.1 km^2 unlikely to support a population.

The synthesized maps allow broad assessment of the distribution and connectivity of the modelled habitat. Most of the larger areas of suitable habitat are in the Ingham region and north to Cardwell (Fig. 2.3; **Appendix S2-10**). This includes the large patch at Wharps Holding (**Appendix S2-10**C) and the fairly continuous large area of habitat from Lannercost State Forest to the Herbert River valley (**Appendix S2-10**B, C). Additionally, an extensive ribbon of predicted high suitability habitat runs along the base of the ranges through much of the species' distribution, with the continuous strip of high suitability habitat along the base of the Paluma Range of particular note (**Appendix S2-10**D). This ribbon of habitat connects with many of the core habitat patches on the coastal flats, particularly in the southern two-thirds of the range. However, many patches, particularly in the north of the range (Kennedy to Tully valley; **Appendix S2-10**A) and in the Ingham region (**Appendix S2-10**C) are disjunct and isolated.

2.6.3. Management recommendations

1. Survey areas of high suitability habitat within the known range, particularly those without sightings records (Fig. 2.5), to identify all remnant populations within the core distribution of the species. Priorities include: large areas west of Ingham (Warps Holding, and Lannercost State Forest; and north along the base of the range up the Herbert River valley); coastal forests east of the Bruce Highway between Big Crystal Creek and Ingham, and between Edmund Kennedy and Tully; and the Big Crystal Creek area in the south (**Appendix S2-10**).
2. Survey areas predicted as moderate to high habitat suitability habitat outside of the known range to resolve the true distribution of the Mahogany Glider. Priorities are: Hinchinbrook Island; lowland woodlands in the Cairns–Yarrabah–Gordonvale areas,

and south of Cooktown; and the Clemant State Forest area at the southern end of Paluma Range (Figs 3, 4; **Appendix S2-9**, **Appendix S2-10**).

3. Identify key populations across the range to establish long-term camera trap monitoring, including in the north (e.g., Edmund Kennedy–Euramo area), centre (e.g., Cardwell Range area), and south (e.g., Paluma Range area) of the range.

2.6.4. Future directions

Attempts have been made to identify key populations of Mahogany Gliders and map corridors between them (Jackson *et al.* 2019) The results gained herein could be used to refine landscape assessments (Tarabon *et al.* 2019) and perform connectivity analyses (Esselman and Allan 2011; Torabian *et al.* 2021) based on the modelled moderate and high suitability patches and corridors (e.g., using the weighted average mapping). Genetic analyses could also be used to test connectivity, focussing on areas with patches of varied size and connectivity.

An updated SDM for Mahogany Gliders is recommended once more recent sighting records accumulate and more advanced spatial data is available. Spatial data that could better refine the models includes additional fine-scale fire layers (Driessen *et al.* 2021), mapping of forest age or structure, to capture important factors such as abundance of tree hollows (Linnell *et al.* 2017), mapping of the impact of recent extreme weather events, in this case cyclones (Bateman *et al.* 2012), and mapping of thin lines of roadside vegetation that may act as species dispersal or movement corridors (Vasudev *et al.* 2015). Additionally, the SDM could be used to model the potential effect of climate change on Mahogany Gliders, as done for other possums and gliders (e.g., Handayani *et al.* 2019), but noting that post-model refining from expert knowledge (e.g., micro-refugia, barriers) (Reside *et al.* 2019) would be required for this species.

2.7. Ethics and permits

No ethics or permits are required in this study.

2.8. Conflicts of interest

The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

2.9. Data availability statement

The data, models, and analysis scripts used in this study are available upon request. A comprehensive record of the species is continuously updated in the WildNet database of Queensland (https://www.qld.gov.au/environment/plants-animals/species-information/wildnet), thanks to the dedicated efforts of the Mahogany Glider Recovery Team.

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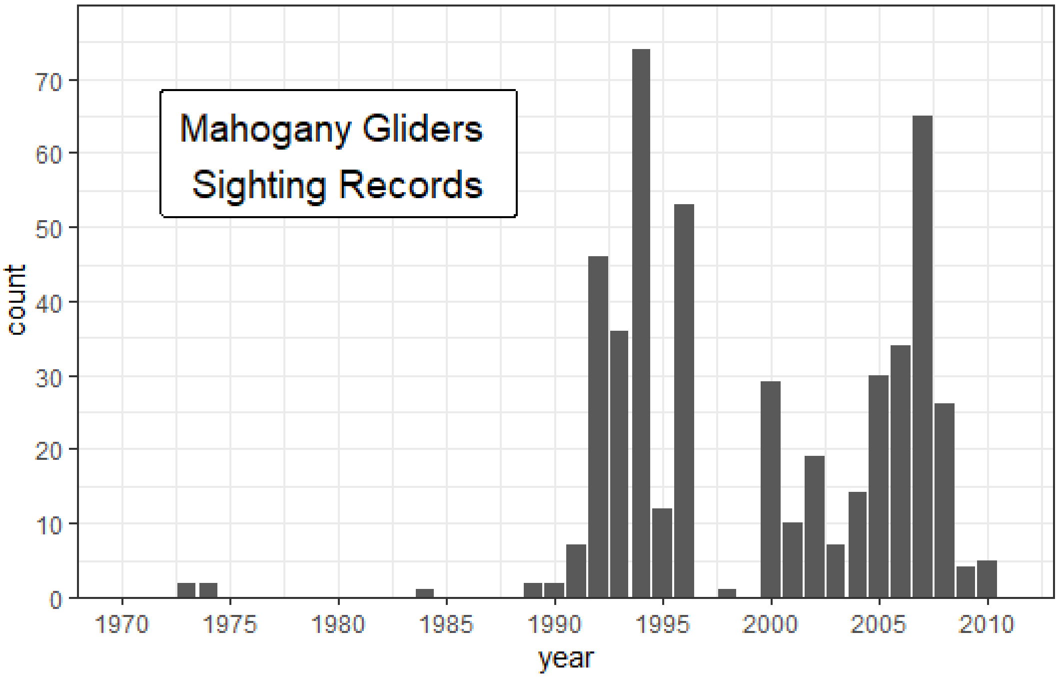
Appendices

Appendix S2-1 Temporal distribution of the sighting records used in the Species Distribution Models. More than 98% of sightings were recorded between 1990 and 2010.



Appendix S2-2 Year coverage, units and the source of the predictor variables (spatial data) used in the SDM models.

Predictor variables	Year coverage	Units	Source
Climatic variables			
Bio_01: Annual Mean Temperature	1996–2015	°C	Storlie *et al.* 2013
Bio_02: Mean Diurnal Range	1996–2015	°C	Storlie *et al.* 2013
Bio_03: Isothermality	1996–2015	°C	Storlie *et al.* 2013
Bio_04: Temperature Seasonality	1996–2015	°C	Storlie *et al.* 2013
Bio_05: Max Temperature of Warmest Month	1996–2015	°C	Storlie *et al.* 2013
Bio_06: Min Temperature of Coldest Month	1996–2015	°C	Storlie *et al.* 2013
Bio_07: Temperature Annual Range	1996–2015	°C	Storlie *et al.* 2013

Bio_08: Mean Temperature of Wettest Quarter	1996–2015	°C	Storlie *et al.* 2013
Bio_09: Mean Temperature of Driest Quarter	1996–2015	°C	Storlie *et al.* 2013
Bio_10: Mean Temperature of Warmest Quarter	1996–2015	°C	Storlie *et al.* 2013
Bio_11: Mean Temperature of Coldest Quarter	1996–2015	°C	Storlie *et al.* 2013
Bio_12: Annual Precipitation	1996–2015	mm	Storlie *et al.* 2013
Bio_13: Precipitation of Wettest Month	1996–2015	mm	Storlie *et al.* 2013
Bio_14: Precipitation of Driest Month	1996–2015	mm	Storlie *et al.* 2013
Bio_15: Precipitation Seasonality	1996–2015	mm	Storlie *et al.* 2013
Bio_16: Precipitation of Wettest Quarter	1996–2015	mm	Storlie *et al.* 2013
Bio_17: Precipitation of Driest Quarter	1996–2015	mm	Storlie *et al.* 2013
Bio_18: Precipitation of Warmest Quarter	1996–2015	mm	Storlie *et al.* 2013
Bio_19: Precipitation of Coldest Quarter	1996–2015	mm	Storlie *et al.* 2013
Geographic variables			
Elevation	2007	meters	Department of Natural Resources, Mines and Energy, 2005
Aspect	2007	degrees	
Slope	2007	degrees	
Distance to major water ways	2016	meters	(Queensland Government 2017)
Environmental variables			
Fire Frequency AVHRR	1997–2011	0–7 burnt times	(Maier and Russell-Smith 2012)
Soil type	2011	14 soil types	Australian Collaborative Land Evaluation Program, 2014
Vegetation	pre-1750, 2006	43 vegetation types*	Department of Environment and Science, 2012
Land use	1999, 2010, 2019	6 land use types	Department of Environment and Science, 2019
Forest coverage	1988–2018	0 (no coverage) –2 (dense coverage)	Department of Industry, 2019

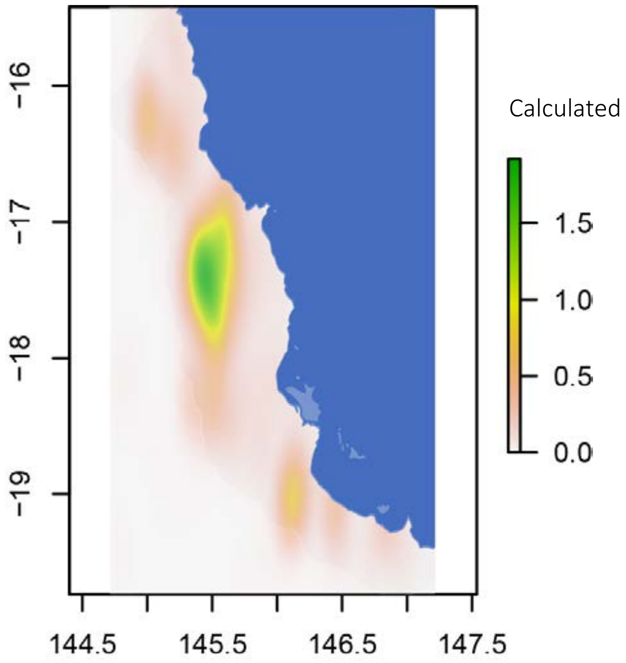
*Only the vegetation types that exist in the Wet Tropics

Appendix S2-3 Distribution of the sighting records (white crossed circles) before and after the Species Thinning process (Aiello-Lammens *et al.* 2015). Sighting records were strongly clustered in some area before the thinning process.

Appendix S2-4 Arboreal species native to the Wet Tropics that were used to construct the kernel map of the Target Group Background (TGB) bias grid.

	Scientific name	Common name
1	*Acrobates pygmaeus*	Feathertail Glider
2	*Antechinus adustus*	Rusty Antechinus
3	*Antechinus flavipes rubeculus*	Yellow-Footed Antechinus (North-East Queensland)
4	*Antechinus godmani*	Atherton Antechinus
5	*Cercartetus caudatus*	Long-Tailed Pygmy-Possum
6	*Dactylopsila trivirgata*	Striped Possum
7	*Dendrolagus bennettianus*	Bennett's Tree-Kangaroo
8	*Dendrolagus lumholtzi*	Lumholtz's Tree-Kangaroo
9	*Hemibelideus lemuroides*	Lemuroid Ringtail Possum
10	*Melomys burtoni*	Grassland Melomys
11	*Melomys cervinipes*	Fawn-Footed Melomys
12	*Mesembriomys gouldii*	Black-Footed Tree-Rat
13	*Petauroides volans*	Greater Glider
14	*Petauroides volans minor*	Northern Greater Glider
15	*Petaurus australis*	Yellow-Bellied Glider (Northern Subspecies)
16	*Petaurus breviceps*	Sugar Glider
17	*Petaurus gracilis*	Mahogany Glider
18	*Petaurus norfolcensis*	Squirrel Glider
19	*Phascogale tapoatafa tapoatafa*	Brush-Tailed Phascogale
20	*Phascolarctos cinereus*	Koala
21	*Pseudocheirus peregrinus*	Common Ringtail Possum
22	*Pseudochirops archeri*	Green Ringtail Possum
23	*Pseudochirulus cinereus*	Daintree River Ringtail Possum
24	*Pseudochirulus herbertensis*	Herbert River Ringtail Possum
25	*Trichosurus vulpecula*	Common Brushtail Possum
26	*Uromys caudimaculatus*	Giant White-Tailed Rat
27	*Uromys hadrourus*	Masked White-Tailed Rat

Appendix S2-5 The kernel density map, also known as the TGB bias grid, (Ripley *et al.* 2013) using observations of 27 arboreal mammals native to the Wet Tropics. The kernel density map serves as a reference of sampling effort in the TGB bias correction method (Phillips *et al.* 2009).



Appendix S2-6 Predictor subsets of the six best-tuned models. Predictors selected by more than three models are marked in bold. The predictor that contributed the most in each model is highlighted in yellow. Attributes of climatic predictors are listed in Supplementary Table 2.1. Measurement of predictor contributions differs across R packages. The values are expressed differently and unitless according to the modelling algorithm: MIAmaxent uses Dsq, fraction of deviation explained; SDMtune uses permutation importance, the same as MaxEnt (Phillips and Dudík 2008; Phillips *et al.* 2017). *radomForest* uses Mean Decreased Accuracy, representing the decreased classification accuracy when the predictor is removed.

R package/ Bias correction	**MIAmaxent TGB**	**MIAmaxent BT**	**SDMtune TGB**	**SDMtune BT**	**randomForest TGB**	**randomForest BT**
Predictors	5	8	13	13	11	7
Bio_01					35.3	42.4
Bio_02						
Bio_03			1.1			
Bio_04	0.044		5.2	0.8		
Bio_05				6		
Bio_06	0.157				35.5	56.2
Bio_07		0.026				
Bio_08					40.1	41.8
Bio_09						
Bio_10					40.1	
Bio_11					31.2	43.3
Bio_12					42	
Bio_13					38	
Bio_14					41.5	
Bio_15	0.023	0.012	2.8	9.8		
Bio_16			1.7	1.8		
Bio_17					43.2	
Bio_18						65.5
Bio_19						
Elevation	0.222	0.101	75.8	64.8	46.3	55
Aspect			0.8	0.9		
Slope		0.02	2.1	1.8		
Fire Frequency		0.008	0.8	0.9		
Soil type	0.159	0.054	2.8	4.4	46.8	
Distance to major water ways		0.004	0.9	2.1		
Vegetation type		0.034	3.1	2		64.5
Land use			0.8	0.9		
Forest coverage			2.1	3.8		
Evaluation unit	Dsq: fraction of deviance explained	Dsq: fraction of deviance explained	permutation importance	permutation importance	Mean Decreased Accuracy	Mean Decreased Accuracy

Appendix S2-7 Vegetation and soil types identified as important in the models. Vegetation code is derived from the Department of Environment Australia (Present Major Vegetation Subgroups - NVIS Version 4.1, 2012). Soil code is derived from Australian Collaborative Land Evaluation Program, endorsed through the National Committee on Soil and Terrain. The vegetation subgroups Freshwater and Sedgelands etc were chosen by some models, likely resulting from sighting records that are close to creeks and swamps.

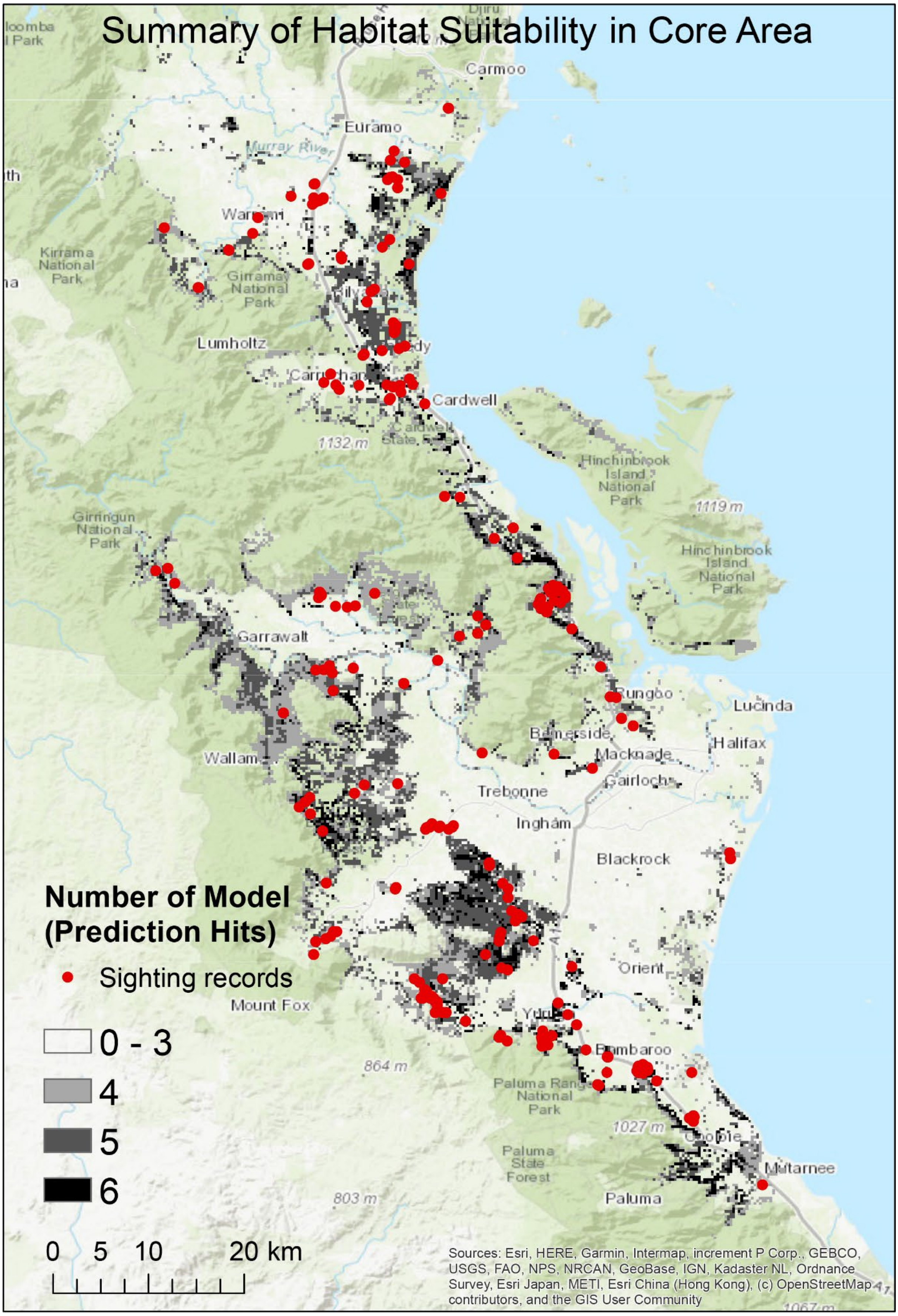
Vegetation code	Selected times	Description
5	2	Eucalyptus open forests with a grassy understory
9	4	Eucalyptus woodlands with a tussock grass understory
14	1	Other Acacia forests and woodlands
15	4	Melaleuca open forests and woodlands
26	1	Casuarina and Allocasuarina forests and woodlands
44	2	Freshwater, dams, lakes, lagoons or aquatic plants
63	1	Sedgelands, rushs or reeds

Soil code	Selected times	Description
1	0	Anthroposols
2	0	Calcarosols
3	1	Chromosols
4	0	Dermosols
5	0	Ferrosols
6	5	Hydrosols
7	1	Kandosols
8	0	Kurosols
9	0	Organosols
10	0	Podosols
11	0	Rudosols
12	0	Sodosols
13	0	Tenosols
14	0	Vertosols

Appendix S2-8 Schoener's D tests of similarity between the six predictions. Schoener's D calculated the overlapping percentage between two raster layers. The tests were conducted using R package *ENMTools* (Warren *et al.* 2010). The background color summarizes the bias-correction method used in each model.

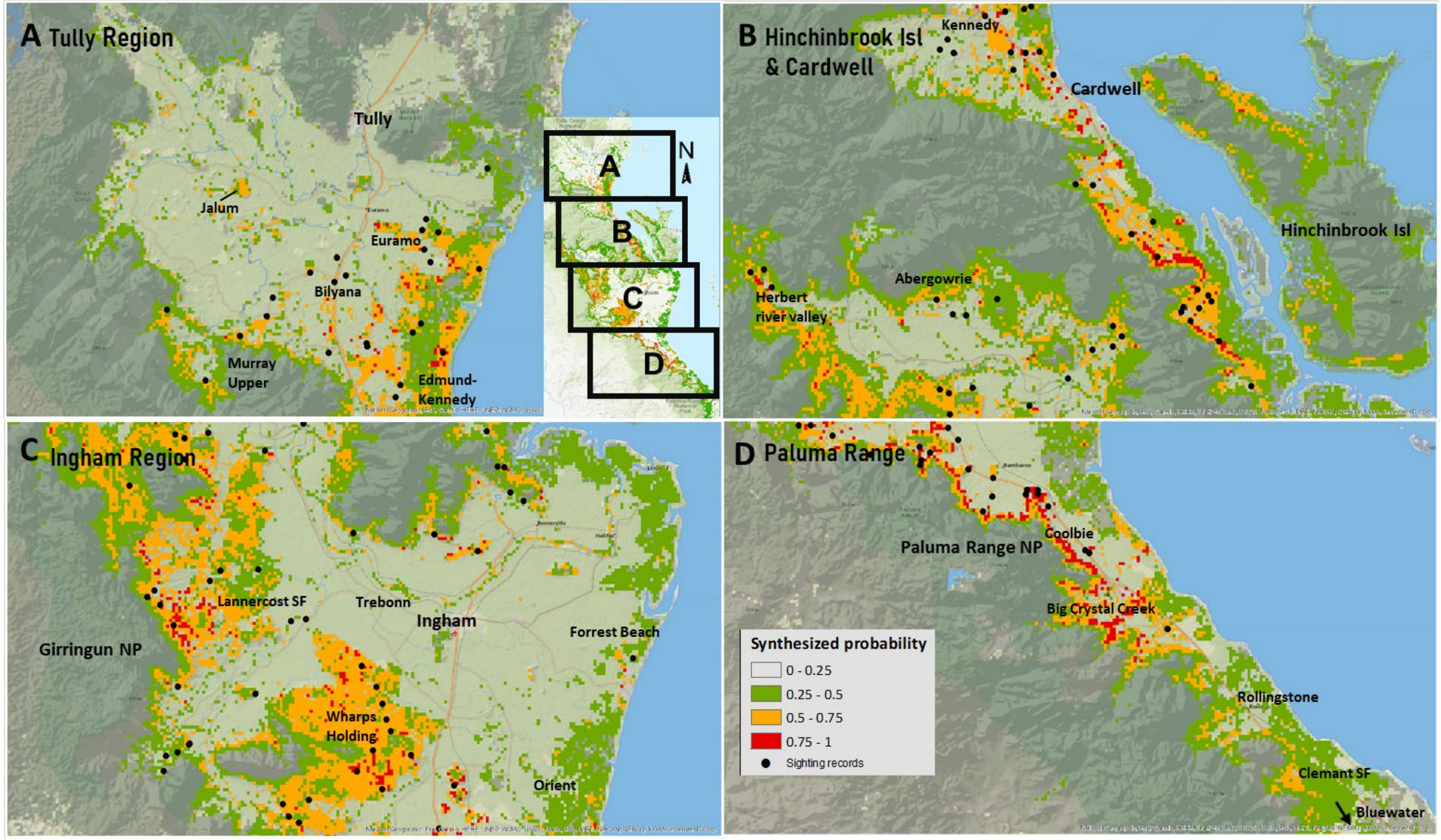
	***SDMtune* (BT)**	***MIAmaxent* (BT)**	***randomForest* (BT)**	***SDMtune* (TGB)**	***MIAmaxent* (TGB)**	***randomForest* (TGB)**
***SDMtune* (BT)**	1.00	0.12	0.07	0.24	0.08	0.09
***MIAmaxent* (BT)**		1.00	0.37	0.26	0.54	0.61
***randomForest* (BT)**			1.00	0.16	0.40	0.44
***SDMtune* (TGB)**				1.00	0.23	0.28
***MIAmaxent* (TGB)**					1.00	0.73
***randomForest* (TGB)**						1.00

Appendix S2-9 Summary of predicted habitat suitability supported by four or more of the six models, for the known extent of the Mahogany Glider distribution. All six model predictions were classified into suitable/unsuitable habitat using a 0.5 probability threshold (or PRO=1 for MIAmaxent models). The summary model shows the sum of these values that are ≥ 4. Colours from grey (4) to black (6) represent the number of models predicting an area as suitable habitat of Mahogany Glider. The red dots are all the sighting records.

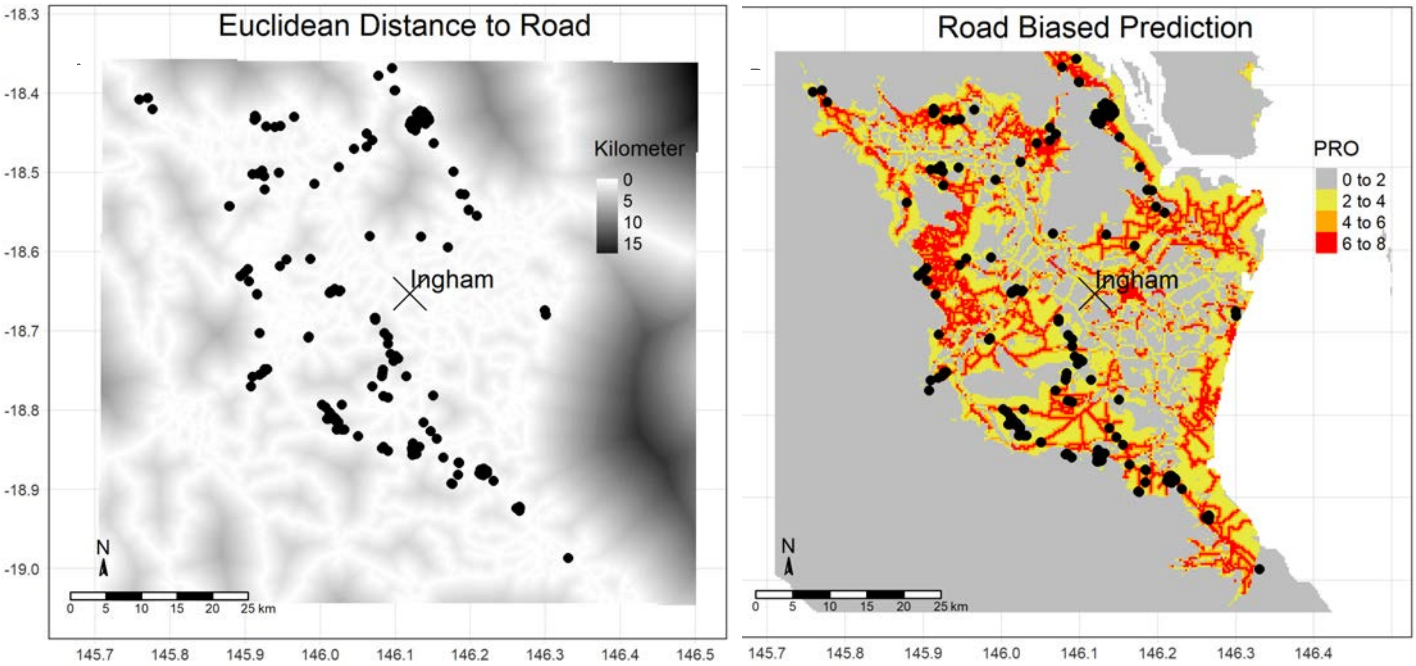


Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

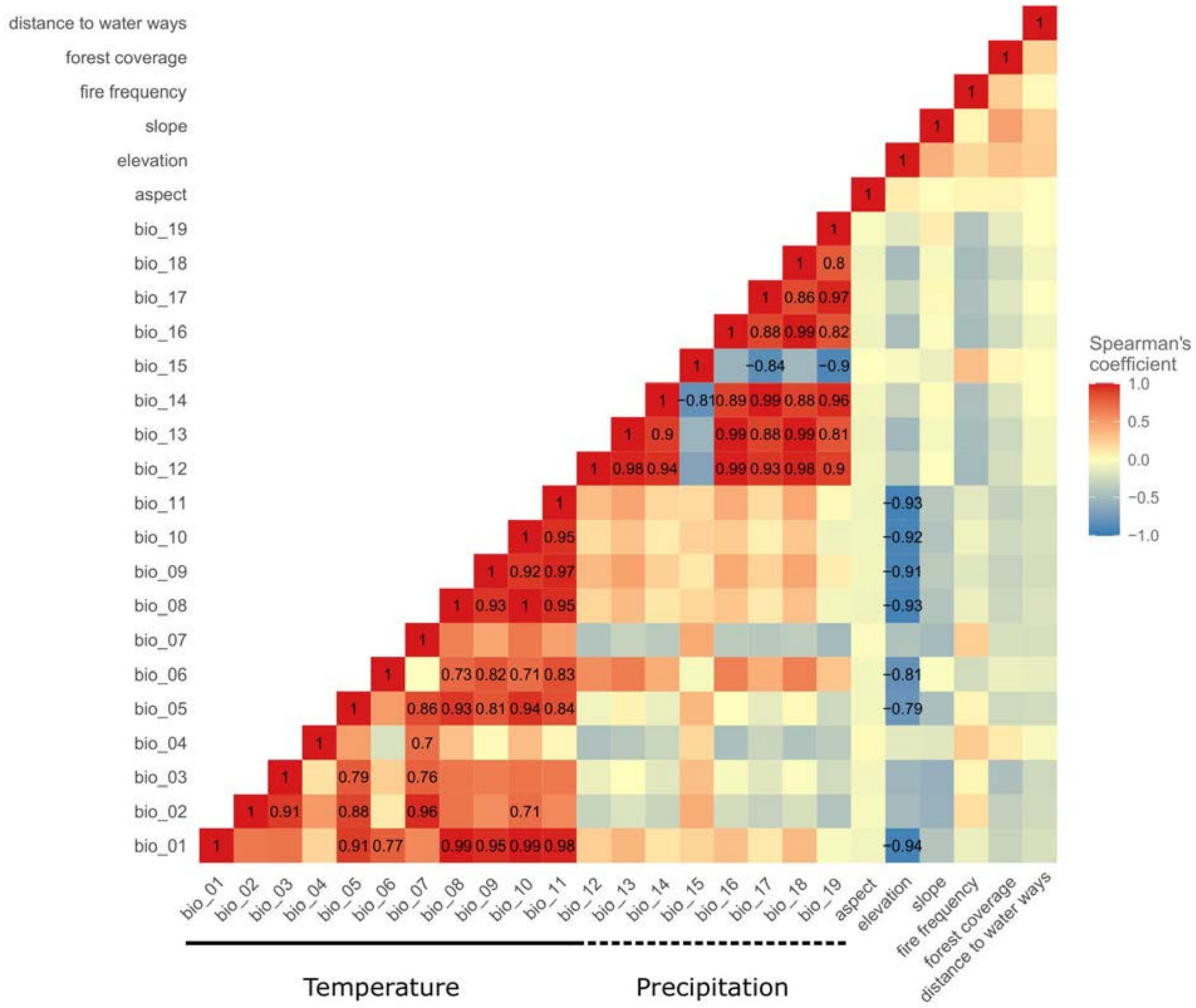
Appendix S2-10 Weighted average maps zoomed for the known range of Mahogany Gliders: (A) Tully Region, (B) Hinchinbrook Island and Cardwell, (C) Ingham Region, and (D) Paluma Range. Coloured pixels represent the synthesized probability (averaged and weighted from the SDMtune and randomForest models). Black dots show the sighting records of Mahogany Gliders. The inset shows how the maps fit together.



Appendix S2-11 (A) A map of the Ingham region shaded by Euclidean distance to roads. (B) Model prediction biased by including Euclidean distance to road as a predictor. The maps show the Ingham region as an example of the road effect. The demonstrated model prediction (B) was built using the *MIAmaxent* R package with TGB bias correction. The prediction with BT correction was similar. Incorporation of distance to roads clearly biased the model.



Appendix S2-12 Spearman's coefficient of the continuous predictors in the SDM models. Categorical predictors were not included. The plot and the correlations were made using the R package *SDMtune.*



Chapter 3.

Estimating the abundance of an endangered arboreal marsupial using camera traps and an integrated species distribution model

Yiyin Chang, Chieh Lin, Conrad J. Hoskin

This chapter has been submitted to *Wildlife Research* and has been reviewed.

Manuscript ID: WR23158 (PDF proof of submission attached)

3.1. Abstract

Population size is critical for species management and planning, particularly for threatened species like the Mahogany Glider, which is endemic to the Wet Tropics of northeastern Australia. Despite its Endangered status, a robust abundance estimate has not been established. We conducted the first extensive arboreal camera trapping surveys for the species, aiming to provide a scientifically rigorous abundance estimate using a Baysian integrated species distribution model (Koshkina *et al.* 2017; Fidino 2021). Survey results revealed substantial variation in glider density across its range. Based on the integrated model, which combines presence-only and presence-absence data, we estimated median abundance at 6,030, 4,834, and 2,820 individuals for home ranges of 9, 16, and 25 ha, respectively. These estimates narrow the previously hypothesized range of 1,200 to 20,000 individuals and provide a critical baseline for future conservation planning. Simulation tests confirmed that the model is robust to camera placement and small sample sizes, although the results were scale dependent. This scale dependency can be mitigated by accounting for home range variations. Our findings underscore the importance of ongoing monitoring and the use of advanced modelling tools to inform effective wildlife management.

3.2. Key words

Mahogany Glider, threatened species, abundance estimates, integrated species distribution model, camera trapping survey, conservation

3.3. Introduction

Estimating the abundance of rare and cryptic species presents significant challenges. Because it is impractical to count every individual, abundance estimates must be derived from sampling, which requires the use of statistical models (Bonar *et al.* 2011). However, sampling inevitably introduces bias and errors, and models are based on assumptions that may not always hold true. These issues are further magnified when dealing with species of low density, as biases and errors become more pronounced, affecting the representativeness of the surveyed data and substantially increasing the required survey effort (e.g., Bonar *et al.* 2011; Linden *et al.* 2017; Burns *et al.* 2019). Consequently, trade-offs must be made between minimizing costs and ensuring data quality (Bailey *et al.* 2007; Jones 2011).

To address these challenges, occupancy modelling, which estimates the probability that a species occupies or uses a sample unit during a specified time, has been developed as an alternative to directly measuring species abundance (MacKenzie and Nichols 2004; Bailey *et al.* 2014). Occupancy models operate under key assumptions, such as constant detection probability across sites, stable occupancy status during the survey period (geographical closure), and the need for repeated sampling to increase precision. Despite these assumptions, models like N-mixture and Royle-Nichols can estimate animal density and abundance from presence-absence data in camera trap surveys, even with imperfect detection and without individual identification (Royle 2004; Royle *et al.* 2005; Nakashima 2020).

The integrated species distribution model (hereafter referred to as the "integrated model") enhances abundance estimates by combining sighting records with repeated presence-absence surveys and spatial data, allowing predictions across larger spatial scales (Koshkina *et al.* 2017). This model is particularly valuable in scenarios where survey coverage is limited, or animal detectability is low (Koshkina *et al.* 2017), making it a powerful tool for assessing rare and threatened species. Fidino (2021) further improved the model's performance by developing it into Bayesian version. Using an inhomogeneous Poisson point process, the integrated model links species distribution to occupancy, accounting for imperfect detections, habitat heterogeneity, and correlated environmental covariates, while remaining flexible across different spatial resolutions (Koshkina *et al.* 2017). While the model assumes no spatial correlation in species presence and requires careful selection of environmental covariates, it has proven effective for estimating abundance in low-density species. For instance, the model successfully estimates the abundance of Yellow-bellied Gliders (*Petaurus australis*) in southeastern Australia (Koshkina *et al.* 2017), large predators in New York State (Twining *et al.* 2024), Baird’s Tapir (*Tapirus bairdii*) in Central America (Schank *et al.* 2017; Schank *et al.* 2019). Additionally, it has also been applied to assess human-wildlife conflicts in urban environment (Fidino *et al.* 2022).

The Mahogany Glider (*Petaurus gracilis*) is a medium-sized gliding marsupial endemic to the Wet Tropics of northeast Australia. It is confined to lowland sclerophyll forests characterized by *Eucalyptus* and *Melaleuca* trees with a grassy understory and pronounced seasonal rainfall (Jackson and Claridge 1999; Chang *et al.* 2022). The glider’s habitat requires diverse tree species to provide essential nectar for foraging and tree hollows for nesting (Van Dyck 1993; Jackson 1998). Mahogany Gliders are reported to be socially monogamous with home ranges of 6–10 ha in fragmented habitats and 19–24 ha in continuous habitats (Jackson 2000). Listed as Endangered under Australia’s Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act, Threatened Species Scientific Committee 2023), the species has suffered from extensive deforestation due to cattle grazing, sugarcane farming, and forestry activities (Jackson *et al.* 2011). In response, a National Recovery Plan and the Mahogany Glider Recovery Team have been established to coordinate conservation efforts aimed at protecting the species and restoring its habitat (Mahogany Glider Recovery Team and Queensland Parks and Wildlife Service 2001; Parson and Latch 2006; Jackson and Diggins 2020).

Conservation efforts to date have focused on collaborating with landowners to maintain and restore habitat, conducting revegetation, and installing glider poles to facilitate road crossings (Asari *et al.* 2010). However, a key gap remains in accurately estimating the census population size across the species' range and developing a long-term monitoring plan. A robust population estimate is essential for assessing population status and tracking trends over time. Based on a capture-recapture study at two sites, the Mahogany Glider's density was estimated at 0.16 individuals per hectare in fragmented habitat and 0.24 in continuous habitat (Jackson 2000). Using these densities, simple extrapolation has suggested a population of 10,000 to 14,000 individuals across the species' known range (Burbidge *et al.* 2014). However, a hypothesis suggesting only 1,200–2,000 remaining individuals, based on unpublished genetic data, has been widely circulated despite lacking scientific foundation (Burbidge *et al.* 2014). The uncertainty around population size has hindered assessments of species decline, including the significant impacts of Cyclone Yasi in 2011 (Starbridge 2012; Holloway 2013).

In this study, we applied the integrated model to estimate the abundance of the Mahogany Glider across its known range, providing a robust baseline for the species' population size. We also assess the potential uncertainty of these estimates by testing the effects of camera placement, sample size, and varying home range sizes. Our camera trapping survey strategies and abundance estimates will serve as a solid foundation for the long-term monitoring of this threatened species.

3.4. Methods

3.4.1. Study sites and timing of surveys

Between 2020 and 2022, camera trapping surveys were conducted in the lowland woodland of the central and southern Wet Tropics bioregion in north-east Australia. Survey locations were selected based on the habitat suitability map (Chang *et al.* 2022) with a minimum criterion of 50% habitat suitability, along with stakeholder consultations. Two camera trapping designs were employed: transects of cameras at eight sites (South Mission Beach, Hinchinbrook Island, Abergowrie, Long-Pocket, Coolbie, Mutarnee, Balgal Beach, Clement State Forest) to determine the presence and absence of Mahogany Gliders, and a grid camera trapping design at four sites, either known for high glider density (Allendale, Bambaroo) or subject to historic or ongoing survey efforts (Muller's Creek, Ollera Creek) (**Fig. 3.1**). The details of these two designs are outlined below. Most surveys were carried out during the dry season, primarily from May to November, due to the swampy and inaccessible nature of the Mahogany Glider habitats during the wet season. The dry season is also the flowering season of several *Eucalyptus* and *Melaleuca* species, which are essential components of the glider's diet.

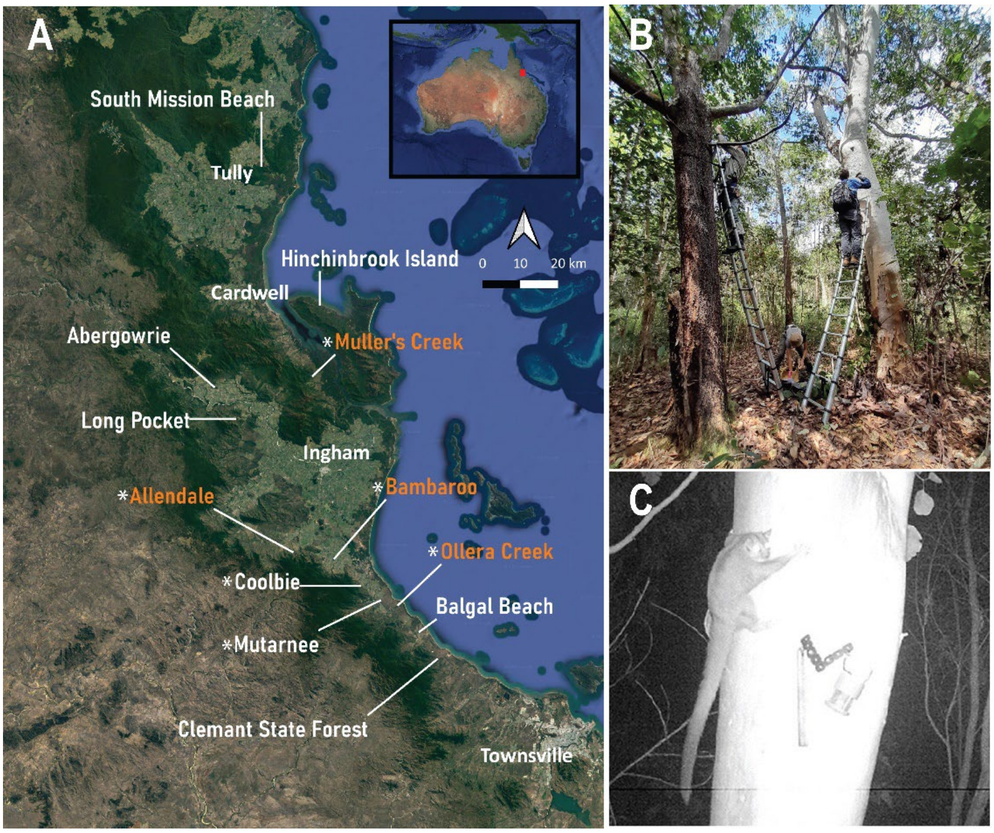


Fig. 3.1 Survey sites and methods. (A) Transect (white) and grid (orange) camera trapping surveys across the Wet Tropics. The asterisks indicate sites where Mahogany Gliders were detected. (B) Installation process of brackets onto the tree pair (one for bait holder, one for camera) for repeat monitoring. Photo credit: Taruna Venkat. (C) A Mahogany Glider captured on a camera trap investigating the bait holder at Muller's Creek. The 21 cm wooden bracket served as a scale bar.

3.4.2. Presence-absence (PA) surveys

Both transect and grid designs were implemented to collect presence-absence data for the integrated model. Each site was monitored using 10 to 20 infrared cameras, with cameras positioned at least 120-150 meters apart, depending on the survey design. The duration of monitoring ranged from 15 to 89 days in transect surveys and 32 to 45 days in grid surveys (Table 3.1).

For transect surveys, camera locations were based on a habitat suitability map (Chang *et al.* 2022), Google Earth satellite imagery, and site accessibility, with exact placement adjusted for habitat conditions and suitable trees. For grid surveys, a grid design was used with a 150-meter spacing between cameras, created using ArcGIS, and a buffer of 75 meters to account for glider home ranges in fragmented habitats (Jackson 2000). Grid sites had 20 cameras deployed for at least four weeks (Kays *et al.* 2020).

At each camera location, a pair of straight-trunked trees spacing 2 to 4 meters apart was selected. One tree was used to mount the bait holder, while the camera was securely fastened to the other. To enhance detectability, a mixture of oats, honey, and peanut butter was used as bait in custom-made PVC and metal bait holders. This setup ensures the bait remained functional without being consumed. Additionally, a diluted honey and raspberry cordial solution was sprayed on the bait tree. A 21 cm wooden scale bar (equivalent to the averaged snout-vent length of Squirrel Gliders) was suspended next to the bait holder for size reference in the images (Fig. 3.1C). Swift Enduro professional-grade motion cameras, equipped with infrared mode and 32 GB SD cards, were used for both survey designs. Cameras were programmed to operate from 5 pm to 7 am, capturing sequences of three photos with a 3-second interval upon detecting animal presence. Cameras were positioned 3 to 4 meters above the ground.

In transect surveys, the bait holder was wrapped around the trunk using jute twine and the cameras were securely fastened with tie-down straps to the tree facing the bait holder. In grid surveys, V-shaped metal brackets and 10 x 10 cm L-shaped brackets were installed for the bait holders and cameras, respectively, to standardize the placements for repeat monitoring (Fig. 3.1B and C).

Upon retrieval, animals captured on camera were catalogued. A detection incident was defined as an animal being photographed at least 30 minutes after the preceding image of that species.

3.4.3. Presence-only (PO) data

We used historical records from the WildNet database and the Mahogany Glider Recovery Team as our presence-only dataset. The data was cleaned by first converting animal counts at each coordinate to presence. We then removed unreliable records, including those before 1990, or lacking year information. This process resulted in a total of 487 valid sighting records in the presence-only dataset.

3.4.4. Environmental Covariates

We used the predictors that showed significance in the latest species distribution modelling (Chang *et al.* 2022) as the environmental covariates in the integrated model (Appendix S1). These spatial rasters were standardised to the same resolution of 250 m and cropped to the known range of the glider (Blakeney 2015). Soil and vegetation types that were significantly correlated with glider presence were recoded into a binary format (1 for relevant, 0 for others). The preferred soil type was hydrosol, while the preferred vegetation types included *Eucalyptus* woodlands with a tussock grass understory and *Melaleuca* open forests (Appendix S1). To account for detection bias, we included distance to road, as this factor is known to influence predictions in species distribution modelling (Chang *et al.* 2022). Missing data representing ocean areas were removed from the environmental covariates. Before model fitting, each variable was scaled and centred (Kruschke 2014).

3.4.5. Integrated model description

The integrated species distribution model consists of an inhomogeneous Poisson process that model the latent species abundance across the area of interest and two sub-models corresponding to two types of monitoring data: 1) a thinned Poisson process that describes the observed presence-only data, and 2) an occupancy model that fits the presence-absence data. Both sub-models are linked to the latent abundance, and the model evaluates the likelihood of all three components simultaneously.

The inhomogeneous Poisson process describes the latent abundance N of the Mahogany Glider in their known extent B as shown in eqn 1:

$$N(B) \sim Poisson\big(\mu(B)\big) \qquad \text{eqn 1}$$

The mean abundance of Mahogany Glider in the range $\mu(B)$ is determined by an intensity function λ as shown in equation 2. In our model, the intensity function depends on an intercept term and nine environmental covariates (eqn 3).

$$\mu(B) = \int_B \lambda(s)ds \qquad \text{eqn 2}$$

$$\log(\lambda) = \beta x(s)^T = \beta_1 \cdot x(s)_1 + \ \dots \ + \beta_{10} \cdot x(s)_{10} \qquad \text{eqn 3}$$

Occupancy models estimate species presence on a spatial grid, and the latent occupancy at gird k (Z_k) was estimated using the probability of glider presence ψ_k through a Bernoulli process (eqn 4) (Fidino 2021). This probability ψ_k depends on the latent abundance at the grid k (N_k) (equation 6 in Koshkina *et al.* 2017)

$$Z_k \sim Bernoulli(\psi_k) \qquad \text{eqn 4}$$

Inferring from the latent abundance $N(B)$, the presence-only sub-model composed of a thinned Poisson process describing the imperfectly detected abundance $\pi(B)$ (eqn 5). The imperfect detection is accounted for by a thinning factor $b(s)$ in eqn 5, which is composed of an intercept term and an observation bias layer (equation 10 in Koshkina *et al.* 2017)

$$\pi(B) = \int_B \lambda(s) \ \cdot b(s)\, ds \qquad \text{eqn 5}$$

The presence-absence sub-model is a typical occupancy model which consist of 1...j survey sites and each site was surveyed w_j days. A successful detection at j site on the w day is a Bernoulli process determined by the latent occupancy Z and observations bias ($p_{j,w}$) as shown in eqn 9.

$$y_{j,w}|Z_{k[j]} \sim Bernoulli\big(p_{j,w} \ \cdot Z_{(k[j])}\big) \qquad \text{eqn 9}$$

We assumed the detection bias to be consistent across sites, thereby only intercept term is used in the $p_{j,w}$ function (equation 4 in Koshkina *et al.* 2017).

The likelihood functions of Dorazio (2014) and MacKenzie *et al.* (2002) were used to estimate the coefficients for each environmental covariate in the intensity function of latent abundance and in the thinning factor (biases) for the presence-only and presence-absence model, respectively (Koshkina *et al.* 2017). Assuming the presence-absence dataset is independent from the presence-only dataset, the joint likelihood of the integrated model can then be expressed by multiplying the likelihood of the submodels (Dorazio 2014; Koshkina *et al.* 2017)

3.4.6. Testing model accuracy

We examined the effects of camera placement, sample size, and aggregation methods on the accuracy of the integrated model, based on the simulation framework of Fidino (2021). In Fidino's framework, animal occurrence was generated according to environmental covariates within a raster, presence-only (PO) data were randomly selected across the raster, and 100 cameras were evenly distributed for presence-absence (PA) data. This simulation process accurately captures the true coefficient values. However, our study differs in two key aspects: (1) our cameras are clustered within 10 sampling sites rather than being evenly distributed, and (2) the number of cameras varies across different resolutions due to subsampling when multiple cameras fall within the same cell.

To ensure the integrated model's applicability to our data, we conducted simulations to test its ability to cover the true values under these conditions. First, we tested the effect of clustered cameras by simulating 25 clusters, each containing four cameras, and compared the modeling results to the evenly distributed 100-camera setup. Second, we evaluated the impact of sample size changes due to subsampling, without altering individual camera observations. Third, we tested three aggregation methods for each cell: averaging all camera observations (mean), retaining only the camera with the highest detection (max), and summing all observations while dividing by 1.7 to ensure totals did not exceed the number of observation nights (sum).

3.4.7. Model Configuration

We fitted the models based on the script of Fidino (2021) using JAGS 4.3.1 (Plummer 2003) through the runjags package 2.2.1-7 (Denwood 2016) in R 4.1.2 (R Development Core Team 2022). We aggregated all environmental variables with factors of 3–5 (Fidino 2021), resulting in three grid sizes that represent the home range of the glider: 9 ha, 16 ha, and 25 ha (Schank *et al.* 2019; personal communication with Mason Fidino). When multiple cameras were present within a single aggregated grid, only the camera with the most detections was retained, based on the optimal method identified in the simulation tests.

The process involved 4 chains, with a 1000-step adaptation phase, followed by a 10000-step burn-in and a thinning factor of 5 to avoid auto-correlation. We subsequently sampled the posterior 5000 times on each chain, which resulted in a total of 20,000 posterior samples. To ensure the model convergence, we visually inspected the trace plots for each variable and verified Gelman-Rubin diagnostics were less than 1.05 (Brooks and Gelman 1998). The Gelman-Rubin statistic, also known as the R-hat statistic, compares the variability within individual chain to the variability between different chains. We then determined the evidence of an effect by calculating 95% credible intervals (CIs) for each variable and assessed whether they overlapped zero.

To capture the range of estimates, we drew 1,000 sets of model coefficients from the posterior distribution and generated 1,000 corresponding abundance predictions. For each prediction, total abundance was calculated by summing the values across all pixels. Finally, we assessed the most likely abundance estimates and their uncertainty by examining the quantiles of the resulting abundance distribution (posterior prediction).

3.4.8. Abundance estimates comparisons

We compared our integrated model's abundance estimates to previous numbers mentioned in Burbidge *et al.* (2014), which included an extrapolation of 10,000 to 14,000 individuals from Jackson (2000b) and a hypothesis of 1,500 to 2,000 individuals based on unpublished genetic data and personal communication with Mark Parsons. Additionally, two reference extrapolations were made using data from Jackson (2000b) and Jackson *et al.* (2019). Extrapolation 1 was calculated by multiplying the total area of primary and secondary subpopulations (12,678 ha; Table 1 in Jackson *et al.* 2019) by the density estimate for fragmented habitats (0.16/ha), resulting in 2,027.28 individuals. Extrapolation 2 used the total area of continuous habitats (Table 1 in Jackson *et al.* 2019) and multiplied it by the density estimate for continuous habitats (0.24/ha). For a conservative estimate, areas larger than 100 ha and 8,000 ha were capped at these values, resulting in $(20 \times 100 + 5 \times 8{,}000) \times 0.24 = 10{,}080$ individuals.

3.5. Results

3.5.1. Camera trapping surveys

The surveys conducted within the known range of the Mahogany Glider generally recorded low detection rates, except for three sites: Allendale, Bambaroo, and Muller’s Creek (Table 3.1). Allendale, situated south of Ingham within continuous habitat, exhibited a very high detection rate. Bambaroo, a small and isolated fragment of primary forest near Allendale, also showed a moderate detection rate. Muller’s Creek, located between Ingham and Cardwell, had a moderate detection rate as well. However, Coolbie, Mutarnee, and Ollera Creek, positioned at the southern end of their range, had low detection rates, with only one to three observations across whole monitoring duration. Surveys at Abergowrie and Long Pocket, both situated in high-probability habitat areas to the west of Ingham, did not yield any Mahogany Glider detections (**Fig. 3.1**A; **Table 3.1**). The visual representation of the spatial-temporal patterns at each site is provided in the Supplementary material S1.

Four of the survey sites were outside of (but close to) the known distributional range of the Mahogany Glider, namely the surveys at Hinchinbrook Island, Clement State Forest, Balgal Beach, and South Mission Beach (Fig. 3.1A). Our surveys failed to detect any Mahogany Glider in these areas. It is worth noting that we were unable to survey the highly suitable habitat on Hinchinbrook Island (Chang *et al.* 2022) to provide solid evidence for the absence of the species. Nevertheless, our surveys did confirm the presence of Krefft's Gliders on the island. Additionally, we observed high densities of Krefft's Gliders in both Clement State Forest and Balgal Beach. In the South Mission Beach habitat, which is predominantly rainforest, we had three detections of Striped Possums.

Table 3.1 Camera trapping survey sites and detection counts of Mahogany Glider (MG) and Kreff's Glider (KG). The location of the sites is shown in Fig. 4.1. The trapping effort is represented as the product of the total number of nights and cameras at each site. Note that operational duration of cameras varied within a site, and the variation of each camera was incorporated in the trapping effort calculation and in the model. The Naïve capture rate was calculated by dividing the Mahogany Glider detections by the total trapping effort.

Site	**Region**	**Survey type**	**Cameras**	**Min. nights**	**Total trapping effort**	**MG**	**KG**	**MG Naïve rate (%)**
Abergowrie	West of Ingham	transect	20	27	540	0	4	0.00
Balgal	North of TSV	transect	20	52	1040	0	40	0.00
Bambaroo	South of Ingham	transect	24	33–89	1016	19	0	1.87
Clemant SF	North of TSV	transect	20	42	840	0	27	0.00
Coolbie	South of Ingham	transect	10	53	530	2	6	0.38
Hinchinbrook	Cardwell	transect	20	57	1140	0	1	0.00
Long Pocket	West of Ingham	transect	20	15	300	0	1	0.00
Mutarnee	North of TSV	transect	20	20	400	2	2	0.50
South Mission Beach	Tully	transect	9	58	522	0	0	0.00

Allendale	South of Ingham	grid	20	41–42	832	78	36	9.38
Bambaroo	South of Ingham	grid	20	30–31	610	25	0	4.10
Muller's Creek	Cardwell	grid	20	44–45	894	22	10	2.46
Ollera Creek	North of TSV	grid	20	42	840	3	0	0.36

3.5.2. Testing model accuracy

In the parameter testing, we used simulated data to assess the effects of camera placement (clustered vs. even), sample size, and aggregation methods. Camera clustering had minimal impact across different resolutions, with most estimated ranges capturing the true values (Appendix S3-4; Appendix S3-5). However, clustering led to a higher estimate of occupied cells at finer resolutions (Appendix S3-4). Aggregation, which combines detections from multiple cameras within a pixel, reduces both the total number of cameras and detections as the aggregation factor increases (lower resolution) (Appendix S2). Despite this reduction in sample size, model estimates were generally unaffected (Appendix S3-5).

The aggregation method was crucial. At a detectability of 0.7, uncertainty increased at finer resolutions (aggregation factors 5 and 10), while at coarser resolutions (aggregation factors 15 and 20), the model underestimated the occupied cells, failing to capture the true value (Appendix S3-6). Overall, the mean and sum methods (averaging or summing detections within a pixel) performed poorly, whereas the max method (selecting the camera with the highest detections) provided the most accurate results (Appendix S3-6).

3.5.3. Abundance estimates using integrated model

As observed in the simulation tests, abundance estimates were scale-dependent, with finer spatial resolutions producing higher estimates (**Error! Reference source not found.**). Below, we reported the quantile of posterior predictions generated from 1,000 sets of coefficients for each home range size. For the smallest estimated home range of 9 ha (aggregation factor

= 3), the quantile ranged from 5,155 to 6,977 individuals, with a median of 6.036. At a home range of 16 ha (aggregation factor = 4), the quantile ranged from 4,018 to 5,755, with a median of 4,834. For the largest home range of 25 ha (aggregation factor = 5), the quantile ranged from 2,236 to 3,487, with a median of 2,820 (**Error! Reference source not found.**, Appendix S3-3). Standard deviations decreased as resolution became coarser, from 1,365.2 in agg3 to 954.9 in agg5.

The coefficients representing species–environment relationships remained relatively stable across the three aggregation factors (pixel sizes). The occupancy intercept exhibited a wider range compared to the abundance and SDM intercepts. The most important environmental covariates in the models were distance to roads (-), elevation (-), preferred vegetation type (Eucalyptus open woodlands) (+), and temperature seasonality (+). Distance to waterways (+) was also significant across all three models. While soil type, precipitation seasonality, and fire frequency were positively correlated with predicted densities, their magnitude of effect varied between models (**Error! Reference source not found.**, Appendix S3-3).

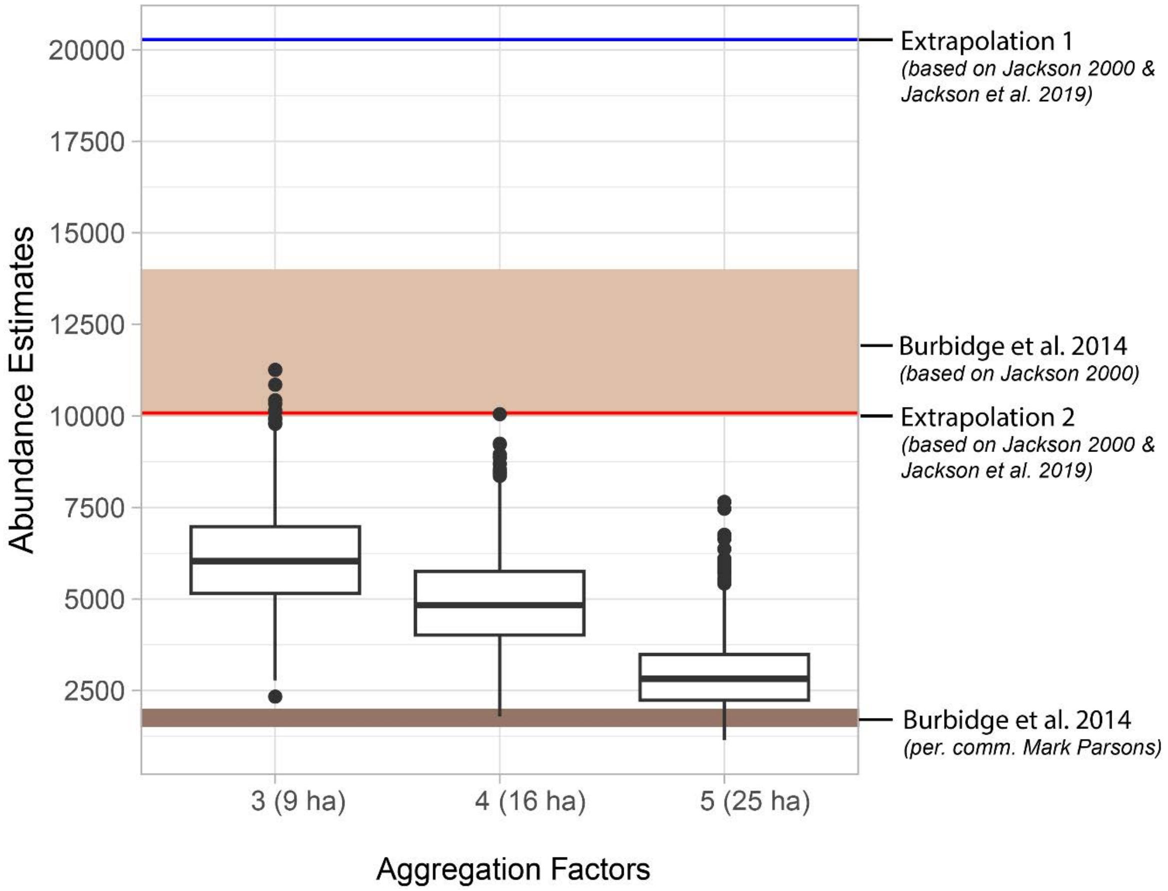


Fig. 3.2 Posterior predictions of the total abundance of Mahogany Gliders across their known range at home range sizes of 9, 16, and 25 ha (aggregation factors 3–5). The Boxplots represent estimates from the 1000 predictions from the integrated species distribution model. The brown ribbons indicate estimates mentioned by Burbidge *et al.* (2014). The blue and red lines represent extrapolations based on density estimates and habitat remnant assessments from Jackson (2000) and Jackson *et al.* (2019) (see Methods).

3.6. Discussions

In this study, we conducted the first extensive camera trapping survey for the Mahogany Glider, covering areas both within and beyond the species' known range. Although both the habitat suitability map and field observations suggested suitable habitat conditions, our surveys did not detect any Mahogany Glider in many of the sampling sites. This absence may be attributed to the small, isolated nature of some habitat fragments and their limited connectivity to source populations, which can impede colonization (Schooley and Branch 2009; Burbidge *et al.* 2014). Additionally, recent habitat changes, such as the spread of vine thickets, may have reduced habitat suitability in northern areas like Abergowrie, Corduroy Creek and Barrett's Lagoon near Tully (Holloway 2013). It is also important to acknowledge that several suitable habitats could not be surveyed due to access limitations. For instance, large patches of suitable habitat on the northwestern side of Hinchinbrook are protected as Aboriginal sacred sites, while areas such as Wharps Holding were inaccessible due to vine thickets and the lack of landowner permission. Similarly, the upper reaches of the Herbert River were not surveyed because of their remote and inaccessible terrain.

We observed variation in detection rates across sampling sites. While detection rates within the known range were generally low, the Allendale and Bambaroo sites exhibited higher-than-expected detections, suggesting that detection rates likely reflect local glider densities. For instance, Bambaroo was surveyed twice using both camera traps and cage traps (Chang 2023), within a clearly defined 64-hectare fragment. Capture-recapture analysis estimated around 30 gliders in this fragment (Chang 2023), resulting in a density of 0.47 individuals per hectare—twice the density reported in continuous habitats by (Jackson 2000). In contrast, Muller's Creek showed much lower detection (2.46%) and capture (2.5%) rates (Chang 2023) compared to the 11% capture rate around 1997 (Jackson 2000). This discrepancy in density estimates highlights several key aspects. First, animal densities can change considerably over time, especially considering that no monitoring has occurred in over 20 years. Second, research and management decisions should not rely on a single density estimate, as densities can vary significantly across different populations and habitats. Lastly, factors beyond habitat suitability, such as fragmentation (Ganzhorn *et al.* 2015), land use (Lenzen *et al.* 2009), range size and geometric constraints (Paudel *et al.* 2018), can also affect density. Moreover, the relationship between abundance and habitat suitability may not always be positive, as species can be density dependent (Souza *et al.* 2022). Investigating and comparing the factors between low and high-density habitats is crucial for the species' recovery (Norris 2004; Mcdonald-Madden *et al.* 2010).

Compared to the wide range of previous estimates (Burbidge *et al.* 2014), the integrated model narrows the abundance estimates to between 2,820 and 6,022 individuals across the known range (~ 400 km^2). Although actual abundance is challenging to determine due to varying home ranges and densities, our estimates provide a scientifically based reference—lower than many extrapolations but more robust than the rough guess of 1,200 (Burbidge *et al.* 2014). The integrated model provides superior abundance estimates in two key aspects. First, it reduces uncertainty by incorporating both sighting records and repeated presence-absence data, outperforming expert opinions and standalone abundance-occupancy models (Koshkina *et al.* 2017). Second, the integrated model enables predictions across larger areas with quantifiable confidence intervals, which is not feasible with traditional abundance-occupancy models. For instance, while estimates for the Yellow-bellied Gliders (*Petaurus australis*) in Richmond Range National Park, NSW, were consistent, they were limited to the twenty 200m transects and could not even be extrapolated to the entire study area (~150 km^2) (Goldingay *et al.* 2017). In contrast, the integrated model has been successfully applied on much larger scales, such as estimating the abundance of Baird's Tapir (*Tapirus bairdii*) across Central America (~ 500,000 km^2) and coyote (*Canis latrans*), bobcat (*Lynx rufus*), and black bear (*Ursus americanus*) populations across New York State (~141,000 km^2) (Schank *et al.* 2017; Schank *et al.* 2019; Twining *et al.* 2024).

While the integrated model provides more reliable abundance estimates and can be applied across larger spatial scales, it is sensitive to the aggregation factor, which in our model represents the species' estimated home range. As the aggregation factor decreases (i.e., resolution increases), abundance estimates rise. This scale dependency is inherent when working with gridded spatial data, accounting for false positives, and in the absence of individual identification—a common challenge in most camera trapping surveys (Steenweg *et al.* 2018; Nakashima 2020). This scale dependency was not addressed in the original model (Koshkina *et al.* 2017) but was later confirmed in a study on Baird's Tapir (*Tapirus bairdii*) using the same model (Schank *et al.* 2019). Defining the aggregation factor based on home ranges is biologically meaningful, but this process can be complex when the home range is dynamic or difficult to determine (Schank *et al.* 2019; personal communication with Mason Fidino). Investigating the animal's home range variability and using the averaged home range are therefore the recommended approach (Schank *et al.* 2019).

Many of the environmental covariate relationships identified in our study aligned with previous species distribution models (SDMs) and the known ecology of the species. However, some minor discrepancies were observed. Soil type and precipitation seasonality, which were key factors in previous SDMs (Chang *et al.* 2022), were not consistently significant in the integrated model. Among the environmental covariates, the temperature of the coldest month appeared to have the least effect on abundance estimates. More notable differences were found in the effects of slope and observation bias. For instance, observation bias related to the Euclidean distance to roads negatively affected abundance estimates, predicting higher abundance further from roads. This prediction behaviour contradicts the previous SDM, where increased sampling near roadways led to a positive bias towards roads. Similarly, slope showed a positive correlation with abundance, despite lower sampling effort in steeper areas compared to flatter regions. This contradicting result was also found in the findings of Schank *et al.* (2019), where steeper slopes unexpectedly had a positive effect on abundance estimates.

Our findings also emphasize the importance of long-term monitoring, as we observed significant fluctuations in population density at a sampling site over a 20-year period. Long-term occupancy monitoring not only improves model accuracy but is essential for tracking population trends over time and offering early warnings about population declines or recovery (e.g., Cassey *et al.* 2007; Rodhouse *et al.* 2019; Weldy *et al.* 2023; Harju and

Cambrin 2023). Since this study, local communities and conservation groups have initiated monitoring efforts using fixed arboreal camera traps at key sites such as Bambaroo, Allendale, and Muller’s Creek. As these efforts expand, abundance estimates for the Mahogany Glider will become more precise, which will also strengthen the role of long-term monitoring in adaptive species management (McCarthy and Possingham 2007; Lindenmayer and Likens 2009).

The integrated model provides a robust baseline for estimating the abundance of this endangered species, especially in situations where traditional occupancy models struggle due to low detection rates or large study areas (e.g., Linden *et al.* 2017; Koshkina *et al.* 2017). Despite its limitations in accounting for population dynamics and variable home ranges, the model offers valuable insights by incorporating both presence and absence data, which can help explain variations in the species' density across different habitats. To further refine these estimates and understand the drivers of population changes, future research should expand camera trapping efforts to additional suitable habitats, including coastal areas within the known range and regions beyond (Chang *et al.* 2022). Investigating other factors—such as level of fragmentation, tree sizes, availability of tree hollows, and human interference—will be essential in understanding the Mahogany Glider’s density and home range variability. Combining these efforts with long-term monitoring and advanced modelling techniques will provide critical insights to effectively address the conservation needs and inform adaptive management.

3.7. Ethics and permits

The research was conducted in accordance with Queensland animal permits for scientific purposes (protected areas: P-PTUKI-100021853; non-protected areas: WA0025939) and animal ethics under James Cook University (A2699).

3.8. Conflicts of interest

The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

3.9. Data availability statement

The model and analysis script used this study are available in FigShare at DOI: 10.6084/m9.figshare.24618996. The supplementary tables and figures of this study are available in the accompanying online supplementary materials.

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Appendices

Appendix S3-1 The Appendix Shows the predictors employed in the integrated species distribution model. The predictors were selected from the subset of variables identified by the latest species distribution model of the species (Chang *et al.* 2022). Categorical variables were transformed into binary values, with 1 and 0 denoting the effective and non-effective category, respectively. The values of each predictor variable were appropriately scaled and centred prior to the modelling process.

Predictor variables	**Year coverage**	**Units**	**Source**
Bio_04: Temperature Seasonality	1996–2015	°C	Storlie *et al.* 2013
Bio_06: Min Temperature of Coldest Month	1996–2015	°C	Storlie *et al.* 2013
Bio_15: Precipitation Seasonality	1996–2015	mm	Storlie *et al.* 2013
Elevation	2007	meters	Department of Natural Resources, Mines and Energy, 2005
Slope	2007	degrees	
Distance to major water ways	2016	meters	Queensland Government Department of Agriculture and Fisheries, 2016
Fire Frequency AVHRR	1997–2011	0–7 burnt times	Maier and Russell-Smith, 2012
Soil: Hydrosol	2011	1, 0	Australian Collaborative Land Evaluation Program, 2014
Vegetation: 9 and 15[†]	pre-1750, 2006	1, 0	Department of Environment and Science, 2012

[†] Eucalyptus woodlands with a tussock grass understory, Melaleuca open forests and woodlands

Appendix S3-2 The Appendix Summarizes the reduction in cells and cameras during the aggregation process in parameter testing using simulated data (detectability = 0.7). Shaded rows indicate results from different aggregation methods. At the original resolution (aggregation factor = 1), cameras and animal presence were randomly assigned across cells, with each camera having a 70% probability of detecting an animal if placed in a cell containing one.

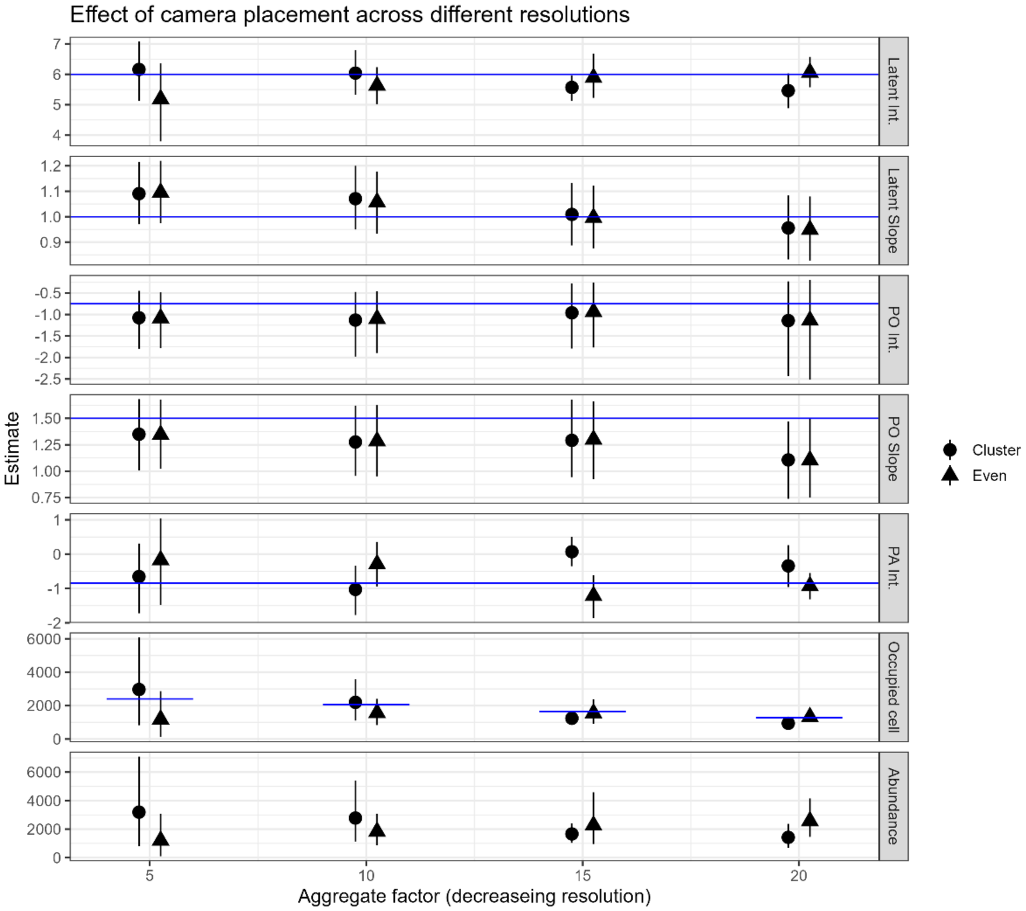
Aggregation factor	**5**	**10**	**15**	**20**
# of cell in the raster	40000	10000	4489	2500
# of cameras in model	100	62	50	43
# of detected cameras: max	8	8	8	8
# of detected cameras: mean	8	5	5	5
# of detected cameras: sum	8	8	8	8

Appendix S3-3 Coefficient estimates for the integrated model at aggregation factors of 3 (9 ha), 4 (16 ha), and 5 (25 ha). Coefficients are presented as medians with their 95% credible intervals, along with means and standard deviations (SD). The effective sample size is denoted as SSeff, and the Gelman-Rubin diagnostic is reported as PSRF.

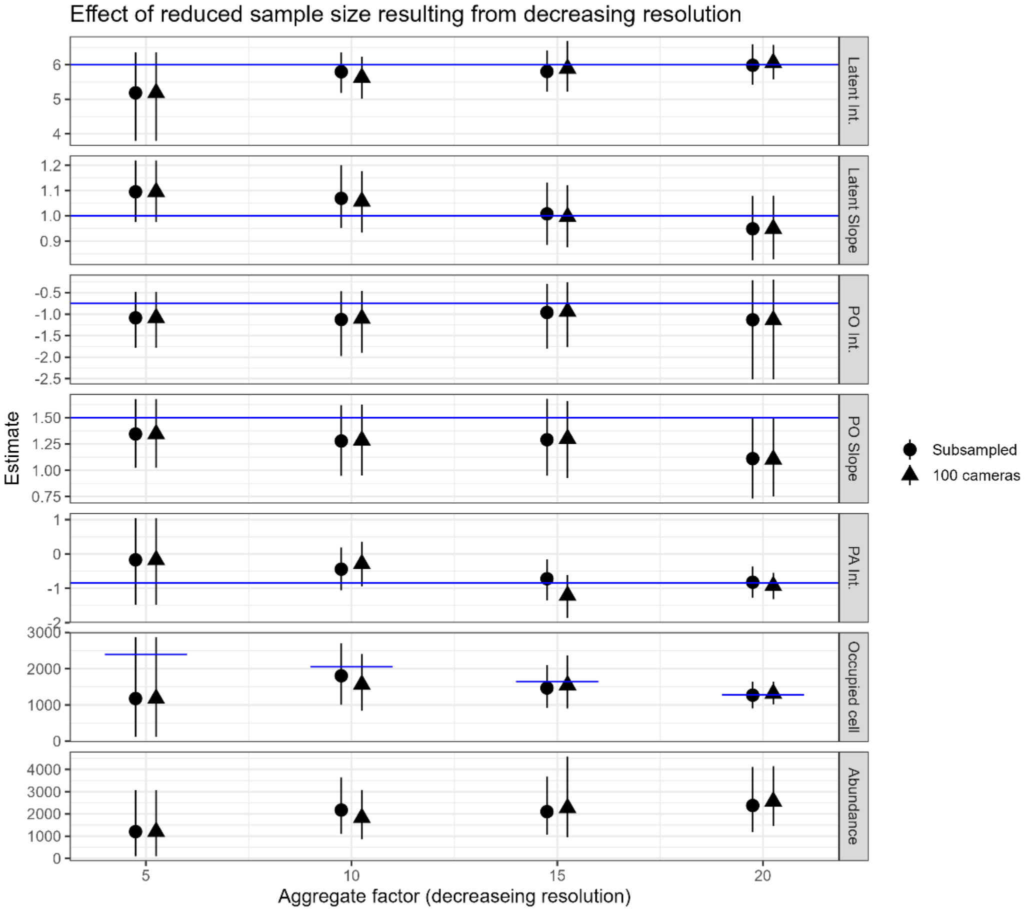
	Lower95	**Median**	**Upper95**	**Mean**	**SD**	**SSeff**	**PSRF**
Aggregation factor = 3							
SDM Intercept	-4.28	-3.17	-2.21	-3.2	0.53	4030	1
Temperature seasonality	0.32	0.63	0.93	0.63	0.15	10373	1
Minimal temperature of the coldest month	-0.06	0.38	0.85	0.38	0.23	9307	1
Precipitation seasonality	0.08	0.24	0.41	0.24	0.09	12598	1
Elevation	-4.43	-3.37	-2.37	-3.4	0.53	3666	1
Slope	-0.1	0.23	0.56	0.23	0.17	6088	1
Fire Frequency	0.09	0.34	0.57	0.34	0.12	18469	1
Soil (Hydrosol)	-0.02	0.08	0.18	0.08	0.05	20204	1
Vegetation type	0.28	0.4	0.52	0.4	0.06	18367	1
Distance to waterways	0.05	0.19	0.32	0.19	0.07	18616	1
PO intercept	-6.86	-4.02	-1.94	-4.22	1.32	19729	1
Observation bias	-2.68	-2.05	-1.45	-2.06	0.31	20234	1
Occupancy intercept	-2.6	-2.35	-2.12	-2.36	0.12	20443	1
Occupancy estimate	3253	5254	7390	5321.34	1073.7	14959	1
Abundance estimate	3527	5879	8658	5981.18	1339.9	15363	1
Aggregation factor = 4							
Intercept	-4.61	-3.38	-2.36	-3.41	0.57	3792	1
Temperature seasonality	0.32	0.64	0.95	0.64	0.16	10601	1
Minimal temperature of the coldest month	-0.16	0.31	0.77	0.31	0.24	9712	1
Precipitation seasonality	0.01	0.19	0.36	0.19	0.09	11630	1
Elevation	-4.66	-3.45	-2.43	-3.49	0.57	3286	1
Slope	-0.03	0.31	0.65	0.31	0.17	5171	1
Fire Frequency	-0.02	0.26	0.51	0.26	0.14	19733	1
Soil (Hydrosol)	-0.01	0.1	0.21	0.1	0.05	20000	1
Vegetation type	0.26	0.39	0.51	0.39	0.07	18245	1
Distance to waterways	0.03	0.17	0.31	0.17	0.07	18476	1
PO intercept	-6.76	-3.95	-1.91	-4.16	1.29	19259	1
Observation bias	-2.93	-2.24	-1.59	-2.25	0.35	19654	1
Occupancy intercept	-2.7	-2.44	-2.19	-2.44	0.13	20467	1
Occupancy estimate	2570	4161	5943	4217.66	874.74	15666	1
Abundance estimate	2757	4804	7213	4906.21	1164.45	16272	1
Aggregation factor = 5							
Intercept	-5.18	-3.91	-2.81	-3.94	0.6	2248	1
Temperature seasonality	0.35	0.67	1.01	0.67	0.17	5043	1
Minimal temperature of the coldest month	-0.23	0.26	0.75	0.26	0.25	4156	1
Precipitation seasonality	-0.08	0.1	0.28	0.1	0.09	6904	1

Elevation	-4.62	-3.45	-2.42	-3.48	0.56	1939	1
Slope	-0.06	0.27	0.63	0.27	0.18	3239	1
Fire Frequency	0.04	0.31	0.56	0.3	0.13	13670	1
Soil (Hydrosol)	0.04	0.15	0.26	0.15	0.06	14601	1
Vegetation type	0.3	0.44	0.57	0.44	0.07	12525	1
Distance to waterways	0.01	0.16	0.31	0.16	0.08	13396	1
PO intercept	-6.48	-3.55	-1.58	-3.75	1.3	13684	1
Observation bias	-2.76	-2.04	-1.4	-2.06	0.35	15888	1
Occupancy intercept	-3.6	-3.05	-2.59	-3.07	0.26	8519	1
Occupancy estimate	1197	2424	3948	2511.68	739.68	7245	1
Abundance estimate	1253	2795	4952	2945.53	1024.44	7327	1

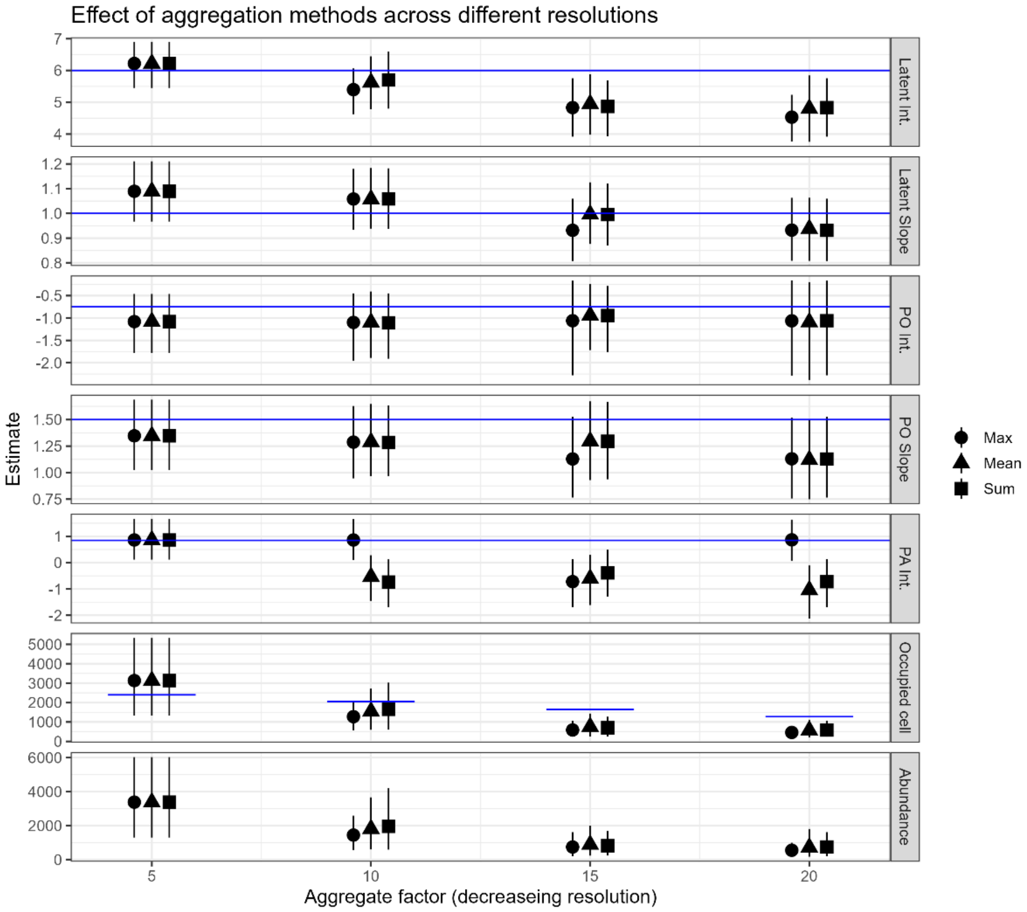
Appendix S3-4 The plot demonstrates the effect of camera placement across different resolutions (aggregation factors). Simulated data were used to test clustered versus evenly placed cameras. The blue line represents the true value, while circles and triangles indicate the medians of clustered and evenly placed camera placements, respectively, with lines showing 95% interval. The plot illustrates whether the estimates capture the true values for the intercepts that serve as a reference for the reliability of the abundance estimates.



Appendix S3-5 The plot demonstrates the effect of reduced sample size resulted from subsampling due to the increasing aggregation factors (decreasing resolutions). Simulated data were used to test subsampled cameras versus original 100 cameras. All cameras were evenly distributed before subsampling. And the aggregation method is to randomly remove cameras from the raster. The blue line represents the true value, while circles and triangles indicate the medians of subsampled and original camera numbers, respectively, with lines showing the 95% interval. The plot illustrates whether the estimates capture the true values for the intercepts that serve as a reference for the reliability of the abundance estimates.



Appendix S3-6 The plot demonstrates the effect of different aggregation methods (max, mean, sum) across various resolutions (aggregation factors) using simulated data. All cameras were evenly distributed before the aggregation. The blue line represents the true value, while circles and triangles indicate the medians of subsampled and original camera numbers, respectively, with lines showing the 95% interval. The plot illustrates whether the estimates capture the true values for the intercepts that serve as a reference for the reliability of the abundance estimates.



Chapter 4.

Conservation genetics of Mahogany Gliders and insights into their evolutionary relationship with Squirrel Gliders

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This chapter has been submitted to *Conservation Genetics* and is currently under review.

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4.1. Abstract

Squirrel Gliders (*Petaurus norfolcensis*) are widely distributed throughout the woodlands of eastern Australia, while the similar but larger Mahogany Glider (*Petaurus gracilis*) inhabits the coastal woodlands of the Wet Tropics in northeastern Queensland. The Mahogany Glider is an Endangered species due to habitat loss and fragmentation. To inform effective conservation management, this study used single nucleotide polymorphism markers (SNPs) from field and museum-derived samples to investigate genetic relationships within the Squirrel/Mahogany Glider complex and conduct a conservation genetics assessment for the Mahogany Glider. Analyses of genetic structure, phylogenomics, and outlier loci identified four genetic groups: Mahogany Glider and three distinct groups in Squirrel Gliders (North Queensland, Cape Cleveland, and mid-eastern/south-eastern Queensland). We found genetic admixture between these groups, but whether the admixture is historic or current remains unclear. Gliders from North Queensland were genetically more similar to Mahogany Gliders in some analyses than to the other Squirrel Glider groups. Morphological analysis confirmed that Mahogany Gliders are distinguishable from other gliders by their larger body size and longer tail. The study emphasizes the taxonomic uncertainty in the Mahogany-Squirrel Glider complex and the need to investigate glider populations at contact zones. When assessing Mahogany

Gliders alone, we found a clear north-south split in genetic structuring, with the southern cluster being more structured than the northern cluster. Genetic diversity within Mahogany Gliders was generally comparable to that of Squirrel Gliders, but some sampling localities indicated loss of genetic diversity and low effective population size. Regardless of whether Mahogany Gliders are classified as a species or subspecies, their Endangered status underscores the need for targeted conservation efforts. The genetic findings offer practical pathways for on-ground management to enhance population recovery and connectivity.

4.2. Key Words

Habitat Fragmentation, *Petaurus* gliders, Threatened Species, Genomics, SNPs, Genetic Structure, Genetic Diversity, Taxonomic Uncertainty

4.3. Introduction

Habitat destruction poses a significant threat to wildlife species, with estimates suggesting this threat impacts nearly 90% of threatened species and is the primary driver of extinction (Hogue and Breon 2022). Loss of habitat often leads to fragmentation, hence transforming once-interconnected habitats into smaller, isolated patches. In these fragmented landscapes, wildlife populations decline and become isolated, suffering from harmful edge effects, habitat degradation, and a loss of connectivity (Bender *et al.* 1998; Laurance *et al.* 2007; Didham 2010). Small, isolated populations are more vulnerable to genetic stochasticity, which can lead to the loss of genetic diversity and inbreeding depression (Willi *et al.* 2007; Frankham *et al.* 2017; Lino *et al.* 2019). Ultimately, loss of genetic diversity diminishes a species' adaptive potential to environmental changes (Hedrick 2000; Charlesworth and Willis 2009) and can lead to extinction (Frankham 2005).

Integrating genetic tools into conservation efforts enhances our understanding of habitat loss and fragmentation impacts, facilitating targeted management strategies (Luikart *et al.* 2003; Kohn *et al.* 2006). One powerful tool is the analysis of Single Nucleotide Polymorphisms (SNPs), which uses thousands of specific genome positions with nucleotide substitutions to provide high-resolution information on individual differences, population structure, and genetic diversity (Marth *et al.* 1999; Schork *et al.* 2000; Primmer 2009; Steiner *et al.* 2013). The results can then be used to target conservation efforts, such as identifying areas for revegetation to improve population connectivity (e.g., Bertola *et al.* 2023) and detecting local adaptation to environment change (e.g., McCulloch *et al.* 2021; Giska *et al.* 2022). Importantly, genomic tools can also reveal cryptic species (Dufresnes *et al.* 2019) and help resolve taxonomic uncertainty, which is crucial because conservation efforts are focussed on formally designated taxa (Dufresnes *et al.* 2019, 2023).

The Squirrel Glider (*Petaurus norfolcensis*) and the Mahogany Glider (*Petaurus gracilis*) are both medium-sized gliding possums inhabiting eucalyptus open forests in eastern Australia. Squirrel Gliders are distributed from Victoria to North Queensland, while Mahogany Gliders are restricted to a 120 km stretch of wet sclerophyll lowland forests in North Queensland between Ingham and Tully (Van Dyck *et al.* 2013). The distributions of the two species are not known to overlap (Van Dyck 1993; Jackson and Claridge 1999; Goldingay and Jackson 2004; Sharpe and Goldingay 2010). Initially considered a subspecies of the Squirrel Glider (Iredale and Troughton 1934), the Mahogany Glider was reclassified as a distinct species due to morphological differences (Van Dyck 1993). The Mahogany Glider is larger, with a body length of 215–265 mm and weight of 255–500 g, compared to the Squirrel Glider's 180–244 mm length and 173–300 g weight. It also has a longer, less fluffy tail (300–390 mm vs. 220–300 mm) (Van Dyck 1993; Jackson 2011; Jackson and Schouten 2012). In skull morphology, the Mahogany Glider has a narrower interorbital width but larger skull length, rostral height, and zygomatic width (Van Dyck 1993; Jackson 2011).

Previous studies have observed morphological and body size variation in Squirrel Gliders but data from gliders in eastern and northern Queensland is limited (Stobo-Wilson *et al.* 2020). The genetic differentiation between Mahogany and Squirrel Gliders also remains unresolved. Earlier research using two mitochondrial genes (ND2 and ND4) and two nuclear markers (ω-globin and ApoB gene) showed low sequence divergence (1.8–2.2%) between the species, and the phylogeny displayed a single admixed clade (Malekian *et al.* 2010; Ferraro 2012). No detailed genomic assessment of genetic differentiation and relatedness between the two species has been conducted to date, thereby creating taxonomic uncertainty that hinders accurate species identification and effective conservation strategies.

The Mahogany Glider is listed as Endangered under the Environment Protection and Biodiversity Conservation (EPBC) Act of 1999. Within its small distribution, the glider relies on mature lowland forests with large, diverse trees that provide essential tree hollows and year-round flower nectar (Jackson 2000). Agricultural deforestation, particularly for sugarcane and cattle farming, has reduced its habitat by approximately 40% (Jackson *et al.* 2011; Jackson *et al.* 2019). Furthermore, suitable habitat is now fragmented and includes more than 400 habitat patches smaller than 1 km^2 (Chang *et al.* 2022). Habitat loss and severe fragmentation can reduce and structure genetic diversity and may have resulted in poor genetic consequences in some isolated, small populations(Frankham *et al.* 2010). Understanding genetic diversity across populations of the Mahogany Glider is a key priority in the recovery plan (Parson and Latch 2006) and other conservation assessments (Curtis 2012; Burbidge *et al.* 2014). Despite the recognition of the importance of population genetic assessments to efficiently manage threatened species (e.g., Frankham *et al.* 2017), none has been conducted for the Mahogany Glider.

Here, we present the first detailed population genetic assessment of the Mahogany Glider, and we place this within the broader context of Squirrel Glider populations in Queensland. Our aims were to: (1) investigate the evolutionary relationship and key morphological characteristics between Mahogany and Squirrel Gliders, and (2) assess the population genetic structure and genetic diversity of the threatened Mahogany Glider. The results provide a foundation for resolving the taxonomy of Mahogany and Squirrel Gliders in Queensland and inform the conservation management of Mahogany Gliders.

4.4. Methods

Fieldwork — surveys and sample collection

A total of 16 trapping surveys were conducted to collect tissue samples from Mahogany Gliders (*Petaurus gracilis*) and Squirrel Gliders (*P. norfolcensis*) at 14 distinct sites between 15th April 2021 and 31st August 2022, for a total of 1,525 trap nights (Fig. 4.1; Appendix S4-1). We also collected tissue samples from Krefft's Gliders (*P. notatus*), a smaller glider species that is sympatric with Mahogany and Squirrel Gliders.

At each site, we strapped 20 wire cage traps (56 x 20 x 20 cm) to trees 2.5–4 m above the ground and 100–400 m apart depending on habitat size and suitability. The back half of each cage trap was covered with waterproof plastic sheeting for rain shelter. Each trap contained a bait ball made of peanut butter, honey and oats to attract gliders to the traps (Jackson 2001; Knipler *et al.* 2021). We squeezed additional honey on top of the bait ball to increase bait smell and keep the bait moist. We also sprayed a solution of water, raspberry cordial and honey above the trap as a scent lure. Traps were baited and opened just before sunset (5 pm) and checked at 11 pm and each morning before sunrise (5 am). Captured individuals were weighed, sexed, and measured (head length and width, body length, and tail length). We collected a tissue biopsy sample from the edge of an ear using a small ear punch and preserved the sample in 90% ethanol. We took photos of the face from the front and the side, and the whole body next to a scale bar. The glider was then released at the point of capture. All equipment was sterilized using 70% ethanol after each capture.

A total of 44 Mahogany Gliders, 6 Squirrel Gliders and 9 Krefft's Gliders samples were trapped and sampled in the field surveys (Appendix S4-1). Five of the 16 surveys conducted yielded no captures. For the sites with catching success, trapping rates were generally low, ranging from 0.8% to 15%. The highest trapping rates were observed in the northern section of Paluma Range National Park, particularly at Bambaroo, Easter Creek, and Allendale (Fig. 4.1; Appendix S4-1). Additional samples were obtained from five rescued Mahogany Gliders (via wildlife-carer Daryl Dickson, MGDD01–05, Appendix S4-2) and from a previous trapping survey during 2008 and 2010 conducted by

Queensland Parks and Wildlife Service (via Mark Parsons, MGMP01–08, Appendix S4-2). We also included historical samples of 10 Mahogany Glider and 43 Squirrel Glider from the Queensland Museum (Appendix S4-2). The Squirrel Glider samples extended from southeastern to far north Queensland (Fig. 4.1). The museum samples, collected between 1989 and 2017, were sourced from fur, skin, liver, or muscle specimens that were obtained from field-specimens, rescued individuals, or deceased animals.

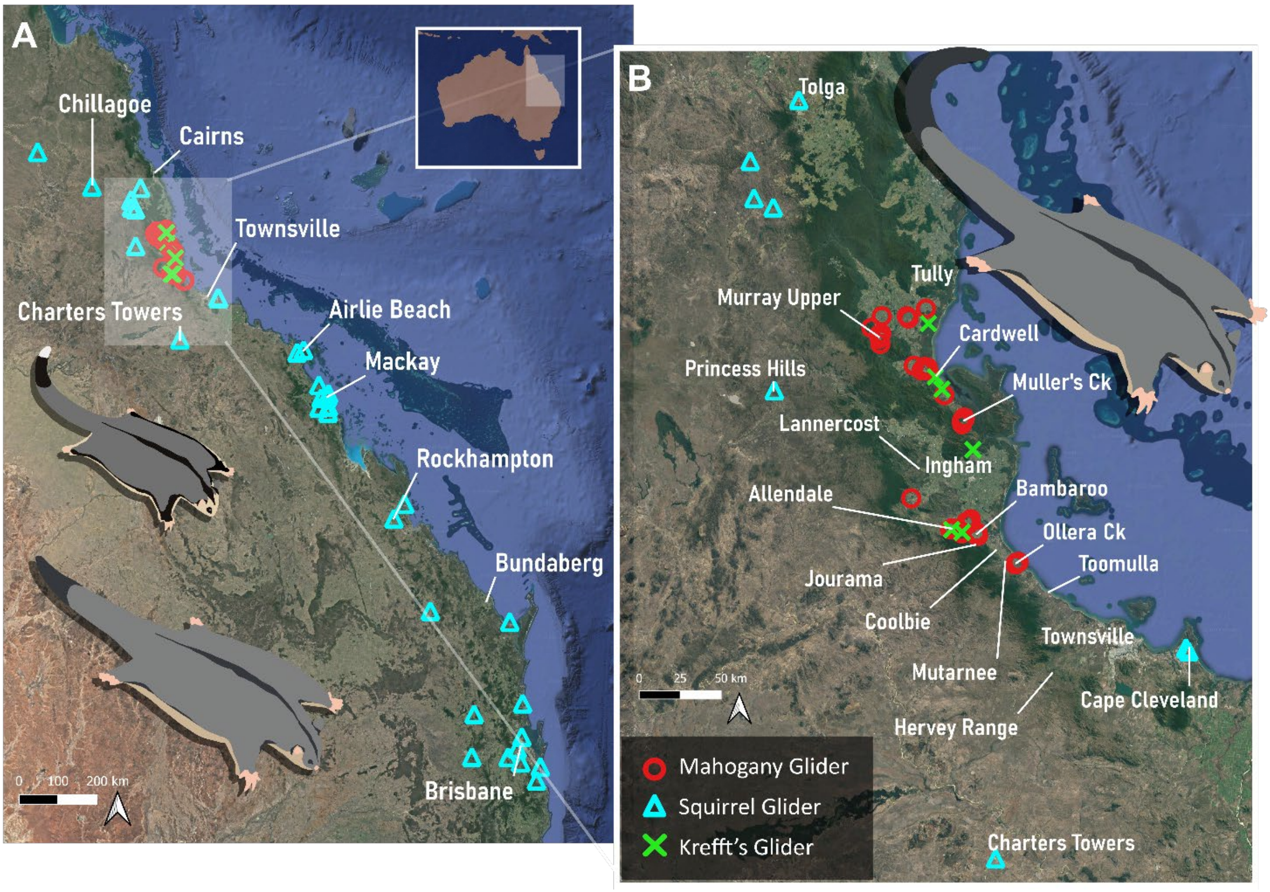

Fig. 4.1 Geographical distribution of sampling localities in (A) Queensland and (B) the Wet Tropics region. Symbols and colours represent different glider species: Squirrel Glider (blue); Mahogany Glider (red); Krefft's

Glider (green). The illustrations of the glider, from the smallest to the largest, are Krefft's Glider (map A), Squirrel Glider (map A), and Mahogany Glider (map B). The illustrations were created by Marine Lechene.

SNP genotyping and filtering

A total of 125 tissue samples were genotyped: 67 from Mahogany Gliders, 49 from Squirrel Gliders, and 9 from Krefft's Gliders (Appendix S4-5; Appendix S4-2). DNA extraction and SNP genotyping were performed at Diversity Arrays Technology (DArTseq) in Canberra, using the DArTseq method with PstI and Sphlv4 restriction enzymes. Genomic DNA was extracted using the Macherey-Nagel NucleoMag Plant kit and subjected to high-density sequencing (2.5 million reads per individual) on an Illumina NovaSeq 6000 S2 flow cell, referencing the *Petaurus* DArTseq (1.0) genomic library (Jaccoud *et al.* 2001; Kilian *et al.* 2012). Single Nucleotide Polymorphism (SNP) calling was performed using the DArTsoft14 algorithm within the KDCompute pipeline developed by Diversity Arrays Technology (http://www.kddart.org/kdcompute.html).

We performed SNP quality control using a customized R script (Appendix S4-5; ESM1) and dartR v2.7.2 (Gruber *et al.* 2018) to ensure standardized sequence quality (R v4.2.2; R Development Core Team 2022; Rstudio team 2023). Individuals with more than 35% missing genotypes (i.e., a low call rate) and single nucleotide polymorphisms (SNPs) with more than 10% missingness were removed. To ensure reliable and consistent genotyping results, SNPs with extreme read depth (<10 & >50) and reproducibility (consistency of SNPs calling result) lower than 0.99 were also removed. Secondary SNPs (i.e., SNPs called from the same locus) were removed by retaining the SNP with the higher reproducibility.

We further applied minor allele count, linkage disequilibrium, and outlier loci filters to both the complete dataset and the species-specific datasets. Briefly, singleton SNPs (minor allele count equals to one) were removed (O'Leary *et al.* 2018). The loci under linkage disequilibrium were filtered out with a threshold of 0.9 using PLINK v1.90b6.26 (Purcell *et al.* 2007) and bigsnpr v1.11.6 (Purcell *et al.* 2007; Prive *et al.* 2018), retaining only one of the linked markers with higher call rate.

To identify loci under selection, we conducted outlier analysis using three distinct methods: OutFLANK v0.2 (Whitlock and Lotterhos 2015), Bayescan v2.1 (Foll and Gaggiotti 2008), and pcadapt v4.3.3 (Luu *et al.* 2017). The results from OutFlank and Bayescan did not reveal any outlier loci. Using pcadapt, we discovered the outlier loci that significantly contribute to the genetic structure. We performed principal component analyses with a false discovery rate of 0.01. Outlier loci were then filtered based on their significance using two thresholds: the highly conservative Bonferroni method and the moderately conservative Benjamini-Hochberg method (Luu *et al.* 2017). To maximize the information retained, we created two distinct datasets based on the outlier filter: (1) a dataset containing only neutral loci, with outlier loci removed using the Bonferroni method, for genetic structure analysis; (2) a separate dataset comprising solely outlier loci, identified through the Benjamini-Hochberg method, for signatures of selection analysis.

First-degree relatives and potentially duplicated samples were identified using the KING method of moments in SNPRelate v1.32.0 (Manichaikul *et al.* 2010; Zheng *et al.* 2012). For first-degree relatives, only the individual with the highest call rate was retained for genetic structure and diversity analyses.

Downstream analyses were conducted in two steps. First, to better understand the evolutionary relationship between Mahogany and Squirrel Gliders, population genetic structure was assessed with a dataset including all three species (Appendix S4-5). For each of the identified genetic clusters, we then evaluated genetic distance, genetic diversity, morphological characteristics, and signatures of selection. Second, we conducted a conservation genetic assessment focusing on the Mahogany Glider.

Different datasets were used based on the assumptions and information required for each analysis (Funk *et al.* 2012) (Table 4.1). Phylogenetic analyses were performed on all loci, including both neutral and outlier loci. Genetic structure and diversity analyses were conducted on neutral loci only, while signature of selection analysis was investigated with outlier loci only. Therefore, the SNPs number varied across datasets. An overview of the analysis workflow is presented in Table 4.1, and the detailed steps to produce the different datasets are summarised in Appendix S4-5.

Table 4.1 Overview of the genetic analyses presented in this study, highlighting the dataset used. The table details the dataset used for each type of analysis for (i) all gliders, (ii) Mahogany and Squirrel Gliders together (MG-SQ), (iii) Mahogany Gliders only (MG), and (iv) Squirrel Gliders only (SQ).

Analysis	Species/Loci subset			
	All gliders	**MG-SQ**	**MG**	**SQ**
DAPC, STRUCTURE	Neutral Loci	Neutral Loci	Neutral Loci	
NetView	Neutral Loci			
AMOVA	All Loci Neutral Loci Outlier Loci	Neutral Loci Outlier Loci		
Mantel test (Isolation by distance)			Neutral Loci	Neutral Loci
Genetic differentiation (F_{ST})		Neutral Loci	Neutral Loci	
Genetic diversity	Neutral Loci	Neutral Loci	Neutral Loci	Neutral Loci
Phylogenetic Tree	All Loci			
Signature of Selection	Outlier Loci	Outlier Loci		

4.4.1. Genetic and morphological assessment of Mahogany and Squirrel Gliders

Interspecific population structure

To identify genetically distinct populations, we analysed genetic structure with a dataset of neutral loci for all three *Petaurus* species sampled (N = 86).

NetView uses the k-nearest neighbours (kNN) approach to visualize genetic distance matrices (Neuditschko *et al.* 2012). These matrices were computed using three distinct methods: Euclidean distance applied on allele frequency within individuals (eucl) (Jombart and Ahmed 2011), pairwise difference on number of loci for which individuals differ (nLoci) (Paradis and Schliep 2019), and number of allelic differences between two individuals (nAllele) (Kamvar *et al.* 2014).

We used the Discriminant Analysis of Principal Components (DAPC) and the unsupervised membership grouping in adegenet v2.1.8 to visualize genetic clustering patterns without assumptions about sampling localities (Jombart and Collins 2015). DAPC reduces the dimensionality of genetic data to identify the underlying population structure (Jombart *et al.* 2010). The unsupervised membership grouping on the sampling localities were compared and visualized using K-means clustering. In response to recent critiques of PCA in genetic analyses (Elhaik 2022), we reported the variance explained by the first two PCs and used additional methods to confirm the population structure.

To investigate genetic structure and admixture jointly, we used the Bayesian clustering method of STRUCTURE v2.3.4 (Pritchard *et al.* 2000; Falush *et al.* 2003; Falush *et al.* 2007; Hubisz *et al.* 2009). Ten replicates for each K value ranging from 1 to 10 were performed and the results were extracted using pophelper v2.3.1 (Francis 2017). The optimal K value was determined by identifying the peak of ΔK in the Evanno plots (Evanno *et al.* 2005).

Isolation by distance for each of Mahogany and Squirrel Gliders was investigated by testing correlations between geographical Euclidean distance and pairwise individual genetic distance (proportion of alleles shared) using Mantel tests (Gruber *et al.* 2018). The results of Mantel tests were then visualized using MASS v.7.3 (Kemp 2002).

Genetic differentiation (F_{ST}) analyses were performed to assess the extent of variation explained between the four genetic groups based on neutral loci. These analyses were performed using the bootstrapped method (hierfstat v0.5, Goudet 2005) and Analysis of Molecular Variance (AMOVA) (poppr v2.9.3, Kamvar *et al.* 2014).

Phylogenomics

To clarify the phylogenetic relationships between Mahogany and Squirrel Gliders, we constructed a maximum likelihood phylogenetic tree using IQ-TREE v2.2.2.2 (Minh *et al.* 2020). The tree was built using both neutral and outlier loci with monomorphic loci and missing data removed (N = 6,501) (Appendix S4-5). We used ModelFinder Plus in IQ-TREE to identify the substitution model (Kalyaanamoorthy *et al.* 2017). A maximum likelihood tree was then computed using the selected substitution model (TVM+F+I+G4), in conjunction with the ultrafast bootstrap method with 30,000 replicates. The resulting phylogenetic tree was visualized using iTOL (Letunic and Bork 2021), with Krefft's Gliders rooted as the outgroup based on available literature (Malekian *et al.* 2010; Cremona *et al.* 2020) and the population structure analyses of this study.

Analysis of signatures of selection among consensus genetic groups

Individual loci that significantly deviate from average genome-wide population divergence patterns may indicate the presence of selection. Therefore, we assessed potential local adaptation of the identified genetic groups using the outlier loci dataset derived from the SNP genotyping and filtering section above. We used DAPC in R package adegenet v2.1.8 to assess clustering patterns of individuals based on the outlier loci (Jombart and Collins 2015).

Morphological assessment of consensus genetic groups

Once the consensus genetic groups were identified across the above analyses, we assessed morphological differences among them. We measured body length (snout-vent length) and tail length on live individuals captured in the field and on specimens housed in the Queensland Museum (Brisbane). The museum specimens included both wet (spirit) and dry (skin) specimens. Additionally, head length and head width were taken when specimens contained skulls. We conducted a Factor Analysis of Mixed Data (FAMD) for the total of 118 Mahogany Glider and 79 Squirrel Gliders. The FAMD analysis integrated both categorical (specimen type, sex, tail character) and continuous data (body, tail, head length and width) into a principal component analysis (Kassambara 2016). To address missing values, the regression method from R package missMDA v1.19 was applied (Husson and Josse 2023). The analysis was conducted using the FactoMineR v2.9 (Lê *et al.* 2008) and factoextra v1.07 (Kassambara and Mundt 2020).

4.4.2. Conservation genetic analyses of Mahogany Gliders

The genetic analyses in this section were based on the Mahogany Glider-only data. Genetic diversity was assessed based on neutral loci and the data was filtered to remove markers monomorphic for Mahogany Gliders. Population genetic structure was assessed following the methodology described in the interspecific population structure section above. Additionally, the effective population size for each sampling locality was estimated using the linkage disequilibrium method (and assuming a monogamous mating system) in NeEstimator v2.1 (Jackson 2000b; Do *et al.* 2014). Only Mahogany Glider samples collected between 2017 and 2022 were used, to prevent overlapping generations.

To evaluate the conservation genetics of Mahogany Gliders, we compared genetic diversity of Mahogany Gliders to that of the consensus genetic groups in Squirrel Gliders. We quantified individual genetic diversity using observed and expected heterozygosity (H_o/H_e) and standardized multi-locus heterozygosity (sMLH), as per the methodology in dartR v2.9.7 (Gruber *et al.* 2018) and inbreedR v0.3.3 (Stoffel *et al.* 2016), respectively. The genetic diversity of each sampling locality, consensus genetic group, and species was assessed using several indices, including averaged sMLH, H_o/H_e, Wright's inbreeding index F_{IS} (Gruber *et al.* 2018), and allelic richness (Ar) corrected using the rarefaction method (Adamack and Gruber 2014). To ensure the accurate estimation of heterozygosity, any loci with missing data were excluded (Schmidt *et al.* 2021). Additionally, we included monomorphic loci to examine their effect on the estimation of genetic diversity (Schmidt *et al.* 2021).

4.5. Results

4.5.1. SNP genotyping and filtering

DArTSeq genotyping identified 67,261 single nucleotide polymorphisms (SNPs) across 115 individuals from all three species (Appendix S4-5). For nine samples, DNA extraction was unsuccessful. The quality control process, which considered call rate, reproducibility, secondary loci, and read depth, filtered out low-quality loci and removed an additional 18 low-quality samples (16 from museums and 2 from old field collections). Most of the failed museum samples were fur samples (Appendix S4-6). After these steps, 97 individuals remained with 10,408 SNPs.

Filtering based on minor allele count and linkage disequilibrium excluded 3,455 loci from the all-species dataset, 948 loci from the Mahogany Glider dataset, 1,598 loci from the Squirrel Glider dataset, and 2,514 loci from the Krefft's Glider dataset. Outlier analysis identified 349, 37, and 32 loci as outliers in the all-species dataset, Mahogany Glider dataset, and Squirrel Glider dataset, respectively (Table 4.1). No outliers were identified in the Krefft's Glider dataset because of the low sample size of nine individuals.

Kinship analyses revealed the presence of three pairs of duplicates (kinship coefficient > 0.354, (Manichaikul *et al.* 2010) indicating three individuals were sampled in the field twice. Additionally, six pairs of first-degree relatives (kinship coefficient > 0.16) were identified among the Mahogany Glider samples in Bambaroo and Easter Creek, as well as one triplet of first-degree relatives among Squirrel Glider samples from near Airlie Beach. Among the first-degree relatives, the individual with the highest call rate was retained for genetic structure and diversity analyses.

The number of SNPs in each of the analysis datasets was: 9,258 for all-species dataset (N = 97), 9,651 for Mahogany-Squirrel Glider dataset (N = 88), 9,719 for Mahogany Glider dataset (N = 58), and 8,941 for Squirrel Glider dataset (N = 30).

4.5.2. Genetic and morphological assessment of Mahogany and Squirrel Gliders

Interspecific population structure

In all analyses, Krefft's Gliders from the Wet Tropics formed a highly distinct group compared to Mahogany and Squirrel Gliders. In the NetView analyses, Krefft's Gliders were not joined to any other species, even when the nearest neighbours (kNN) parameter was set to 30 (Fig. 4.2A; Appendix S4-7). In the DAPC analyses, Krefft's Gliders were identified as a highly distinct group that is well-distinguished from the other two species with a high eigenvalue (7608 with all loci, 2927 with neutral loci) (Fig. 4.2B). In the STRUCTURE analyses, Krefft's Glider also emerged as genetically distinct, showing no evidence of genetic admixture with other species (Fig. 4.2C). Results of AMOVA also showed that the outlier loci (N = 542) explained 70% of variation when Krefft's gliders were included (Appendix S4-11). Therefore, below we present results based on neutral loci of Mahogany and Squirrel Glider only.

The genetic structure of Mahogany Gliders exhibits some degree of differentiation from Squirrel Gliders, although the extent of this differentiation varies across different analyses. NetView analyses utilizing Euclidean distance matrices (eucl) consistently delineated Mahogany and Squirrel Gliders into two distinct groups (Appendix S4-7), maintaining separation even up to a kNN value of 42. Conversely, the other two distance matrices (nLoci and nAllele) demonstrated a convergence between Squirrel and Mahogany Gliders at kNN values of 15 and 25, respectively. DAPC distinguished Mahogany and Squirrel Gliders with a high eigenvalue of 1890 (Fig. 4.2B), although only 37% of total variance was explained. STRUCTURE analyses also suggested an optimal clustering at K = 2, demarcating the Mahogany Glider from the Squirrel Glider (Fig. 4.2C; Appendix S4-9).

Three distinct groups of Squirrel Gliders were identified: (1) gliders from the mid-eastern and south-eastern regions of Queensland, extending from Brisbane to Charters Towers (SQ), (2) gliders from Cape Cleveland (CC), and (3) gliders from Chillagoe, Tolga, and Princess Hills north of Townsville (NQ) (Fig. 4.2). The SQ group exhibited considerable variation and consistently formed its own cluster, distinct from the Mahogany Gliders (Fig. 4.2). The assignment of the CC group varied across analyses. In most structure analyses, these gliders were grouped with the Squirrel Gliders (Fig. 4.2A; Appendix S4-8A), but in some analyses, they formed their own distinct cluster (Fig. 4.2B, C; Appendix S4-8A, B). The NQ samples, which comprise a broad distribution from Townsville to Chillagoe in north Queensland, were particularly interesting. Unlike the SQ group, these samples were grouped with Mahogany Gliders in most of the structure analyses, rather than with Squirrel Gliders (Fig. 4.2A, B; Appendix S4-8A).

Despite the clear genetic distinction between Mahogany Gliders and Squirrel Gliders, evidence of introgression between the two species is evident. A gradient of admixture is observed in Squirrel Gliders from north of Mackay to the southern and northwestern range of the Mahogany Glider (Fig. 4.2C). In the STRUCTURE analysis (K = 2), minor introgression is detected between Mahogany Gliders

(MG) and Squirrel Gliders north of Mackay, but more than half of the genetic composition of the CC and NQ groups originates from Mahogany Gliders (Fig. 4.2C). The NQ group, identified as Squirrel Gliders based on morphology and collection localities, were connected with Mahogany Gliders in the NetView analysis at kNN = 30 (Fig. 4.2A). This pattern persisted in the unsupervised membership grouping, where these samples consistently clustered with Mahogany Gliders (Appendix S4-8). Even in the STRUCTURE analysis (K = 2 and K = 5), the NQ samples predominantly displayed genetic components from Mahogany Gliders, with some admixture from CC (Fig. 4.2C).

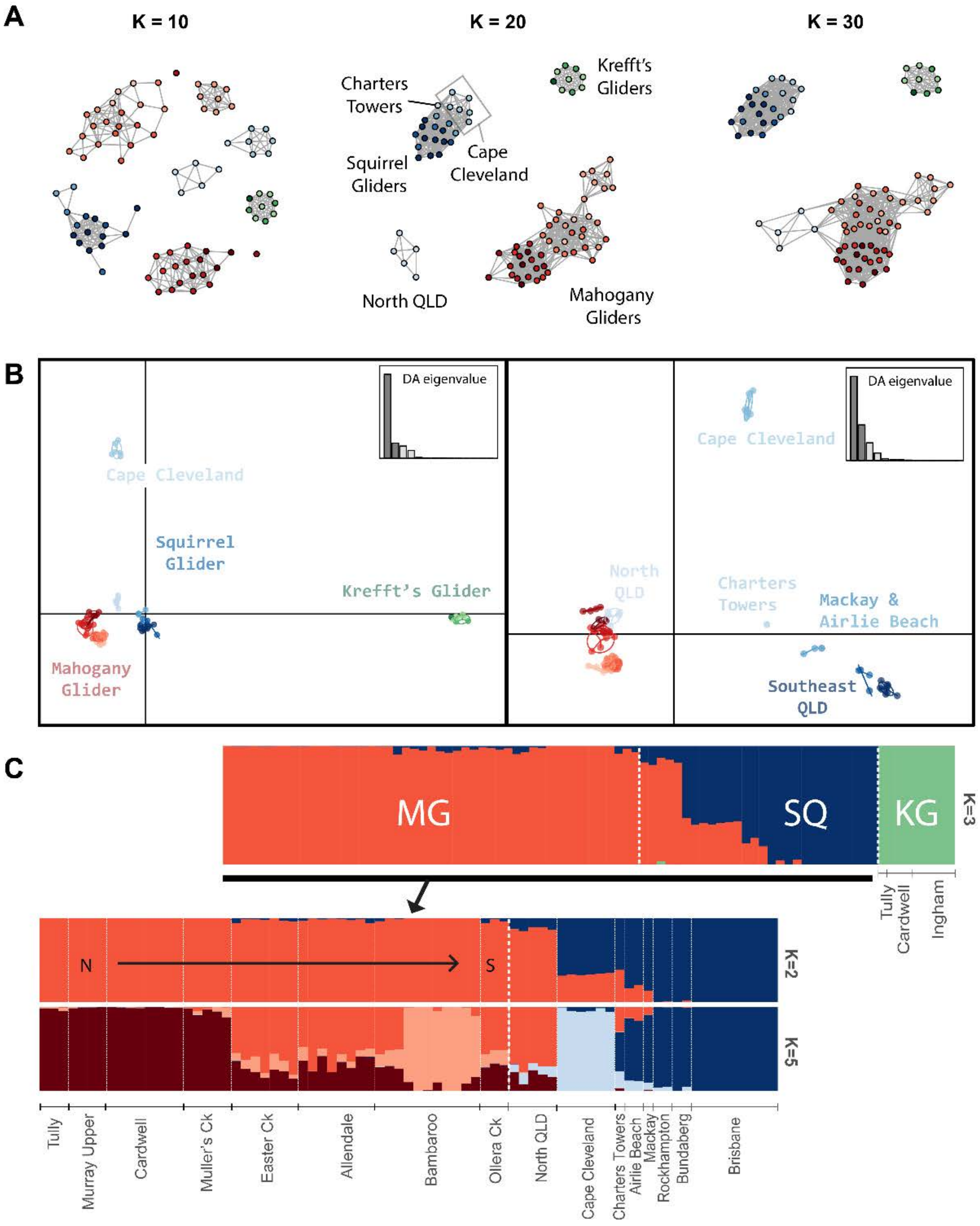

Fig. 4.2 Structure analyses of Mahogany Glider (*P. gracilis*), Squirrel Glider (*P. norfolcensis*), and Krefft's Glider (*P. notatus*): (A) NetView networks for the neutral dataset of the three species. Individuals are coloured based on sampling locality. Krefft's Gliders are depicted in greens, Mahogany Gliders in reds, and Squirrel Gliders in blues. (B) DAPC for all three glider species (left) and Mahogany and Squirrel Gliders only (right). (C) STRUCTURE plots for all three glider species (top) and Mahogany and Squirrel Glider only (bottom), with optimal and second optimal clustering

identified by the ΔK method. See Appendix S4-8 for STRUCTURE plots exclusively for Mahogany and Squirrel Gliders, encompassing K values ranging from 2 to 10.

Phylogenomic analysis further support recognition of four genetic groups

The maximum likelihood tree based on the all-species dataset using both neutral and outlier loci conforms with the population genetic results presented above (Fig. 4.3; Appendix S4-5). Krefft's Gliders form a distinct and divergent group, while the relationships among Mahogany and Squirrel Gliders are complex. All Mahogany Glider samples cluster into a single clade, yet this clade is nested within the broader Squirrel Glider clade. Within this broader clade, the North Queensland (NQ) Squirrel Gliders are the most divergent group, forming a sister clade to the clade that includes the subclades of Mahogany Glider, Cape Cleveland Squirrel Gliders (CC), and mid-eastern/south-eastern Queensland Squirrel Gliders (SQ). These clades and subclades have high bootstrap support (98–100; Fig. 4.3). Additionally, the Mahogany Glider clade is divided into two groups: a northern group (North MG) and a southern group (South MG), separated by the Cardwell Range.

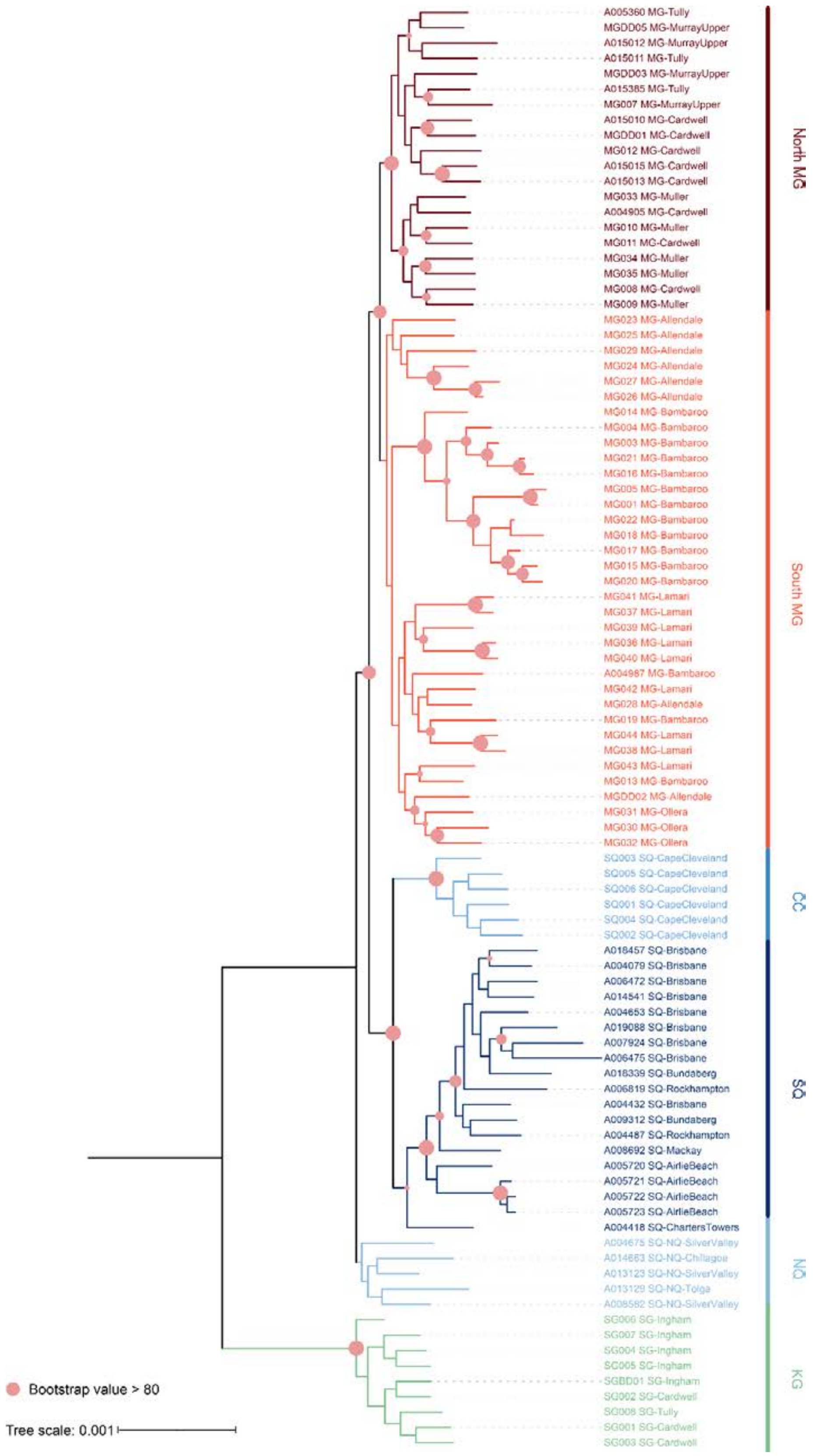
A005360 MG-Tully
MGDD05 MG-MurrayUpper
A015012 MG-MurrayUpper
A015011 MG-Tully
MGDD03 MG-MurrayUpper
A015385 MG-Tully
MG007 MG-MurrayUpper
A015010 MG-Cardwell
MGDD01 MG-Cardwell
MG012 MG-Cardwell
A015015 MG-Cardwell
A015013 MG-Cardwell
MG033 MG-Muller
A004905 MG-Cardwell
MG010 MG-Muller
MG011 MG-Cardwell
MG034 MG-Muller
MG035 MG-Muller
MG008 MG-Cardwell
MG009 MG-Muller
MG023 MG-Allendale
MG025 MG-Allendale
MG029 MG-Allendale
MG024 MG-Allendale
MG027 MG-Allendale
MG026 MG-Allendale
MG014 MG-Bambaroo
MG004 MG-Bambaroo
MG003 MG-Bambaroo
MG021 MG-Bambaroo
MG016 MG-Bambaroo
MG005 MG-Bambaroo
MG001 MG-Bambaroo
MG022 MG-Bambaroo
MG018 MG-Bambaroo
MG017 MG-Bambaroo
MG015 MG-Bambaroo
MG020 MG-Bambaroo
MG041 MG-Lamari
MG037 MG-Lamari
MG039 MG-Lamari
MG036 MG-Lamari
MG040 MG-Lamari
A004987 MG-Bambaroo
MG042 MG-Lamari
MG028 MG-Allendale
MG019 MG-Bambaroo
MG044 MG-Lamari
MG038 MG-Lamari
MG043 MG-Lamari
MG013 MG-Bambaroo
MGDD02 MG-Allendale
MG031 MG-Ollera
MG030 MG-Ollera
MG032 MG-Ollera
SQ003 SQ-CapeCleveland
SQ005 SQ-CapeCleveland
SQ006 SQ-CapeCleveland
SQ001 SQ-CapeCleveland
SQ004 SQ-CapeCleveland
SQ002 SQ-CapeCleveland
A018457 SQ-Brisbane
A004079 SQ-Brisbane
A006472 SQ-Brisbane
A014541 SQ-Brisbane
A004653 SQ-Brisbane
A019088 SQ-Brisbane
A007924 SQ-Brisbane
A006475 SQ-Brisbane
A018339 SQ-Bundaberg
A006819 SQ-Rockhampton
A004432 SQ-Brisbane
A009312 SQ-Bundaberg
A004487 SQ-Rockhampton
A008692 SQ-Mackay
A005720 SQ-AirlieBeach
A005721 SQ-AirlieBeach
A005722 SQ-AirlieBeach
A005723 SQ-AirlieBeach
A004418 SQ-ChartersTowers
A004675 SQ-NQ-SilverValley
A014663 SQ-NQ-Chillagoe
A013123 SQ-NQ-SilverValley
A013129 SQ-NQ-Tolga
A008582 SQ-NQ-SilverValley
SG006 SG-Ingham
SG007 SG-Ingham
SG004 SG-Ingham
SG005 SG-Ingham
SGBD01 SG-Ingham
SG002 SG-Cardwell
SG008 SG-Tully
SG001 SG-Cardwell
SG003 SG-Cardwell
North MG
South MG
CC
SQ
NQ
KG
● Bootstrap value > 80
Tree scale: 0.001

Fig. 4.3 The maximum likelihood phylogenetic tree of all glider samples. Krefft's Gliders form a distinct clade, and four subclades were found in Mahogany and Squirrel Glider clade: North Queensland (NQ), Mahogany Gliders (MG), Cape Cleveland (CC) and mid-eastern/south-eastern Queensland individuals (SQ). The Mahogany Glider clade is further split into northern (brown) and southern (orange) individuals. The unit for the tree scale represents the number of substitutions per site. The tree was built using IQ-TREE v2.2.2.2 (Minh *et al.* 2020) with 30,000 bootstrap replicates and was rooted with Krefft's Glider in iTOL (Letunic and Bork 2021).

Genetic differentiation among consensus genetic groups

Pairwise genetic differentiation (F_{ST}) was calculated based on neutral loci among the four genetic groups (Table 4.2). The F_{ST} estimates are moderate between groups, ranging from 0.14 to 0.19. The exception to this is the lower estimate of 0.07 between the NQ Squirrel Gliders and Mahogany Gliders (Table 4.2). Notably, the F_{ST} estimates between Mahogany Gliders and the three Squirrel Glider groups (NQ, CC, and SQ) were lower (0.07–0.14) compared to the differentiation observed among the three Squirrel Glider groups themselves (0.17–0.19; Table 4.2)

Table 4.2 Pairwise F_{ST} calculated based on neutral loci (lower unshaded diagonal) between the four consensus genetic groups as determined by the results of population genetic structure and phylogenetic analyses. These groups are Mahogany Gliders (MG), the North Queensland individuals (NQ), the Cape Cleveland individuals (CC), and the remaining Squirrel Gliders (SQ).

F_{ST}/ Group	**MG**	**NQ**	**CC**	**SQ**
MG	NA			
NQ	0.07	NA		
CC	0.14	0.19	NA	
SQ	0.14	0.19	0.17	NA

Signatures of selection

In the analysis of molecular variance (AMOVA) of the all-species dataset, the outlier loci explained around 65% of the variance between species, whereas only about 10% of the variance was attributed to the four consensus genetic groups (Appendix S4-11). However, in the AMOVA focusing only on Mahogany and Squirrel Gliders, the variance explained between species became negative. Instead, nearly 75% of the genetic variation was explained by the outlier loci within the four genetic groups (Appendix S4-11).

The DAPC plot based on 101 outlier loci explained 82% of the total variance among the genetic groups (Fig. 4.4). PC1 (x-axis) had a high eigenvalue of 1908 and primarily differentiated CC Squirrel Gliders from Mahogany Glider and NQ Squirrel Gliders. PC2 (y-axis), with an eigenvalue of 691, further distinguished mid-eastern/south-eastern Queensland (SQ) Squirrel Gliders from the other three genetic groups. The plot also shows distinct genetic clustering of CC and SQ, while MG and NQ show significant overlap (Fig. 4.4).

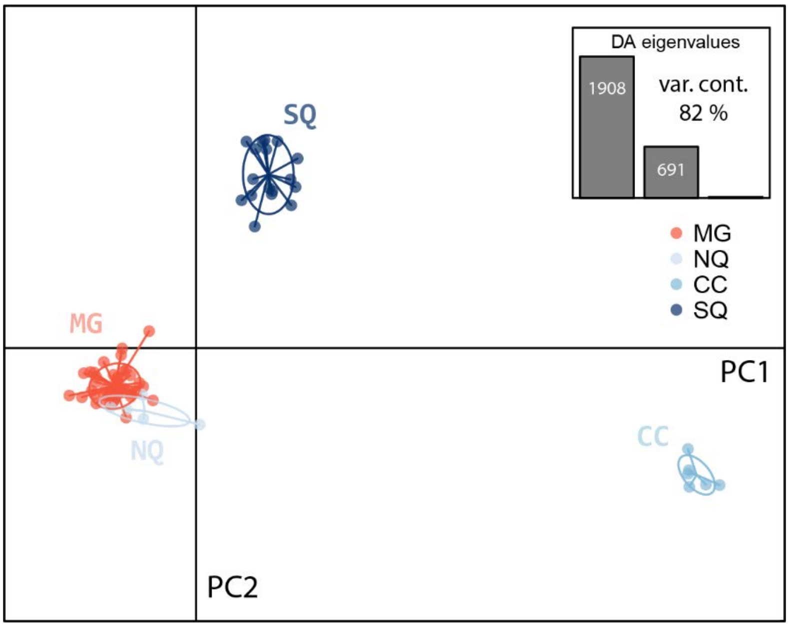

Fig. 4.4 The Discriminant Analysis of Principal Components (DAPC) of outlier loci from Mahogany and Squirrel Gliders. The individuals are marked by the four consensus genetic groups based on genetic structure. Mahogany Gliders (MG) are represented in red, North Queensland individuals (NQ) and Cape Cleveland individuals (CC) in light blue, and mid-eastern/south-eastern Queensland

individuals (SQ) in dark blue. The eigenvalues and the total variance contribution (var. cont.) of the DAPC plot are displayed in the top right corner.

Morphological assessment among consensus genetic groups

The Mahogany Glider was originally described as a larger glider, with a relatively longer and more slender tail, compared to Squirrel Gliders. The measurements in this study generally confirmed these morphological differences (Fig. 4.5A). MG individuals were larger, with longer bodies and longer tails compared to NQ, CC, and SQ (Fig. 4.5A). However, they are not distinct for relative tail length, with the mean tail-to-body length ratio for NQ and CC being similar to that of Mahogany Gliders (Fig. 4.5A). Compared to the other groups, SQ have relatively shorter tails. However, larger sample sizes are required for NQ and CC.

The Factor Analysis of Mixed Data (FAMD) revealed that individuals identified as Mahogany versus Squirrel Gliders could be distinguished by a combination of body length, tail length, head length, head width, and tail base thickness (slender versus wide/fluffy tail base); however, there was some overlap (Fig. 4.5B). The first dimension of the FAMD accounted for 36.5% of the variation, with body length, head length, and tail length contributing 26.25%, 26.15%, and 24.65%, respectively. Nevertheless, it is important to interpret the results cautiously due to different specimen types and limited numbers of individuals for NQ and CC.

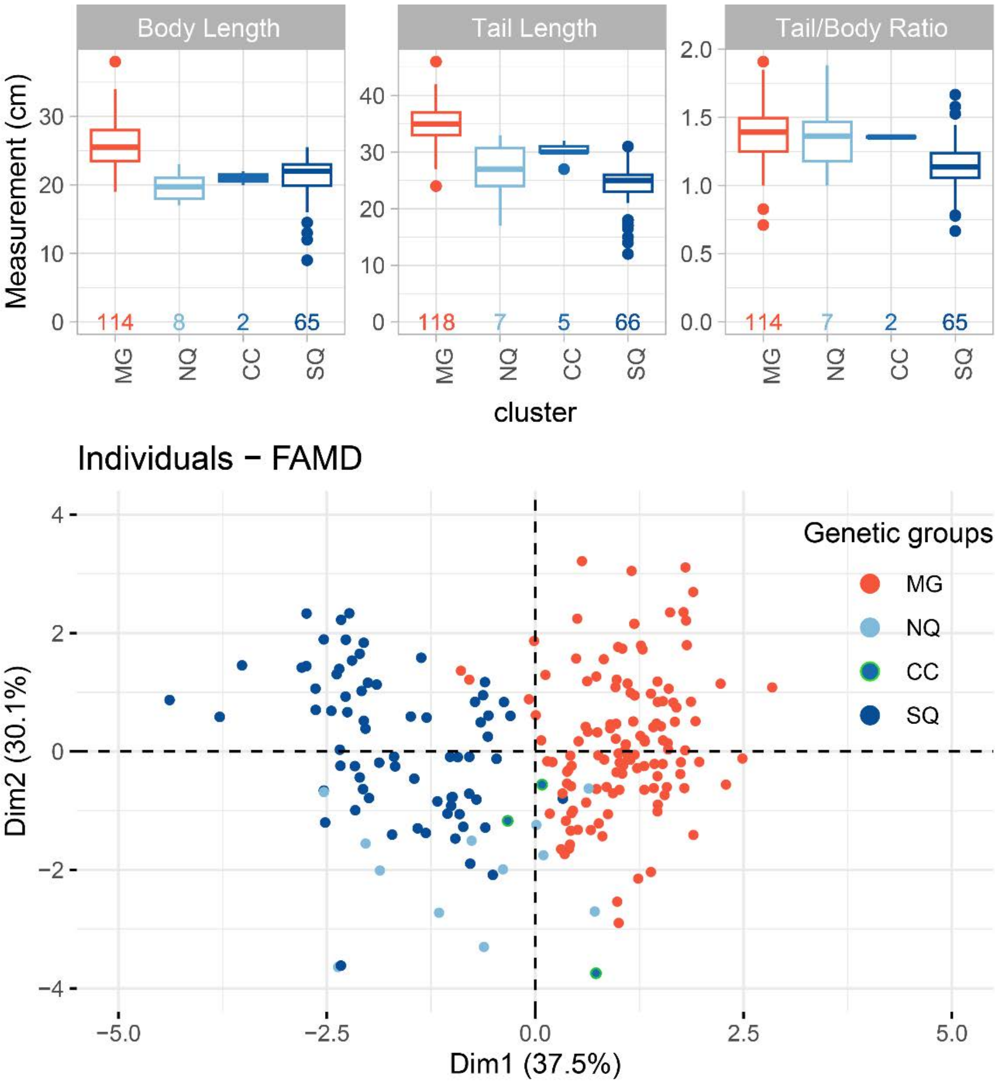

Fig. 4.5 Boxplots (A) and Factor Analysis of Mixed Data (FAMD) (B) for morphological traits for Mahogany and Squirrel Glider consensus genetic groups. The boxplots illustrate body length (cm), tail length (cm), and tail-to-body length ratio for the four consensus genetic groups: Mahogany Gliders (MG), North Queensland individuals (NQ), Cape Cleveland individuals (CC), and mid-eastern/south-eastern Queensland Squirrel Gliders (SQ). Sample sizes for each measurement are indicated under the boxplot. The FAMD plot (B) demonstrates the four genetic groups based on five morphological measurements: body length, tail length, head length, head width, and tail character.

4.5.3. Conservation genetics of Mahogany Gliders

After confirming that Mahogany Gliders are a moderately distinct genetic and phenotypic group through the analyses above, we conducted a genetic assessment of this Endangered taxon.

Mahogany glider monitoring and abundance

Genetic structure analysis

Two distinct genetic clusters were identified within Mahogany Gliders. These clusters correspond to the sampling localities north of the Herbert River/Cardwell Range (Muller's Creek, Cardwell, Murray Upper, and Tully) versus the sampling localities south of the Herbert River (Ollera Creek, Bambaroo, Allendale, and Easter Creek) (Fig. 4.1; Fig. 4.6). In the Discriminant Analysis of Principal Components (DAPC), K-means clustering identified two clusters as optimal, explaining 44% of total variation. The northern and southern clusters were separated by the first eigenvalue (811.8), while the second eigenvalue (106) showed some discrimination among localities within each of the northern and southern clusters (Fig. 4.6A). The Evanno plots generated during the STRUCTURE analysis supported the identification of two clusters (K) as optimal, aligning with the clustering observed in the DAPC analysis (Appendix S4-9). However, F_{ST} between the northern and southern clusters was relatively low ($F_{ST} = 0.054$, 95% CI: 0.051–0.058), and the unsupervised membership grouping only identified one cluster within Mahogany Gliders.

The northern cluster demonstrated greater genetic homogeneity, while the southern cluster showed more genetic substructure (Fig. 4.6B). Upon identifying the optimal two clusters (K = 2) in the STRUCTURE analysis, the southern cluster demonstrated genetic admixture from the northern cluster, though not reciprocally. At the second optimal clustering (K = 6), the northern cluster remained virtually homogenous, but the southern cluster showed more substructure. Interestingly, the Bambaroo site displayed its own genetic subcluster and had the least genetic admixture compared to other sampling localities in the southern cluster (Fig. 4.6B). NetView analyses yielded similar results — while all Mahogany Gliders form a distinct cluster when the nearest neighbours were set to 20 (kNN = 20), at kNN = 10, three distinct groups emerged: northern, southern, and Bambaroo groups (Appendix S4-7).

The Mantel test results showed a statistically significant but weak isolation by distance, with only 12.6% ($R^2 = 0.126$) of the variation explained by geographical distance among the Mahogany Glider samples (Appendix S4-13A). Notably, after grouping the gliders into northern and southern clusters based on genetic structure analysis, genetic distances within the northern cluster exhibit a stronger correlation with geographical distance ($R^2 = 0.236$) (Appendix S4-13C).

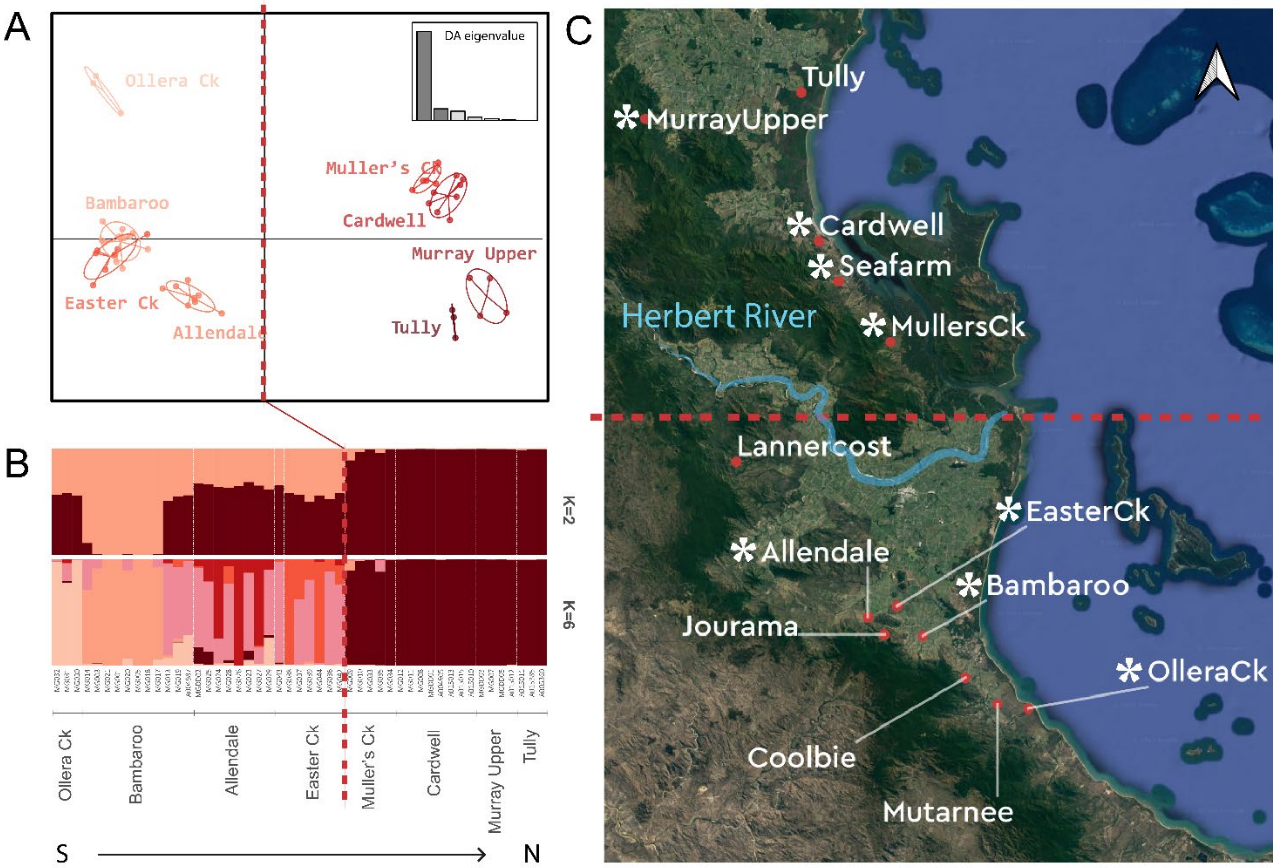

Fig. 4.6 Population genetic structure of Mahogany Gliders. (A) Discriminant Analysis of Principal Components (DAPC) across all sampling localities, with the first DA eigenvalue (PC1, x-axis) explaining most of the variation. (B) STRUCTURE analysis illustrating the optimal (K = 2) and second optimal (K = 6) clustering, with sampling localities arranged from south (left) to north (right). (C) Map of sampling localities, with the Herbert River marked in blue. The red dashed line in plots A, B, and C signifies the separation between northern and southern populations based on optimal clustering results. Asterisks on the map in panel C show sampling sites with trapping success (Appendix S4-1). Comparative genetic diversity and effective population size estimates

Genetic diversity and effective population size estimates

The neutral genetic diversity between Mahogany Gliders and Squirrel Gliders is similar. Mahogany Gliders exhibit a standardized multi-locus heterozygosity (sMLH) of 1.13, while Squirrel Gliders have a sMLH of 0.895. The observed heterozygosity (Ho) is 0.116 for Mahogany Gliders and 0.089 for Squirrel Glider, and the expected heterozygosity (He) is 0.13 for Mahogany Gliders and 0.118 for

Squirrel Glider (Appendix S4-3). Note that the inbreeding coefficient (F_{IS}) is higher in Squirrel Gliders in comparison to Mahogany Gliders, likely due to the mixture of structured populations (Wahlund effect) (De Meeûs 2018).

Within Mahogany Gliders (MG), the sMLH ranges from 0.78 to 1.06, with an average of 0.98. The H_o varies from 0.14 to 0.19, averaging at 0.17, and the F_{IS} ranged from 0.01 to 0.20, with an average of 0.07 (Table 4.3; Appendix S4-3). The northern cluster showed lower genetic diversity indices compared to the southern cluster, with individuals from Murray Upper—the northernmost site of their current known range—exhibiting the lowest genetic diversity (sMLH = 0.776, FIS = 0.201). Bambaroo, despite its small size and isolation, displayed a wide range of sMLH (0.75–1.26) and H_o (0.13–0.22) values, with a low F_{IS} of 0.05 (Appendix S4-12; Table 4.3).

The effective population size could only be estimated for the three sampling localities with more than six samples: Allendale, Bambaroo, and Easter Creek (Table 4.3; Appendix S4-4). In Allendale, the effective population size was low, with a mean of 37 individuals (parametric CI: 35.4–38.8, Jackknife CI: 7.8–infinite). Bambaroo also exhibited a low effective population size, with a mean of 27.6 individuals (parametric CI: 27.1–28.1, Jackknife CI: 19–45.1). Conversely, Easter Creek displayed a notably high effective population size, with a mean of 431.2 individuals (parametric CI: 324.4–640.6, Jackknife CI: 45.8–infinite).

Table 4.3 Genetic diversity metrics and effective population size estimates for Mahogany Gliders, including south and north populations, and sampling localities. Metrics provided are the number of individuals (nInd), standardized multilocus heterozygosity (sMLH), observed heterozygosity (Ho), expected heterozygosity (He), inbreeding coefficient (FIS), and effective population size estimates (Ne). Refer to Appendix S4-3 and S4 for a full table with standard deviations and confidence intervals that includes Squirrel Glider genetic groups.

Dataset	Group	nInd	sMLH	Ho	He	FIS	Ne
All-species	MG	49	1.13	0.116	0.13	0.114	-
Mahogany Glider	South MG	29	1.04	0.184	0.204	0.111	-
	North MG	20	0.942	0.167	0.186	0.124	-
	Allendale	8	1.063	0.188	0.189	0.068	64.7
	Bambaroo	11	1.028	0.182	0.184	0.054	27.6
	Cardwell	8	0.973	0.172	0.177	0.085	-
	Easter Ck	7	1.044	0.185	0.186	0.077	431.2
	Muller	5	1.039	0.184	0.175	0.053	-
	Murray Upper	4	0.776	0.138	0.151	0.201	-
	Ollera Ck	3	1.014	0.18	0.158	0.053	-
	Tully	3	0.921	0.163	0.149	0.085	-

4.6. Discussion

4.6.1. Genetic and morphological assessment of Mahogany and Squirrel Gliders

Aiming to inform effective conservation management of the Endangered Mahogany Glider, we utilised genomic tools at both broad and fine scales. We firstly examined the population genetic structure of the Mahogany Glider (*Petaurus gracilis)*, Squirrel Glider (*P. norfolcensis*) and Krefft's Glider (*P. notatus*) to gain insight on their evolutionary relationships and genetic distinctiveness of the Mahogany Glider. Subsequently, we conducted a conservation genetic assessment for the Mahogany Glider. The analyses confirmed that the Krefft's Glider is highly divergent from the other two species. In contrast, genetic relationships between Mahogany and Squirrel Gliders are more complex. Genetic structure and phylogenetic analyses consistently identified four genetic groups: Mahogany Gliders from the lowlands of the Wet Tropics, 'Squirrel Gliders' from inland North Queensland (NQ), 'Squirrel Gliders' from Cape Cleveland near Townsville (CC), and Squirrel Gliders from mid-eastern and south-eastern Queensland (i.e., from about Charters Towers and Proserpine south).

Mahogany Gliders are generally distinct from the other three genetic groups in the genetic analyses but with genetic admixture evident with the NQ and CC genetic groups (Fig. 4.2). The genetic admixture between Mahogany and Squirrel Gliders suggests that historical or contemporary introgression has occurred between these species. The complexity of relationships between Mahogany and Squirrel Gliders has been previously suggested in phylogenetic studies on the Petaurid gliders. For instance, Malekian *et al.* (2010) revealed a genetic difference of only 1.8–2.2% between Mahogany and Squirrel Gliders for two mitochondrial genes (ND2 and ND4) and one nuclear marker (ω-globin). A different phylogenetic study, based on ND2 mitochondrial gene and ApoB1 nuclear gene, clustered Mahogany Glider samples with Squirrel Glider samples from Hervey Range (west of Townsville) and Einasleigh Uplands (west of Atherton Tablelands) (Ferraro 2012). The phylogenomic relationship we present here shows Mahogany Gliders nested within the broad Squirrel Glider clade but does show Mahogany Gliders as a highly supported, distinct clade (Fig. 4.3).

We found substantial introgression between Mahogany Gliders and the gliders from North Queensland (NQ) (samples collected near Princess Hills, Atherton Tablelands, and Chillagoe) (Fig. 4.2C). The NQ gliders also group closely to Mahogany Gliders in signature of selection based on outlier loci and structure analyses based on neutral loci (e.g., NetView, Fig. 4.2A; DAPC, Fig. 4.2B; Signature of selection, Fig. 4.4). The low F_{ST} value between NQ gliders and Mahogany Gliders further support the close relationship between them (Table 4.2). Interestingly, in the SNPs-based phylogeny (Fig. 4.3), the NQ samples are divergent to a monophyletic group of Mahogany and Squirrel Gliders, rather than being clustered within it (Fig. 4.3). The morphology is interesting for the NQ gliders — they are of similar body size to Squirrel Gliders, but their relative tail length is more akin to Mahogany Gliders (albeit based on a small sample size) (Fig. 4.5). Overall, the results suggest a close genetic relationship between NQ gliders and Mahogany Gliders, and whether hybridisation or cryptic (sub)species exist in NQ gliders requires further sampling and analyses (Malinsky *et al.* 2018).

The gliders from Cape Cleveland (CC) are identified as a genetically distinct group in most of the analyses. They are more closely related to Squirrel Gliders but show signs of introgression from Mahogany Gliders (e.g., NetView, Fig. 4.2A; Structure, Fig. 4.2C; phylogeny, Fig. 4.3). In some analyses, they appear as a distinct group (e.g., DAPC, Fig. 4.2B; Pairwise F_{ST}, Table 4.2) and exhibit a relatively long and slender tail, similar to that of Mahogany Gliders. Additionally, CC samples exhibit a unique signature of selection that differs from both Mahogany and Squirrel Gliders (Fig. 4.4). It is likely that the gliders from Cape Cleveland are adapted to their local coastal habitat, a peninsula of tropical lowland eucalyptus woodlands, rainforest, and wetlands. The genetically and ecologically distinct CC gliders are therefore potentially qualified as a subspecies of Squirrel Glider with further sampling and analyses. Furthermore, we recorded a high glider density at Cape Cleveland, with a catch rate of 15.4%. This high density, along with their greater genetic diversity compared to other Squirrel Gliders (Table 4.3), indicates that the CC population is genetically healthy.

While genetic admixture exists between the Mahogany Glider and other genetic groups, compelling evidence supports the classification of the Mahogany Glider as at least a highly distinct subspecies. This classification finds support in their status as a monophyletic clade, distinct clustering, and characteristic morphology (e.g., phylogeny, Fig. 4.3; NetView, Fig. 4.2A; Morphology, Fig. 4.2C;), which suggest a distinct evolutionary path despite their close genetic relationship to the Squirrel Gliders (Fig. 4.3). Morphological features are also unique in Mahogany Gliders, as seen in the FAMD analysis (Fig. 4.5). These morphological distinctions are consistent with the species description of the Mahogany Glider by Van Dyck (1993) and measurements presented elsewhere (e.g., Ferraro 2012). Furthermore, as for CC gliders, signature of selection analysis suggests potential local adaptation in the Mahogany Glider (Fig. 4.4). These findings indicate that the Mahogany Glider has potentially adapted in a unique way to the lowland open forests of the Wet Tropics. Further research is needed to fully understand the factors driving local adaptation and its implications for the conservation of this species.

4.6.2. Conservation genetics of Mahogany Gliders

Genetic diversity of the Mahogany Glider is generally comparable to the non-threatened Squirrel Gliders analysed in this study. Comparisons of heterozygosity based on SNPs, employing similar filtering methods, indicate that the observed heterozygosity (H_o) of the Mahogany Glider is comparable to other threatened marsupials listed in the EPBC Act 1999 (Threatened Species Scientific Committee 2023), such as the Koala (Phascolarctos cinereus), Northern Bettong *(Bettongia tropica*), Western Barred Bandicoot (*Perameles bougainville*) and Greater Glider (*Petauroides volans*) (Table 4.3). However, this range of observed heterozygosity is lower when compared to species with a vulnerable status, such the Greater Bilby (*Macrotis lagotis*), Burrowing Bettong (*Bettongia lesueur*), Long-nosed Potoroo (*Potorous tridactylus*), and Golden Bandicoot (*Isoodon auratus*) (Table 4.4). Caution should be taken when comparing genetic indices across species, as these indices are heavily dependent on the evolutionary history and population genetics of each species and thus can be influenced by biases introduced through different filters, thresholds, and sample sizes (Schmidt *et al.* 2021). For instance, despite being categorized as Least Concern in terms of conservation status, the Sugar Glider (*P. breviceps*) and Krefft’s Glider consistently exhibit low observed heterozygosity (Knipler *et al.* 2022), as also seen for Krefft’s Gliders in our study here (Appendix S4-3).

Table 4.4 Observed SNPs heterozygosity (H_o) ranges of selected Australian marsupials with EPBC conservation status.

Species	**Scientific name**	**EPBC Status**	**H_o (range)**	**Reference**
Mahogany Glider	*Petaurus gracilis*	Endangered	0.12 (0.16–0.19)	This study
Koala	*Phascolarctos cinereus*	Endangered	(0.22–0.29)	Kjeldsen *et al.* 2019
Northern Bettong	*Bettongia tropica*	Endangered	(0.15–0.22)	Todd *et al.* 2023
Western Barred Bandicoot	*Perameles bougainville*	Endangered	(0.14–0.22)	White *et al.* 2018
Greater Glider (south)	*Petauroides volans*	Endangered	0.14 (0.09–0.21)	Knipler *et al.* 2023
Greater Bilby	*Macrotis lagotis*	Vulnerable	0.26	White *et al.* 2018
Burrowing Bettong	*Bettongia lesueur*	Vulnerable	(0.18–0.31)	White *et al.* 2018
Long-nosed potoroo	*Potorous tridactylus*	Vulnerable	0.34	Mulvena *et al.* 2020
Golden Bandicoot (mainland)	*Isoodon auratus*	Vulnerable	(0.28–0.31)	Rick *et al.* 2023
Red-tailed Phascogale	*Phascogale calura*	Vulnerable	(0.19–0.20)	Pierson *et al.* 2023
Squirrel Glider	*P. norfolcensis*	Least Concern	0.18	Knipler *et al.* 2021
Sugar Glider	*P. breviceps*	Least Concern	(0.15–0.16)	Knipler *et al.* 2022

Structure analyses have revealed two distinct genetic clusters within Mahogany Gliders — the northern and the southern cluster (Fig. 4.6). The Cardwell Range, situated between these two clusters, appears to serve as a natural barrier. Interestingly, despite this geographical division, genetic admixture persists between the northern and southern groups. This admixture could be a result of natural gene flow through the upper catchment of the Herbert River, or movements across the Herbert River (which is narrow in places). Interestingly, there is a significant northern genetic component in the southern cluster, and this asymmetry cannot be explained based on data to date.

The northern cluster is characterized by lower genetic diversity comparing to the southern cluster, a more homogeneous genetic structure (Fig. 4.8B), and moderate isolation by distance (24% of genetic variation in this cluster is explained by isolation by distance; Appendix S4-13). Acceptable connectivity of populations may exist through this area, but perhaps only until recently. The catch rate at Muller's Creek was previously recorded between 7.5–15% in 1995–1996 (Jackson 1998) and around 11.5% in 2008 (personal communication with Mark Parsons, Queensland Government 2020). These high catch rates suggest high glider density in a quality habitat. In contrast, recent catch rate at Muller's Creek was lower in our study using similar field techniques — just 2% and 3% in 2021 and 2022, respectively (Appendix S4-1). Furthermore, individuals from Murray Upper, the northernmost known population of the species, exhibit worryingly low individual heterozygosity (H_o and sMLH; Table 4.3), indicating the population is inbred to some degree. The massive clearance and sugar cane farming in the Tully region from 1880 to 1905 removed and fragmented much suitable habitat (QImaginary 1957; Bolton 1970; The University of Queensland 2018), a situation exacerbated by further clearing over the following decades and widespread habitat damage during Cyclone Yasi (Holloway 2013). However, ongoing forest thickening due to changes in fire regimes (Stanton *et al.* 2014a; Stanton *et al.* 2014b) may be a key issue in reducing habitat suitability in recent times in the northern half of the range (Chang *et al.* 2022).

The southern cluster of the Mahogany Glider is genetically more structured across different sampling localities (Fig. 4.6), and only 10% of genetic variation is explained by isolation by distance (Appendix S4-13). Therefore, factors other than distance are likely contributing to the population structure. The most likely explanation is habitat fragmentation and hence restricted movement between populations. However, catch rates at some southern sites were high, suggesting considerable abundance within the habitat fragments. Catch rates were high at Bambaroo, Allendale and Easter Creek (Appendix S4-1), and these sites had higher genetic diversity than sites in the northern cluster (Table 4.3). These sites are intriguing given how small these fragments are and low Ne estimates for Bambaroo (Ne = 27.6) and Allendale (Ne = 64.7). This discrepancy may reflect a delay in the loss of neutral genetic diversity because neutral genetic diversity lags behind population isolation and decline (Pinto *et al.* 2023). The connectivity between Bambaroo and adjacent coastal forest was lost in 1988 (QImaginary 1951; Google Earth imagery through time) and Easter Creek only became fragmented during extensive logging from 1987 to 1997 (QImaginary 1993; Google Earth imagery through time). Given population isolation only occurred in the past 40 years, the full impact of habitat loss and fragmentation on the density and genetic diversity of the Mahogany Gliders in this area is yet to be seen.

4.6.3. Conclusion and Management Recommendations

This study has shown that the genetics of Mahogany and Squirrel Gliders is complex in Queensland, but that four consensus genetic groups are supported: Mahogany Glider, North Queensland gliders, Cape Cleveland gliders and Squirrel Gliders from mid-eastern/south-eastern Queensland. Evidence of genetic introgression between these groups was found, but whether it is historical or ongoing remains unclear. A first step for conservation is resolving the taxonomic uncertainty associated with these four genetic groups. It is possible that all four groups represent subspecies of the Squirrel Glider, but this requires further genetic and morphological investigation. Sampling should focus on the broad areas of introgression and narrow in on areas of potential contact zones of the four genetic groups. Genetic and phenotypic investigations at these contact zones could resolve the current level of genetic isolation (e.g., Hoskin *et al.* 2005; Harrison and Larson 2016; Malinsky *et al.* 2018; Caeiro-Dias *et al.* 2021) and help resolve the taxonomy. Key sampling areas are located at the southern and western edge of the Mahogany Glider distribution (for contact with NQ and CC), and the Charters Towers–Townsville–Ayr region (for contact between NQ, SQ and CC).

In regard to the ongoing conservation of the Mahogany Glider, the genetic and morphological data presented here suggest that this taxon is at least a subspecies, that is, either as a full species or a subspecies of the Squirrel Glider complex. In Australia, subspecies receives the same conservation status as species under the EPBC Act 1999 (Threatened Species Scientific Committee 2023). Given the ongoing threats of habitat loss for the Mahogany Glider, it is imperative that current conservation efforts continue to ensure the long-term survival of these genetically and morphologically distinct gliders. The next critical conservation step involves monitoring population trends and developing tailored conservation strategies for the northern and southern genetic clusters. These strategies should aim to increase population sizes and genetic diversity in the northern cluster and increase connectivity and effective population sizes in the fragmented southern cluster. The latter can be achieved through a combination of assisted gene flow and revegetation of functional habitat corridors. Continuous genetic monitoring of vulnerable populations, particularly those with low effective population sizes and poor genetic diversity, is essential. Additional surveys should continue to better resolve the fine-scale distribution and local densities of the Mahogany

Glider, to better understand habitat determinants, connectivity, and target future conservation genetic research.

4.7. Ethics and permits

The research was conducted in accordance with Queensland animal permits for scientific purposes (protected areas: P-PTUKI-100021853; non-protected areas: WA0025939) and animal ethics under James Cook University (A2699).

4.8. Conflicts of interest

The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

4.9. Data availability statement

The model and analysis script used this study are available in FigShare at DOI: 10.6084/m9.figshare.24618996. The supplementary tables and figures of this study are available in the accompanying online supplementary materials.

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Appendices

Appendix S4-1 Summary of trapping results and effort across sites, ordered from south to north of the Mahogany Glider range in the Wet Tropics. The gliders caught indicated Mahogany Glider except for the site at Cape Cleveland. The table includes information on the number of cages used, the duration of trapping in nights, the number of gliders caught, trapping effort calculated as the product of cages and nights, and the trapping rate expressed as a percentage, calculated as the total number of gliders caught by the total trapping effort for the site.

Region	**Site**	**Cages**	**Nights**	**Gliders Caught**	**Trapping Effort†**	**Trapping rate (%)**
Southern Paluma	Ollera Ck	20	5	3	100	3.0
	Mutarnee	20	5	0	100	0.0
Northern Paluma	Jourama	20	2	0	40	0.0
	Coolbie	20	5	0	100	0.0
	Jourama & Bamabroo	20	5	6	100	6.0
	Easter Ck	20	5	9	100	9.0
	Bambaroo	20	5	10	100	10.0
	Jourama + Allendale	20	5	7	100	7.0
Ingham	Lannercost SF	20	5	0	100	0.0
Cardwell	Murray Upper	21	6	1	126	0.8
	Cardwell SF	23	5	1	115	0.9
	Muller's Ck	20	5	2	100	2.0
	Seafarm	21	5	2	105	1.9
	Muller's Ck	20	5	3	100	3.0
Tully	Tully Euramo	20	5	0	100	0.0
Townsville	Cape Cleveland	13	3	6	39	15.4
Total			318	50	1525	

†Trapping effort = number of cages*number of nights
SF = State Forest; Ck = Creek

Appendix S4-2 Summary of genetic samples used in this study. The table comprises 67 Mahogany Gliders (44 from cage trapping, 13 from rescued and previously studied individuals, 10 sourced from Queensland Museum), 49 Squirrel Gliders (6 from cage trapping and 43 sourced from the Queensland Museum), and 9 Krefft's Gliders (all from cage trapping in the Wet Tropics). The table details the unique identification (ID), common species name, sex, sampling location, year of collection, specimen type, collection source, sampling latitude, longitude, and the associated accuracy of these coordinates.

ID	Species	Sex	Sampling Locality	Year	Type	Source	Lat	Lon	GPS Accuracy
MGDD01	Mahogany Glider	F	Cardwell	2021	fur	Acquired	-18.23	145.94	high
MGDD02	Mahogany Glider	M	Allendale	2021	ear	Acquired	-18.84	146.08	high
MGDD03	Mahogany Glider	F	Murray Upper	2021	fur	Acquired	-18.13	145.80	low
MGDD04	Mahogany Glider	F	Murray Upper	2021	fur	Acquired	-18.15	145.80	high
MGDD05	Mahogany Glider	F	Murray Upper	2022	skin	Acquired	-18.11	145.80	high
MGMP01	Mahogany Glider	NA	Muller's Ck	2008	ear	Acquired	-18.42	146.13	medium
MGMP02	Mahogany Glider	NA	Muller's Ck	2008	ear	Acquired	-18.43	146.14	medium
MGMP03	Mahogany Glider	NA	Muller's Ck	2008	ear	Acquired	-18.43	146.14	medium
MGMP04	Mahogany Glider	M	Cardwell	NA	ear	Acquired	-18.25	145.97	medium
MGMP05	Mahogany Glider	M	Ingham	2011	ear	Acquired	-18.86	146.13	low
MGMP06	Mahogany Glider	M	Tully	2011	ear	Acquired	-18.05	145.91	low
MGMP07	Mahogany Glider	F	Cardwell	2010	ear	Acquired	-18.23	145.98	medium
MGMP08	Mahogany Glider	F	Tully	2011	ear	Acquired	-18.05	145.91	low
SGBD01	Krefft’s Glider	M	Ingham	2021	muscle	Acquired	-18.55	146.17	low
MG001	Mahogany Glider	F	Bambaroo	2021	ear	Field	-18.87	146.18	high
MG002	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.86	146.18	high
MG003	Mahogany Glider	F	Bambaroo	2021	ear	Field	-18.86	146.19	high
MG004	Mahogany Glider	F	Bambaroo	2021	ear	Field	-18.86	146.19	high
MG005	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.87	146.18	high
MG006	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.87	146.19	high
MG007	Mahogany Glider	F	Murray Upper	2021	ear	Field	-18.11	145.81	high
MG008	Mahogany Glider	M	Cardwell	2021	ear	Field	-18.25	145.99	high
MG009	Mahogany Glider	M	Muller's Ck	2021	ear	Field	-18.45	146.13	high
MG010	Mahogany Glider	F	Muller's Ck	2021	ear	Field	-18.42	146.14	high
MG011	Mahogany Glider	F	Cardwell	2021	ear	Field	-18.34	146.06	high
MG012	Mahogany Glider	M	Cardwell	2021	ear	Field	-18.34	146.06	high
MG013	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.86	146.18	high
MG014	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.86	146.19	high
MG015	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.86	146.18	high
MG016	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.87	146.19	high
MG017	Mahogany Glider	F	Bambaroo	2021	ear	Field	-18.86	146.18	high
MG018	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.86	146.18	high
MG019	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.87	146.19	high
MG020	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.86	146.19	high
MG021	Mahogany Glider	F	Bambaroo	2021	ear	Field	-18.87	146.19	high
MG022	Mahogany Glider	M	Bambaroo	2021	ear	Field	-18.86	146.18	high
MG023	Mahogany Glider	M	Allendale	2022	ear	Field	-18.85	146.09	high
MG024	Mahogany Glider	F	Allendale	2022	ear	Field	-18.85	146.09	high
MG025	Mahogany Glider	M	Allendale	2022	ear	Field	-18.84	146.09	high
MG026	Mahogany Glider	F	Allendale	2022	ear	Field	-18.85	146.09	high
MG027	Mahogany Glider	M	Allendale	2022	ear	Field	-18.84	146.09	high
MG028	Mahogany Glider	F	Allendale	2022	ear	Field	-18.84	146.09	high
MG029	Mahogany Glider	F	Allendale	2022	ear	Field	-18.86	146.13	high
MG030	Mahogany Glider	M	Ollera Ck	2022	ear	Field	-18.97	146.34	high

MG031	Mahogany Glider	F	Ollera Ck	2022	ear	Field	-18.98	146.34	high
MG032	Mahogany Glider	M	Ollera Ck	2022	ear	Field	-18.97	146.35	high
MG033	Mahogany Glider	F	Muller's Ck	2022	ear	Field	-18.44	146.13	high
MG034	Mahogany Glider	F	Muller's Ck	2022	ear	Field	-18.44	146.13	high
MG035	Mahogany Glider	M	Muller's Ck	2022	ear	Field	-18.44	146.13	high
MG036	Mahogany Glider	M	Easter Ck	2022	ear	Field	-18.82	146.15	high
MG037	Mahogany Glider	M	Easter Ck	2022	ear	Field	-18.82	146.16	high
MG038	Mahogany Glider	M	Easter Ck	2022	ear	Field	-18.81	146.16	high
MG039	Mahogany Glider	M	Easter Ck	2022	ear	Field	-18.82	146.16	high
MG040	Mahogany Glider	M	Easter Ck	2022	ear	Field	-18.82	146.15	high
MG041	Mahogany Glider	M	Easter Ck	2022	ear	Field	-18.82	146.16	high
MG042	Mahogany Glider	F	Easter Ck	2022	ear	Field	-18.82	146.14	high
MG043	Mahogany Glider	F	Easter Ck	2022	ear	Field	-18.82	146.16	high
MG044	Mahogany Glider	F	Easter Ck	2022	ear	Field	-18.81	146.16	high
SG001	Krefft's Glider	M	Cardwell	2021	ear	Field	-18.27	146.02	medium
SG002	Krefft's Glider	F	Cardwell	2021	ear	Field	-18.27	146.02	medium
SG003	Krefft's Glider	M	Cardwell	2021	ear	Field	-18.32	146.05	high
SG004	Krefft's Glider	F	Ingham	2022	ear	Field	-18.85	146.09	high
SG005	Krefft's Glider	M	Ingham	2022	ear	Field	-18.85	146.09	high
SG006	Krefft's Glider	M	Ingham	2022	ear	Field	-18.85	146.09	high
SG007	Krefft's Glider	M	Ingham	2022	ear	Field	-18.86	146.13	high
SG008	Krefft's Glider	M	Tully	2022	ear	Field	-18.07	145.99	high
SQ001	Squirrel Glider	F	Cape Cleveland	2021	ear	Field	-19.30	147.03	high
SQ002	Squirrel Glider	F	Cape Cleveland	2021	ear	Field	-19.29	147.01	high
SQ003	Squirrel Glider	M	Cape Cleveland	2021	ear	Field	-19.29	147.02	high
SQ004	Squirrel Glider	M	Cape Cleveland	2021	ear	Field	-19.29	147.02	high
SQ005	Squirrel Glider	M	Cape Cleveland	2021	ear	Field	-19.29	147.02	high
SQ006	Squirrel Glider	M	Cape Cleveland	2021	ear	Field	-19.30	147.03	high
A004079	Squirrel Glider	NA	Brisbane	2006	muscle	Museum	-27.65	152.78	low
A004418	Squirrel Glider	NA	NQ-Charters Towers	2000	muscle	Museum	-20.08	146.26	low
A004432	Squirrel Glider	NA	Brisbane	2006	muscle	Museum	-27.50	152.96	low
A004487	Squirrel Glider	NA	Rockhampton	2001	NA	Museum	-23.38	150.51	low
A004653	Squirrel Glider	NA	Brisbane	2008	muscle	Museum	-28.06	153.34	low
A004675	Squirrel Glider	NA	NQ-Silver Valley	2001	NA	Museum	-17.63	145.38	low
A004905	Mahogany Glider	NA	Cardwell	1996	liver	Museum	-18.04	145.91	low
A004987	Mahogany Glider	NA	Bambaroo	1995	muscle	Museum	-18.87	146.19	low
A005360	Mahogany Glider	NA	Tully	1989	liver	Museum	-18.04	145.81	low
A005720	Squirrel Glider	NA	Airlie Beach	2005	NA	Museum	-20.27	148.72	low
A005721	Squirrel Glider	NA	Airlie Beach	2005	NA	Museum	-20.31	148.59	low
A005722	Squirrel Glider	NA	Airlie Beach	2005	NA	Museum	-20.31	148.59	low
A005723	Squirrel Glider	NA	Airlie Beach	2005	NA	Museum	-20.31	148.59	low
A006472	Squirrel Glider	NA	Brisbane	2009	liver	Museum	-26.70	153.07	low
A006475	Squirrel Glider	NA	Brisbane	2010	muscle	Museum	-27.82	153.42	low
A006476	Squirrel Glider	NA	Brisbane	2010	muscle	Museum	-27.82	153.42	low
A006819	Squirrel Glider	NA	Rockhampton	2009	muscle	Museum	-23.11	150.72	low

A007924	Squirrel Glider	NA	Brisbane	2007	muscle	Museum	-27.75	153.03	low
A008582	Squirrel Glider	NA	NQ-Silver Valley	NA	NA	Museum	-17.60	145.30	low
A008692	Squirrel Glider	NA	Mackay	2013	muscle	Museum	-21.32	149.21	low
A009312	Squirrel Glider	NA	Bundaberg	2007	muscle	Museum	-25.05	151.23	low
A009916	Squirrel Glider	NA	Mackay	2013	muscle	Museum	-21.34	149.02	low
A013109	Mahogany Glider	NA	Ingham	2016	NA	Museum	-18.73	145.93	low
A013123	Squirrel Glider	NA	NQ-Silver Valley	2005	muscle	Museum	-17.45	145.29	low
A013129	Squirrel Glider	NA	NQ-Tolga	2012	muscle	Museum	-17.22	145.48	low
A013130	Squirrel Glider	NA	NQ-Princess Hills	1995	liver	Museum	-18.32	145.38	low
A014541	Squirrel Glider	NA	Brisbane	2014	muscle	Museum	-26.89	152.10	low
A014663	Squirrel Glider	NA	NQ-Chillagoe	2016	NA	Museum	-17.20	144.51	low
A015010	Mahogany Glider	NA	Cardwell	2012	skin	Museum	-18.24	145.97	low
A015011	Mahogany Glider	NA	Tully	2010	skin	Museum	-18.01	145.98	low
A015012	Mahogany Glider	NA	Murray Upper	2010	skin	Museum	-18.09	145.77	low
A015013	Mahogany Glider	NA	Cardwell	2017	skin	Museum	-18.23	145.98	low
A015015	Mahogany Glider	NA	Cardwell	2017	skin	Museum	-18.24	145.99	low
A015067	Squirrel Glider	NA	Mackay	2005	fur	Museum	-21.14	149.19	low
A015068	Squirrel Glider	NA	Mackay	2005	fur	Museum	-21.14	149.19	low
A015069	Squirrel Glider	NA	Mackay	2005	fur	Museum	-21.14	149.19	low
A015071	Squirrel Glider	NA	Mackay	2005	fur	Museum	-21.14	149.19	low
A015072	Squirrel Glider	NA	Mackay	2005	fur	Museum	-21.14	149.19	low
A015073	Squirrel Glider	NA	Mackay	2005	fur	Museum	-21.14	149.19	low
A015075	Squirrel Glider	NA	Mackay	2006	Fur	Museum	-21.16	149.06	low
A015078	Squirrel Glider	NA	Mackay	2006	fur	Museum	-21.08	149.21	low
A015079	Squirrel Glider	NA	Mackay	2006	fur	Museum	-21.43	149.20	low
A015081	Squirrel Glider	NA	Mackay	2006	fur	Museum	-21.43	149.20	low
A015082	Squirrel Glider	NA	Mackay	2006	fur	Museum	-21.08	149.21	low
A015088	Squirrel Glider	NA	Mackay	2006	fur	Museum	-21.16	149.06	low
A015089	Squirrel Glider	NA	Mackay	2006	fur	Museum	-20.93	149.02	low
A015245	Squirrel Glider	NA	NQ-Mitchell River	2003	skin	Museum	-16.54	143.43	low
A015246	Squirrel Glider	NA	NQ-Silver Valley	NA	skin	Museum	-17.60	145.30	low
A015385	Mahogany Glider	NA	Tully	2007	muscle	Museum	-18.04	145.91	low
A018339	Squirrel Glider	NA	Bundaberg	2006	NA	Museum	-25.25	152.81	low
A018457	Squirrel Glider	NA	Brisbane	2012	muscle	Museum	-27.65	152.06	low
A019042	Squirrel Glider	NA	Brisbane	2010	muscle	Museum	-27.82	153.42	low
A019088	Squirrel Glider	NA	Brisbane	2016	muscle	Museum	-27.30	153.05	low

Appendix S4-3 Calculated genetic diversity indices for each species, genetic groups, and sampling locality, with the number of individuals (nInd), loci (nloc), polymorphic loci (polyLoc), and monomorphic loci (monoLoc) displayed. Observed heterozygosity (H_o), expected heterozygosity (He), and inbreeding coefficient (F_{IS}) were calculated using dartR (Gruber *et al.* 2018). The confidence interval of F_{IS} was determined through bootstrapping using Hierfstat (Goudet 2005). The abbreviations used are: MG for Mahogany Glider, SQ for mid-eastern/south-eastern Queensland Squirrel Glider, CC Cape Cleveland Squirrel Glider, NQ for North Queensland Squirrel Glider, and KG for Krefft's Glider

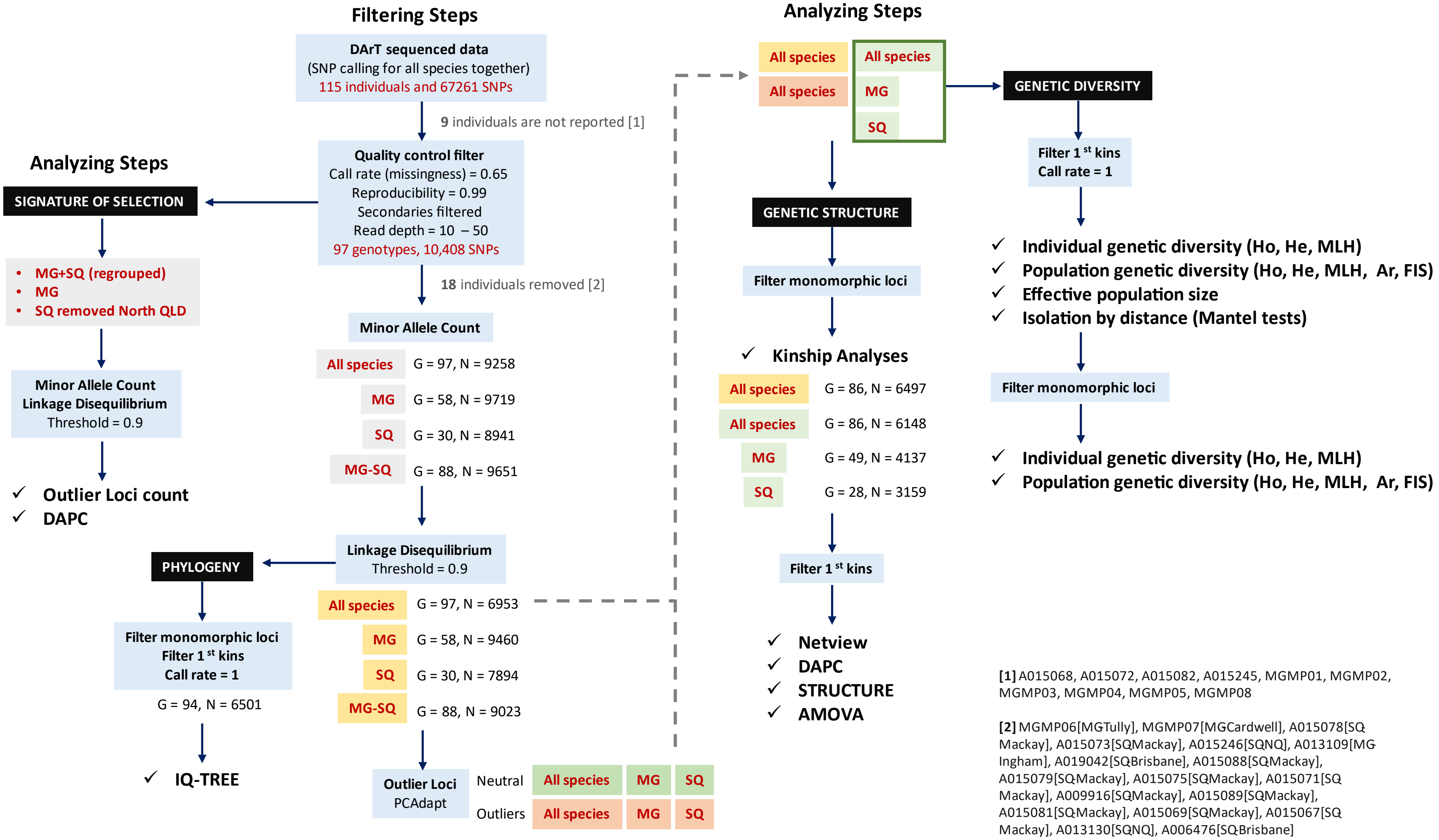
	Group	**nInd**	**nLoc**	**polyLoc**	**monoLoc**	**sMLH**	**sMLH.SD**	**Ho**	**HoSD**	**He**	**HeSD**	**uHe**	**uHeSD**	**FIS**	**FIS_2.5Q**	**FIS_97.5Q**
Species (All data)	Mahogany	49	2424	1834	590	1.13	0.14	0.116	0.131	0.13	0.142	0.131	0.144	0.114	0.104	0.125
	Squirrel	28	2424	1675	749	0.895	0.189	0.089	0.108	0.118	0.14	0.121	0.143	0.265	0.253	0.282
	Krefft's	9	2424	497	1927	0.572	0.042	0.061	0.145	0.07	0.152	0.074	0.161	0.17	0.15	0.207
MG-cluster (MG data)	South MG	29	2877	2675	202	1.04	0.094	0.184	0.143	0.204	0.148	0.207	0.151	0.111	0.102	0.122
	North MG	20	2877	2282	595	0.942	0.132	0.167	0.154	0.186	0.16	0.191	0.164	0.124	0.114	0.138
Sampling locality (MG data)	Allendale	8	2877	1974	903	1.063	0.053	0.188	0.19	0.189	0.169	0.202	0.181	0.068	0.054	0.095
	Bambaroo	11	2877	1964	913	1.028	0.137	0.182	0.189	0.184	0.173	0.193	0.181	0.054	0.041	0.076
	Cardwell	8	2877	1808	1069	0.973	0.08	0.172	0.187	0.177	0.172	0.188	0.183	0.085	0.072	0.108
	Easter Ck	7	2877	1882	995	1.044	0.052	0.185	0.196	0.186	0.171	0.2	0.184	0.077	0.065	0.104
	Muller	5	2877	1596	1281	1.039	0.055	0.184	0.22	0.175	0.181	0.194	0.201	0.053	0.033	0.081
	Murray Upper	4	2877	1277	1600	0.776	0.182	0.138	0.203	0.151	0.184	0.172	0.211	0.201	0.203	0.256
	Ollera Ck	3	2877	1246	1631	1.014	0.09	0.18	0.251	0.158	0.191	0.19	0.229	0.053	0.04	0.091
	Tully	3	2877	1173	1704	0.921	0.065	0.163	0.243	0.149	0.189	0.178	0.226	0.085	0.066	0.133
SQ-cluster (SQ data)	SQ	17	1912	1667	245	0.958	0.232	0.163	0.137	0.216	0.159	0.222	0.164	0.265	0.257	0.288
	CC	6	1912	1094	818	1.209	0.055	0.206	0.233	0.195	0.193	0.213	0.211	0.031	0.015	0.056
	NQ	5	1912	1037	875	0.891	0.129	0.152	0.195	0.178	0.186	0.198	0.206	0.232	0.226	0.284

*Interpretation of genetic diversity indices should be approached with caution when the sample size comprises fewer than 10 individuals.

Appendix S4-4 Estimated Effective Population Sizes for Mahogany Glider Sampling Localities. The effective population size is determined through the linkage equilibrium method and is reported at three critical values (0.05, 0.02, 0.01). Confidence intervals are provided using both parametric and jackknife (non-parametric) methods, offering a comprehensive view of the estimated variability (Do *et al.* 2014).

Site	Sample Size	Crit.Value	Ne.est	CI.para.low	CI.para.high	CI.jk.low	CI.jk.high
Allendale	8	0.05	64.7	62	67.6	16.1	Infinite
		0.02	64.7	62	67.6	16.1	Infinite
		0.01	64.7	62	67.6	16.1	Infinite
Bambaroo	10	0.05	27.6	27.1	28.1	19	45.1
		0.02	27.6	27.1	28.1	19	45.1
		0.01	27.6	27.1	28.1	19	45.1
Cardwell	4	0.05	-21.2	Infinite	Infinite	Infinite	Infinite
		0.02	-21.2	Infinite	Infinite	Infinite	Infinite
		0.01	-21.2	Infinite	Infinite	Infinite	Infinite
Easter Creek	7	0.05	431.2	324.4	640.6	45.8	Infinite
		0.02	431.2	324.4	640.6	45.8	Infinite
		0.01	431.2	324.4	640.6	45.8	Infinite
Muller's Creek	5	0.05	-56.2	Infinite	Infinite	Infinite	Infinite
		0.02	-56.2	Infinite	Infinite	Infinite	Infinite
		0.01	-56.2	Infinite	Infinite	Infinite	Infinite
Murray Upper	3	0.05	-6.2	Infinite	Infinite	Infinite	Infinite
		0.02	-6.2	Infinite	Infinite	Infinite	Infinite
		0.01	-6.2	Infinite	Infinite	Infinite	Infinite
Ollera Creek	3	0.05	-5.6	Infinite	Infinite	Infinite	Infinite
		0.02	-5.6	Infinite	Infinite	Infinite	Infinite
		0.01	-5.6	Infinite	Infinite	Infinite	Infinite

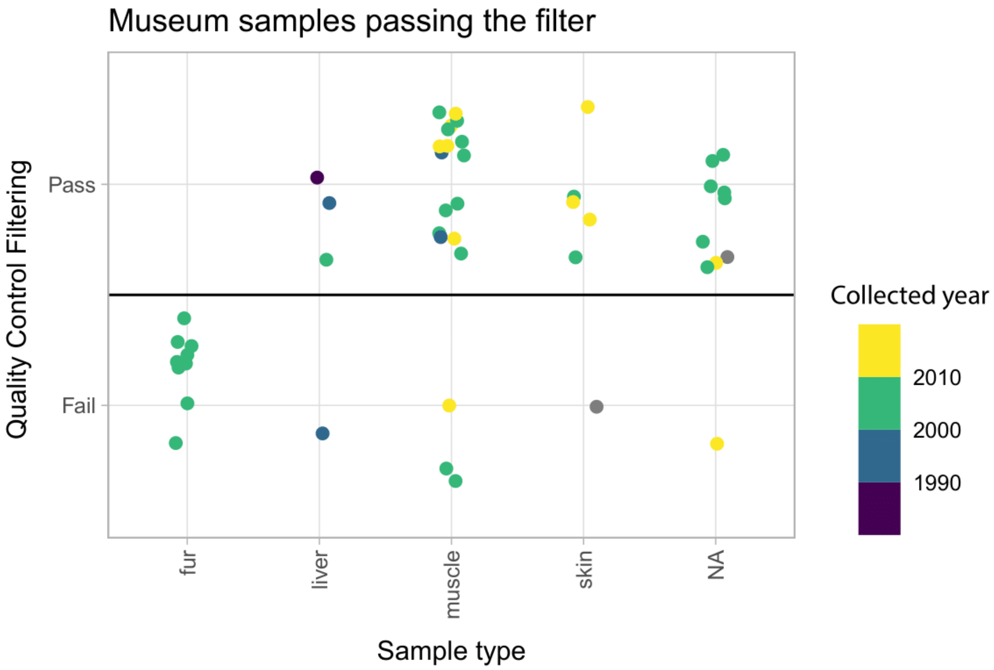
Appendix S4-5 A flowchart illustrating the customized filtering process in this study for the analysis of genetic structure and genetic diversity.



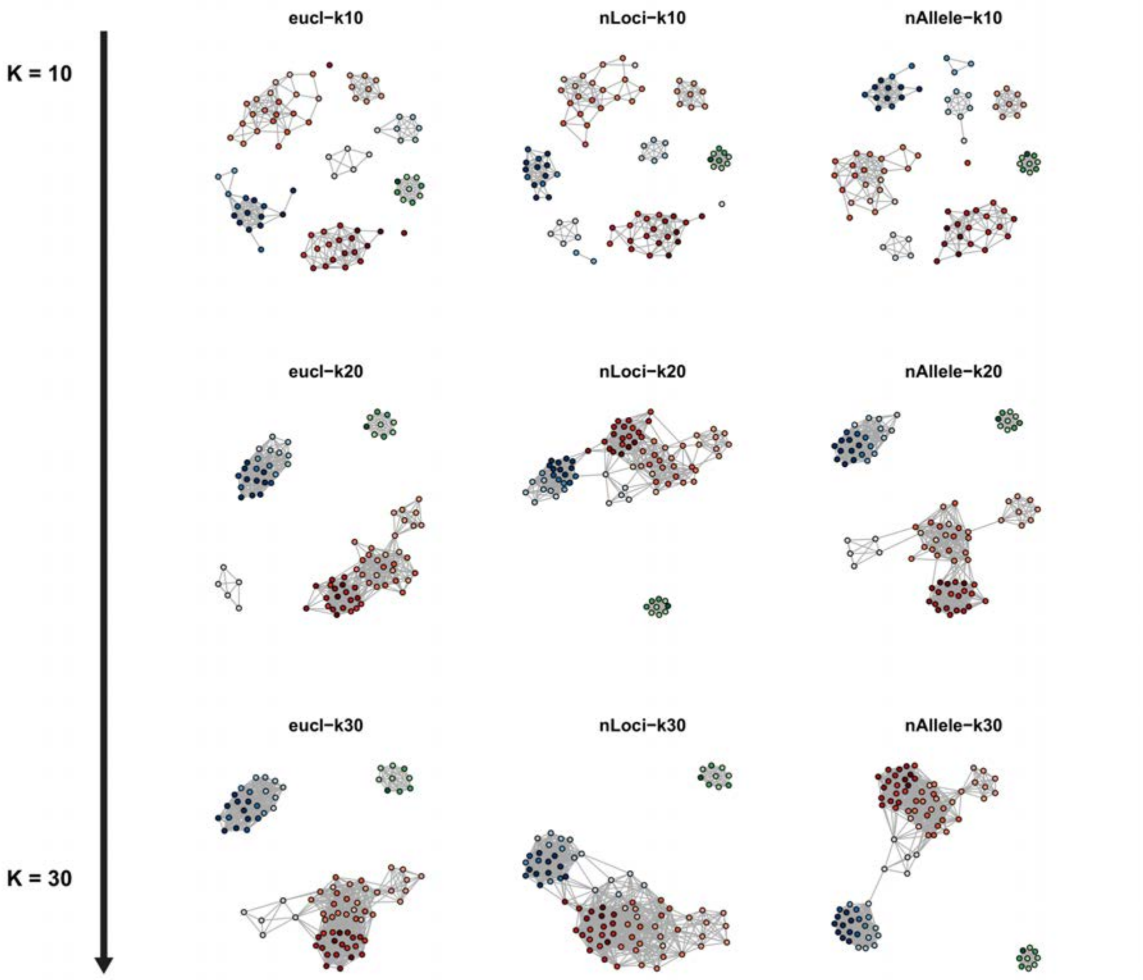
[1] A015068, A015072, A015082, A015245, MGMP01, MGMP02, MGMP03, MGMP04, MGMP05, MGMP08

[2] MGMP06[MG-Tully], MGMP07[MG-Cardwell], A015078[SQ-Mackay], A015073[SQ-Mackay], A015246[SQ-NQ], A013109[MG-Ingham], A019042[SQ-Brisbane], A015088[SQ-Mackay], A015079[SQ-Mackay], A015075[SQ-Mackay], A015071[SQ-Mackay], A009916[SQ-Mackay], A015089[SQ-Mackay], A015081[SQ-Mackay], A015069[SQ-Mackay], A015067[SQ-Mackay], A013130[SQ-NQ], A006476[SQ-Brisbane]

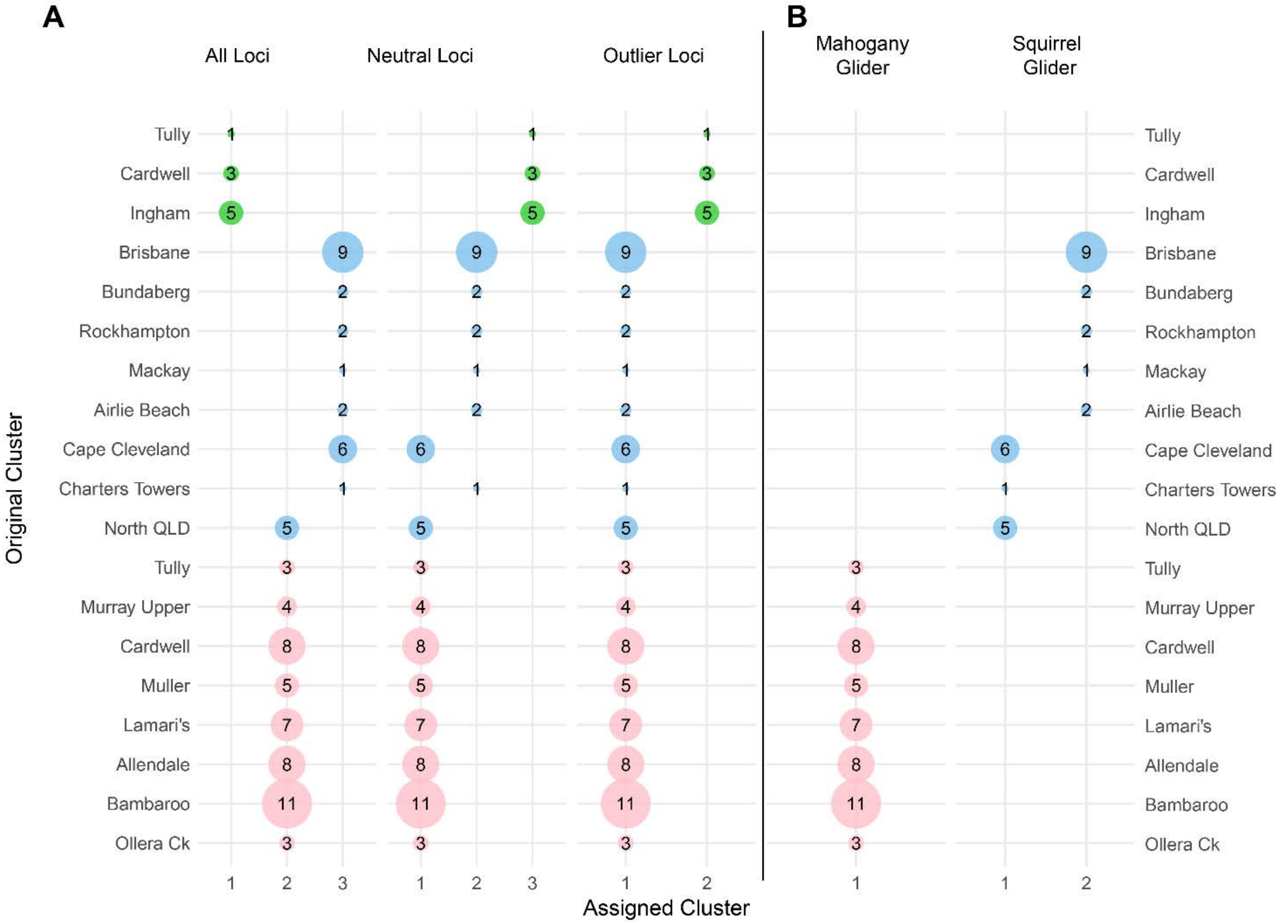
Appendix S4-6 Types of museum samples passing/failing SNP quality control filters



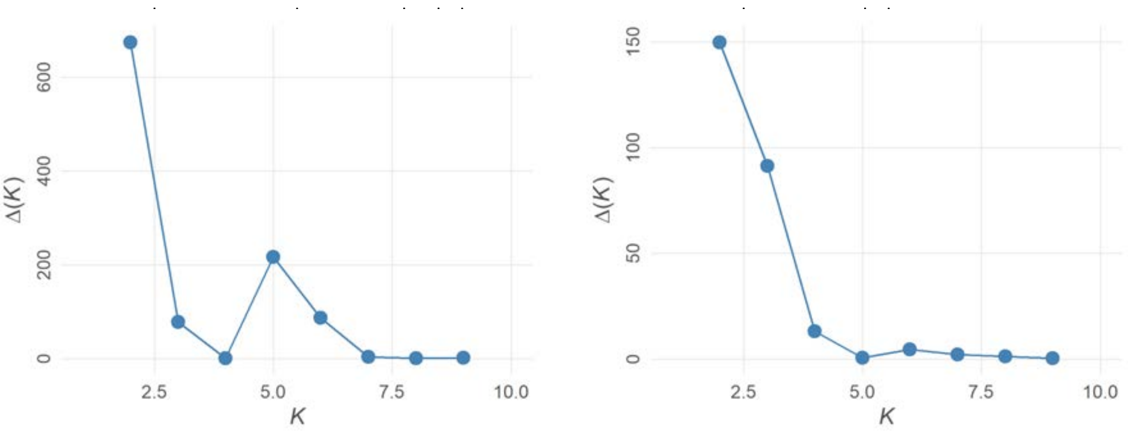
Appendix S4-7 Netview network on three different distance matrices connecting 10, 20, and 30 nearest neighbors. The three distance matrices presented Euclidean distance (eucl) applied on allele frequency within individuals (Jombart and Ahmed 2011), pairwise difference on number of loci for which individuals differ (nLoci) (Paradis and Schliep 2019), and number of allelic differences between two individuals (nAllele) (Kamvar *et al.* 2014).



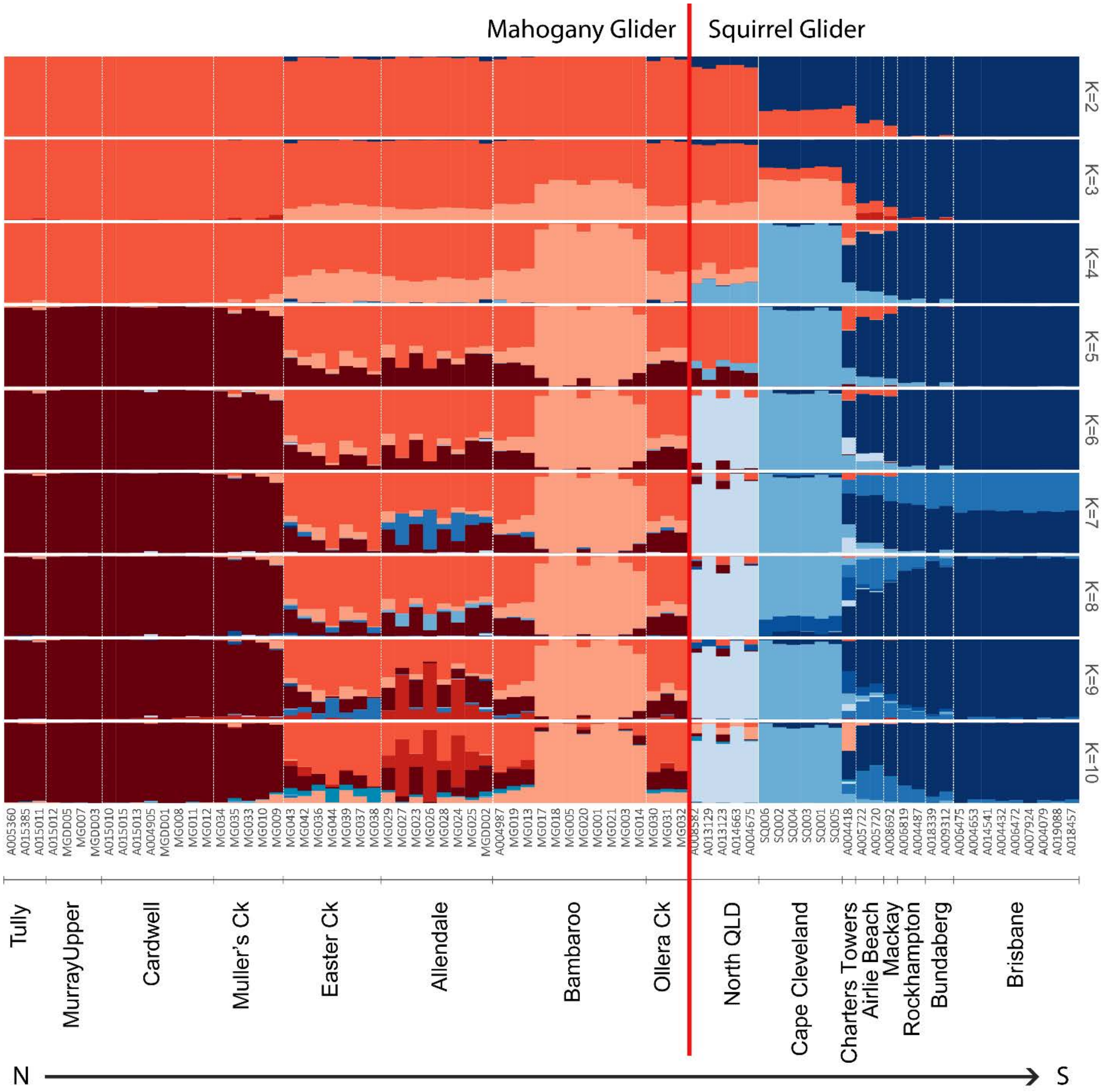
Appendix S4-8 Unsupervised K means clustering using R adegenet package (Jombart and Ahmed 2011) on all-species datasets (A) and two species datasets of neutral loci (B). The y-axis represents the original cluster, and the x-axis indicates the assigned cluster. The sampling localities identified as Mahogany Glider are shown red, Squirrel Gliders are shown in blue, and Krefft's Glider are shown in green.



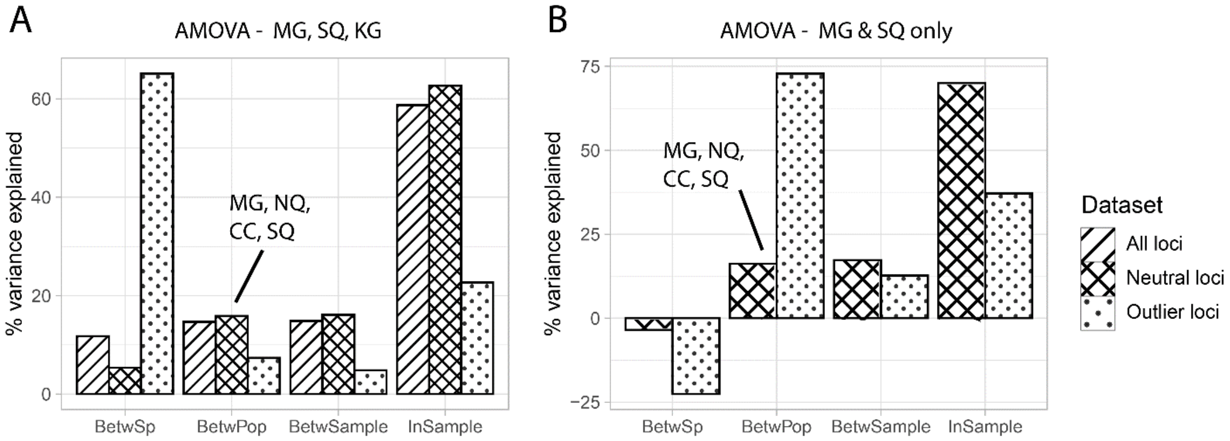
Appendix S4-9 Delta K (ΔK) in the Evanno plots (Evanno *et al.* 2005) determining the optimal cluster K in the STURCTURE analyses for Mahogany and Squirrel Glider dataset (A) and Mahogany Glider only dataset (B)



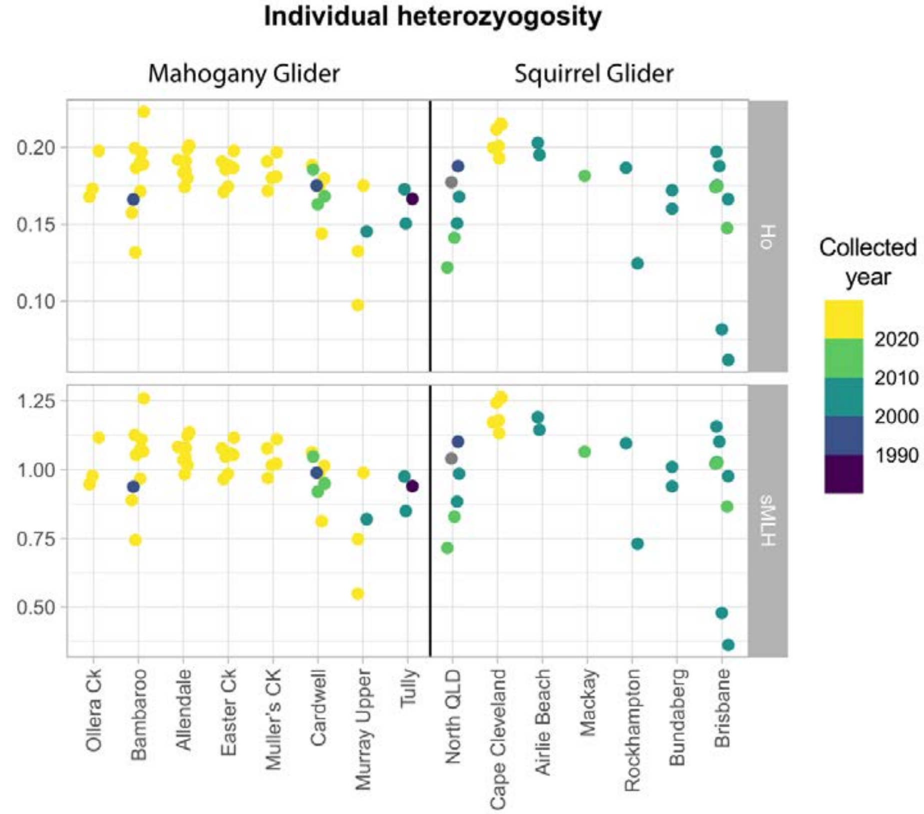
Appendix S4-10 Structure Plot of Mahogany and Squirrel Glider presenting the genetic components of Mahogany and Squirrel Gliders, with K values ranging from 2 to 10. The gliders are arranged geographically from north to south. The red lines separate the Squirrel Gliders and Mahogany Glider. The genetic component of the Mahogany Glider is represented in orange for the southern population and brown for the northern population. In contrast, the genetic component of the Squirrel Gliders is depicted in various shades of blue. The hypothetical optimal K and the second optimal K value for the Mahogany-Squirrel Glider cluster is determined to be K=2 and K=5, respectively (**Error! Reference source not found.**).



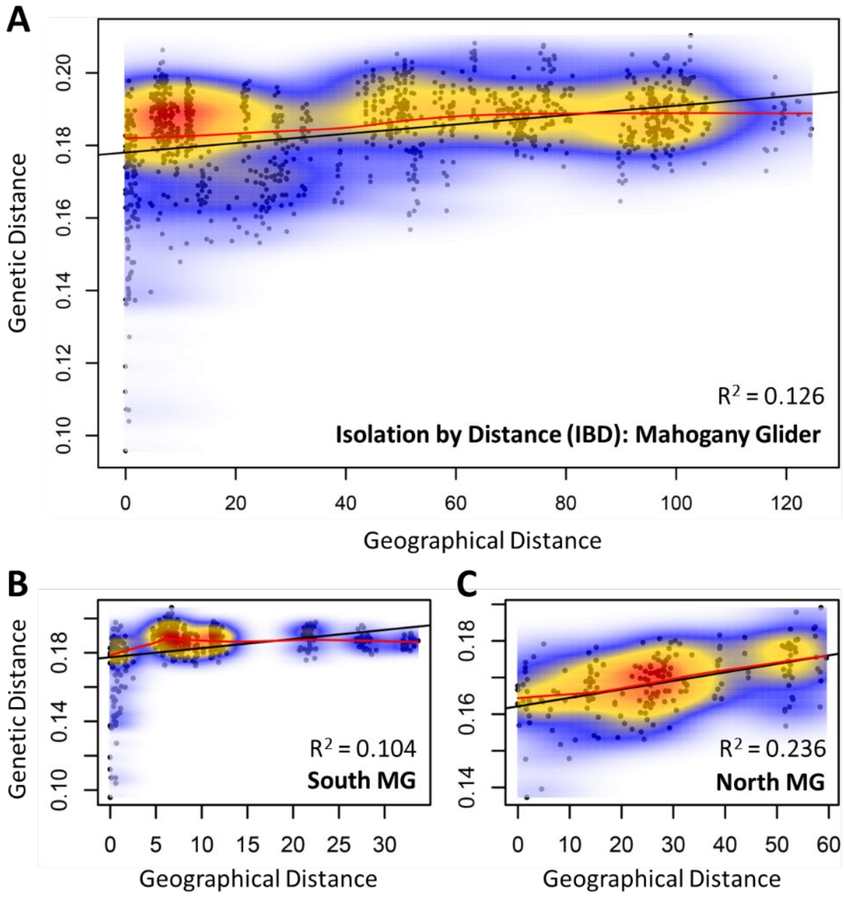
Appendix S4-11 Analysis of molecular variance (AMOVA) of all-species datasets (A) and Mahogany-Squirrel Glider only datasets. Bar plots depict variances contributing to population structure among species (Mahogany, Squirrel, and Krefft's Glider), within the four consensus genetic groups (MG, NQ, CC, SQ), and among and within samples. The percentage of explained variance was significant at all levels.



Appendix S4-12 Observed heterozygosity (H_o) and standardized multi-locus heterozygosity (sMLH) of individual Mahogany Glider and Squirrel Glider with monomorphic loci filtered. The populations of Mahogany Glider are arranged geographically from south (left) to north (right). The samples are colour-coded by the year of collection.



Appendix S4-13 Analysis of isolation by distance (IBD) based on the proportion of shared alleles among individual Mahogany Gliders (MG). The x-axis represents the Euclidean distance in kilometres, while the y-axis depicts the proportion of shared alleles between individuals. The colour gradient reflects the kernel density of individuals within the plot, and the trend lines illustrate the correlation. (A) The IBD for all Mahogany Gliders (B) The IBD for the southern cluster (C) The IBD for the northern cluster. Despite the Mantel tests for all groupings being statistically significant, the correlations are relatively weak



Chapter 5.

Summary and Synthesis

This research project was initiated to address significant knowledge gaps and to inform the conservation management of the Endangered Mahogany Glider (*Petaurus gracilis*), a species that had been relatively understudied despite its Endangered status. Recognizing the urgent need for updated information and long-term management strategies, the project aimed to provide detailed distribution of the species in the fragmented landscape of the Wet Tropics lowlands, monitor population trends and abundance, and assess the genetic health and population connectivity. The approaches involved applying the latest advancements in conservation science. First, I used species distribution models to update the glider's habitat suitability maps, which in turn guided targeted survey efforts. The surveys, coupled with subsequent occupancy and genetic analyses, provided crucial insights into glider density, total abundance, genetic health, population structure, and relationships with Squirrel Glider in Queensland. The results highlight the importance of updating habitat suitability maps and the invaluable role of genetic assessment in elucidating population status and functional connectivity. Moreover, the findings emphasize the necessity of further field surveys and establishing long-term monitoring. This collective effort not only contributes to the conservation of the Mahogany Glider but also sets a precedent for the effective management of other threatened species.

5.1. Key Findings

5.1.1. Species distribution model and updated habitat suitability

Chapter 2 focused on updating the habitat suitability map of the Mahogany Glider by applying advanced machine learning algorithms to comprehensive spatial data. Our results revealed a concerning degree of fragmentation both within and outside the known range of the species. Notably, more than 400 potential habitat patches were smaller than 1 km^2, and many historical records were found within areas that had been subsequently cleared of suitable vegetation. The model also predicted large and continuous suitable habitats within the broadly known range that warrant surveys, such as the Wharps Holding and the forested areas near Lannercost State Forest, both west of Ingham. Some areas outside of the known range also showed high habitat suitability and may support unknown glider populations. These areas include Little Mulgrave and Yarrabah near Cairns, northwestern areas of Hinchinbrook Island, and forests beyond the known southern limit of the species between Paluma Range National Park and Townsville.

5.1.2. Low detection rate and the population size estimates

The fine-scale habitat suitability maps formulated in Chapter 2 have provided guidance for the implementation of cage and camera trapping surveys within this project. These maps also facilitated a more comprehensive understanding of the factors influencing habitat suitability, as well as enabling the estimation of population size for the species. Chapter 3 introduced the first scientifically estimated total abundance for the Mahogany Glider, achieved by applying a comprehensive integrated species distribution modelling that combines the presence-absence (camera trapping surveys) and presence-only (sighting records) data. Based on the integrated model, which combines presence-only and presence-absence data, I estimated median abundance at 6,030, 4,834, and 2,820 individuals for home ranges of 9, 16, and 25 ha, respectively. These estimates narrow the previously hypothesized range of 1,200 to 20,000 individuals and provide a robust baseline for future conservation planning. The chapter also emphasized the importance of accounting for home range and density variability during modelling process.

The detection rate and cage trapping success remained consistently low across the surveyed sites, encompassing areas previously designated as optimal habitat in previous studies and regions anticipated by the models to exhibit high habitat suitability. Notably, while the cage trapping design employed may not have precisely replicate the previous methodologies, the catch rates observed at Muller's Creek notably diminished, ranging from 2% to 3% during 2021–2022 (see Appendix I). This stands in stark contrast to previous trapping efforts conducted by Jackson during 1995–1996, which yielded catch rates ranging from 7.5% to 15%, and those in 2008, which recorded an 11.5% catch rate (personal communication with Mark Parsons). Although surveys conducted at most suitable habitats throughout the recognized range revealed catch rates ranging from 0% to 3%, certain southern sites demonstrated notably higher catch rates, exceeding 10% and reaching as high as 24%. For instance, surveys conducted at Bambaroo yielded catch rates around 10%. This finding is particularly noteworthy considering the relatively small size of the habitat fragment at 0.67 km² and its surrounding of sugarcane fields.

5.1.3. Conservation genetics of Mahogany Gliders

In Chapter 4, I explored the genetic structure of the species, revealing distinct northern and southern clusters approximately separated by the Herbert River. The presence of genetic admixture between these clusters suggests recent or historical gene flow. However, it remains uncertain whether this interchange is sufficient for long-term genetic exchange across the species range. The overall genetic diversity of the species generally comparable to that of Squirrel Gliders. Notably, Murray Upper, the northernmost site in this study, exhibits concerning genetic health. It displays exceptionally low genetic diversity and a high inbreeding index.

Additionally, two sites with high glider density south of Ingham—Bambaroo and Allendale—have estimated effective population sizes below 100 individuals. The low effective population sizes indicate limited evolutionary potential and pose a significant challenge to the long-term survival of these populations.

5.1.4. Genetic admixture between Mahogany and Squirrel Gliders

The genetic assessment in Chapter 4 have elucidated a gradient of genetic admixture between the southern cluster of Mahogany Gliders and the Squirrel Gliders from north of Mackay. However, discerning whether this genetic admixture is presently ongoing or pertains to historical interactions remains unresolved. Squirrel Glider populations manifest into three distinct genetic groups. Gliders originating from the northwest extent of the known Mahogany Glider range, encompassing Princess Hills, Tolga, and Chillagoe, exhibit closer genetic affinities with Mahogany Gliders than with their Squirrel counterparts. Nevertheless, instead of nested within Mahogany Gliders, they constitute a basal group relative to the clade comprising Mahogany and Squirrel Gliders in the phylogenetic tree. Gliders sampled from Cape Cleveland, despite clustering with conventional Squirrel Gliders from southeastern Queensland, exhibit distinct genetic profiles. These individuals demonstrate a unique signature of divergent selection, setting them apart from both Squirrel and Mahogany Gliders. This discovery underscores the complexity of genetic interactions among these glider populations and emphasizes the need for further investigation to resolve the taxonomy uncertainty.

Central to this project and thesis is the investigation into historical or ongoing introgression between Mahogany and Squirrel Gliders. This scrutiny raises questions regarding the species status of Mahogany Gliders. However, despite the observed genetic admixture, analyses encompassing signatures of selection, SNP phylogenetics, genetic structure, and morphological comparisons consistently reaffirm the distinctiveness of Mahogany Gliders from Squirrel Gliders. This distinctiveness suggests a significant degree of genetic isolation and unique evolutionary adaptations of Mahogany Glider. The scientific evidence provided from this study implies that Mahogany Gliders should be considered at least as a distinct subspecies. This assertion not only highlights the importance of recognizing and preserving intraspecific diversity but also underscores the necessity for targeted conservation efforts aimed at safeguarding this taxon. Furthermore, this conclusion aligns with existing conservation frameworks such as the EPBC Act, which explicitly acknowledges the significance of subspecies delineation (EPBC 1999). By recognizing the distinctiveness of Mahogany Gliders, conservation efforts can be appropriately tailored to address the specific needs and vulnerabilities of this genetically and ecologically unique population.

5.2. Insights and Questions Arising

5.2.1. Taxonomic uncertainty of North Queensland glider populations

The genetic study in Chapter 4 highlighted taxonomic uncertainty regarding the glider populations in North Queensland, particularly between Mahogany and Squirrel Gliders. Despite evident genetic admixture between these species, both genetic and morphological analyses consistently delineate Mahogany Gliders as a distinct group. Nevertheless, uncertainties persist in the identity of glider populations inhabiting areas of potential contact or overlapping zone. For instance, populations situated at the southern areas of the Wet Tropics region, spanning between Townsville and Paluma, as well as those open woodlands west of the Mahogany Glider range, warrant thorough surveys to assess their morphological and genetic relationships. To identify the evolutionary history of Mahogany Glider within the Petaurus gliders, constructing a comprehensive phylogenetic tree is crucial. This tree should include a complete sampling of the *Petaurus* gliders and be based on genomic data and should incorporate fossil records, morphology and instances of introgression. Such an approach will significantly enhance our understanding of the taxonomic relationships among glider populations in North Queensland and guide targeted conservation efforts aimed at preserving their unique genetic and ecological attributes.

5.2.2. Unexpected low catch rate across the known range of Mahogany Glider

The surveys encountered unexpectedly low catch rates at numerous sampling localities. Notably, some large and continuous habitats within the known range, such as Lannercost State Forest west of Ingham and the coastal forests east of Tully, yielded no glider captures (Appendix I). This outcome was unexpected given that these areas are highly suitable for the gliders (Chapter 4) with historical records. However, it is important to note that many suitable sites were inaccessible. Some sites (i.e., upper catchment of Herbert River) were either extremely remote or difficult to access, even with 4WD vehicles. Given that cage trapping required the team to camp for up to five days, safety considerations were the priority. Additionally, certain areas, such as Wharps Holding, are privately owned. Unfortunately, despite efforts to engage with the landowners, we were unable to secure permission to access these properties.

Only one unknown population (Mutarnee) was discovered beyond the known range during the study (Chapter 2). The survey at sites along the northern border (South Mission Beach), western border (Hinchinbrook Island), and southern border (Clement State Forest & Balgal Beach) failed to detect Mahogany Glider (Chapter 3). Nevertheless, the survey effort beyond the known range was relatively limited in these areas due to time and logistical constraints.

These results prompt an inquiry into why glider density is low in seemingly suitable areas within the known range and why they are absent from apparently suitable Sites beyond that range. Habitat loss and fragmentation in specific regions over recent decades may have contributed to population decline, raising concerns about population viability at these sampling localities. Some suitable habitats may have lost Mahogany Gliders due to extreme isolation and degradation, such as forest thickening, cattle farming, establishment of pine plantations, and potentially unknown influences. This degradation may be particularly severe in the northern region of the range due to early agricultural development and heavier forest thickening. The impacts of extreme weather events, such as Cyclones Yasi, cannot be overlooked. The catastrophic events may have caused substantial habitat destruction, leading to further declines in glider populations in affected areas.

The determination of range limits is a multifaceted issue. It is plausible that certain habitats are unsuitable for Mahogany Gliders due to reasons that are not readily discernible. Historical effects on habitats, such as changes in vegetation composition or distribution, could also play a role. Furthermore, competition with other species, such as Squirrel Gliders, may influence the range limits of Mahogany Gliders through mechanisms such as resource competition or territorial displacement.

In conclusion, understanding the factors driving the distribution and abundance of Mahogany Gliders requires a comprehensive examination of habitat quality, historical influences, interspecific interactions, and the impacts of anthropogenic and natural disturbances. Such insights are crucial for informing conservation strategies aimed at preserving and restoring suitable habitats for the Mahogany Glider.

5.2.3. High density sites in the southern range of Mahogany Glider

This project has identified high-density sites (Bambaroo, Allendale, and Easter Creek) south of Ingham, which are characterized by notably fragmented but suitable habitats. Genetic data reveals interesting patterns within these sites. While genetic assessment suggests low effective population sizes of 27.6–37 individuals at Bambaroo and Allendale, Easter Creek represents a fragmented habitat patch that still supports a high density of gliders and maintains a considerable effective population size of over 400 individuals.

The factors enabling these southern localities to sustain such high glider suggest that these sites may represent optimal habitat conditions for Mahogany Gliders. The habitat characteristics in these areas typically consist of mature open woodlands with minimal evidence of rainforest thickening and large, hole-bearing trees. Furthermore, narrow but functional corridors may possibly exist within the fragmented landscape, thus allowing movement and genetic exchange among glider populations. Additionally, the gliders inhabiting these patches may not yet be experiencing negative genetic effects due to the relatively recent habitat loss. As a result, the full extent of genetic isolation and its consequences may not have manifested.

The southern sites of the study area thus offer invaluable opportunities for investigating the key factors contributing to these high densities. Future research could focus on understanding the unique characteristics of these sites that make them conducive to supporting high glider populations. For instance, a standardized method to quantify and measure the quality of suitable habitats for the Mahogany Gliders can be established to quantify the forest structure, forest thickness, vegetation community, tree holes, size and species of the trees, microclimate, etc. This knowledge could then be leveraged to inform effective conservation strategies and habitat management plans aimed at increasing census/effective population size of Mahogany Glides.

Moreover, given the significance of these southern sites in sustaining high glider densities, they represent clear targets for long-term monitoring efforts. Continuous monitoring of population dynamics, habitat conditions, and other relevant parameters will be essential for assessing the effectiveness of conservation interventions over time and guiding adaptive management strategies as needed.

5.3. Management Recommendations for the Mahogany Glider

Irrespective of its taxonomic classification as a species or a subspecies, the Mahogany Glider is afforded protection under the Environment Protection and Biodiversity Conservation (EPBC) Act in Australia. This legislation provides a robust framework for the protection and management of significant species and ecological communities at national and international levels. In addition to the legal protection, the Mahogany Glider should receive ongoing conservation attention to recover populations, including but not limited to habitat preservation and restoration, population monitoring, research, and public education about the species. These concerted efforts are integral to ensuring the long-term survival and recovery of the Mahogany Glider.

5.3.1. Assess functional connectivity and species distribution models based on new information and techniques

Evaluating habitat connectivity emerges as a critical task, particularly given the severe fragmentation identified as a significant factor impacting the genetic health of sampled populations. The findings of this study suggest that some corridors may be ineffective, leading to potential loss of connectivity between key populations. Consequently, restoring functional connectivity entails accurately identifying both functional and non-functional corridors, implementing policies to protect potential corridors, and installing gliding poles equipped with monitoring devices to quantify and track their functionality.

Recent advancements in species distribution models have equipped researchers with tools capable of incorporating population dynamics and connectivity. In light of these advancements, regularly updating the Mahogany Glider distribution model is recommended. This update should integrate new sighting records, the latest climatic data and anthropogenic changes to provide more accurate future predictions. Such updated models will prove invaluable in identifying potential threats and opportunities for the species and guiding targeted conservation efforts. It is proposed that the next update be conducted in 2025 to ensure that conservation strategies remain informed by the most current and relevant data available.

5.3.2. Increasing effective and census population size

Assessing population condition and viability relies heavily on estimates of effective population size at various sites. However, due to limited sample sizes at most sampling localities, I was unable to calculate effective population sizes comprehensively. Therefore, it is imperative to obtain effective population size estimates at these locations through additional sampling efforts aimed at achieving a minimum sample size of ten individuals per site.

The considerable variation in density and effective population size observed across sampled sites in this study underscores the urgent need for tailored conservation strategies. The first crucial step involves pinpointing the key factors contributing to this variation in glider densities across the range, as well as the apparent population declines observed at certain sites. Monitoring the populations based on the camera trapping method established in this study can be helpful. By comparing monitoring results to the abundance baseline provided in Chapter 3, population trends can be assessed over time. Additionally, correlating these findings with various environmental factors at and around these sites will provide insights into the underlying drivers of density variation and declines. These environmental factors may include habitat degradation, predation pressure, availability of food and tree holes, and the impacts of anthropogenic disturbances, among others. By systematically evaluating these factors, we can identify priority areas for conservation intervention and develop targeted strategies to mitigate threats and support the recovery of glider populations.

The subsequent step entails increasing both the census and effective population size of the Mahogany Glider. This can be accomplished by improving habitat connectivity and preparing for genetic rescue based on the genetic assessment detailed in Chapter 4. Implementing these strategies will be paramount in ensuring the survival and recovery of this Endangered species.

5.3.3. Implementing and expanding long-term monitoring

With the baseline estimation of occupancy and abundance at reference sites identified in Chapter 3, a medium to long term annual monitoring plan would provide valuable insights into population trends of this species. Chapter 3 also demonstrated that the camera trapping surveys have played a fundamental role, not only in detecting species presence and abundance estimation, but also in the development of a long-term monitoring plan. In collaboration with Terrain NRM and the Mahogany Glider Recovery Team, a long-term monitoring program was established at three high-density reference sites of Bambaroo, Allendale, and Muller’s Creek. The subsequent monitoring activities were successfully carried out by stakeholders under the leadership of Terrain Natural Resource Management. The standardized methodology documented in Appendix II can be extended to include additional sites. Long-term monitoring offers an invaluable early warning system to detect signs of population decline, thereby aiding in the conservation management of the Mahogany Glider. It also shows if conservation efforts at and around a site are leading to the increase of population size.

5.3.4. Implementing adaptive management and enhancing collaboration with stakeholders

In light of the challenges posed by habitat heterogeneity and fragmentation, adopting adaptive management strategies is imperative for the conservation of the Mahogany Glider. Adaptive management, characterized by its iterative approach, enables the adjustment of conservation strategies based on ongoing actions and newly acquired information. The overarching goal is to integrate adaptive management into real-world conservation practices, addressing inquiries, bridging knowledge gaps, and prioritizing strategies to enhance the long-term survival of the species. For instance, adaptive management for the Mahogany Glider may entail assessing the availability of limiting resources within its habitat, such as tree holes or food sources. By identifying these constraints, conservation efforts can be tailored to increase the availability of these critical resources, thereby improving habitat quality. This adaptive approach ensures that conservation actions remain dynamic and responsive to changing ecological conditions, ultimately contributing to effective and measurable outcomes.

Collaboration with conservation practitioners and stakeholders plays a pivotal role in facilitating information exchange and bridging the divide between research findings and on-the-ground conservation efforts. In this study, proactive communication has ensured timely dissemination of survey activities and results to property owners and relevant authorities, thus fostering transparency and mutual understanding. Establishing and nurturing long-term relationships with stakeholders and property owners are paramount for continued collaboration in the conservation of Mahogany Glider. Regular stakeholder meetings, such as the Mahogany Glider Recovery Team meetings, has proved to be invaluable for knowledge exchange, communication, collaboration, stakeholder engagement, and brainstorming innovative conservation strategies grounded in scientific evidence.

5.4. Conclusion and Remarks

This thesis has contributed to the conservation science of the Endangered Mahogany Glider through a versatile framework encompassing habitat mapping, conservation genetics, and camera monitoring. By meticulously examining the species distribution and habitat suitability at a landscape scale, this study has revealed the environmental factors, such as vegetation type, soil type, and seasonality, affect the habitat suitability for the glider. The updated habitat suitability map also provided insights for the glider distribution under severe fragmentation and guided the targeted surveys. Furthermore, the study detailed the baseline abundance for the glider within the known range and established a framework for long-term monitoring programs which will be beneficial for tracking the population trends in the future. The study also delved into conservation genetics, thereby providing an in-depth understanding of population status and genetic admixture with the Squirrel Glider that were otherwise undetectable in standard surveys and management practices. This knowledge is of paramount significance, as it forms the foundation for critical conservation strategies, including genetic rescue, translocation, and captive breeding. This thesis stands as a valuable blueprint for conservation initiatives of the Mahogany Glider, and the comprehensive framework may hold a great value for broader application to other threatened species.

Thesis Appendix I

Mahogany Glider (*Petaurus gracilis*) Cage Trapping Survey Report 2021-2022

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Thesis Appendix ll

Long-term Camera Trap Monitoring SOP for the Mahogany Glider (available upon request)