Title

Taxonomic revisions, strategic decisions: research and management priorities for the threatened greater glider complex

Authors

Luke D. Emerson[1, 2]*, Kristal N. Kostoglou[1], Kita R. Ashman[3,4,5], Jemma K. Cripps[6], Louise K. Durkin[6], Teresa J. Eyre[7], Ana Gracanin[5], David B. Lindenmayer[5], Amanda Lo Cascio[1], Karen J. Marsh[8], Rachel T. Mason[1], Vivianna Miritis[9], Jenny L. Nelson[6], Benjamin Wagner[10], Kara Youngentob[5], and Euan G. Ritchie[1]

Affiliations

[1] Life and Environmental Sciences, Deakin University, Burwood, 3125, Melbourne, Victoria, Australia.

[2] Environmental and Life Sciences, University of Newcastle, Callaghan, 2308, New South Wales, Australia.

[3] Gulbali Institute for Agriculture, Water and Environment, Charles Sturt University, Thurgoona, 2640, New South Wales, Australia.

[4] WWF-Australia, Suite 3.01, Level 3/45 Clarence Street, Sydney, 2000, New South Wales, Australia.

[5] Fenner School of Environment and Society, The Australian National University, Canberra, 2601, Australian Capital Territory, Australia.

[6] Arthur Rylah Institute for Environmental Research, Department of Energy, Environment and Climate Action, Heidelberg, 3084, Melbourne, Victoria, Australia.

[7] Department of Environment, Tourism, Science and Innovation, Queensland Herbarium and Biodiversity Science, Toowong, 4066, Brisbane, Queensland, Australia.

[8] Research School of Biology, The Australian National University, Canberra, 2601, Australian Capital Territory, Australia.

[9] School of Life and Environmental Sciences, The University of Sydney, Sydney, 2000, New South Wales, Australia.

[10] School of Agriculture, Food, and Ecosystem Sciences, The University of Melbourne, 500 Yarra Boulevard, Richmond, 3121, Melbourne, Victoria, Australia.

*Corresponding author. Email: lukedanielemerson@hotmail.com

ABSTRACT

Collating and synthesising ecological information is critical for guiding effective conservation policy and management plans. This is especially pertinent for species of conservation concern. This task may be further complicated when taxonomic revisions of species and species complexes occur. Species previously managed as a single taxon may be reclassified into multiple species, and hence species-specific concerns and management requirements may need to be revised rapidly. Until 2020, greater gliders were widely recognised as a single species (*Petauroides volans*) with an extensive distribution along Australia's east coast. However, recent genetic evidence supports earlier descriptions of three separate greater glider species: *Petauroides minor* (northern greater glider), *P. armillatus* (central greater glider), and *P. volans* (southern greater glider). However, the current Environment Protection and Biodiversity Conservation Act 1999 currently recognises only *P. volans* (southern and central) and *P. minor* (northern) as unique species, which are listed as Endangered and Vulnerable, respectively. We conducted a systematic review of all literature relating to ecological research on greater gliders. Our aim was to inform appropriate conservation and management actions and identify future research priorities for the three species. We identified 178 unique greater glider studies and categorised them by geographic location and thematic focus, assigning them to each species based on previous work on distributional boundaries to evaluate the ecological knowledge base for each species. Most research addressed factors associated with occurrence, abundance, anthropogenic habitat destruction, fire, and spatial distribution, with a marked research bias toward the southern greater glider. Ecological knowledge for the central and northern species remains limited, potentially compromising species-specific conservation and management for these two taxa. Climate change, habitat destruction, and wildfire are considered key threats to greater glider populations. Additional research across all greater glider species is needed to understand key drivers of population dynamics, including the role of climate change and associated extreme weather events, life history traits, genetics, physiology, predation, competition, disease, habitat quality, planned burning, and spatial ecology. Such information is essential for accurate extinction risk and effective threat mitigation. Ensuring the long-term survival of greater gliders requires coordinated, species-specific conservation strategies informed by research, supported by legislative reform, and underpinned by strong environmental protections and habitat restoration. Our synthesis highlights the broader utility of re-evaluating existing research in the context of taxonomic reclassification, particularly for directing future research and informing targeted and effective conservation responses for threatened species.

KEY WORDS

biodiversity conservation, environmental policy, threatened species conservation, mammal extinction, systematic literature review, arboreal mammals, extinction crisis, Petauroides, taxonomic uncertainty

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I. INTRODUCTION

Effective biodiversity conservation and management relies on a robust evidence base (Sutherland *et al.*, 2004). However, decision-makers often struggle to utilise this evidence due to the sheer volume of relevant literature (Pullin & Knight, 2005). Instead, they may rely on subsets of information, such as published reviews (Pullin & Knight, 2005). Thus, the review and collation of evidence is fundamental to the development of effective conservation policy and subsequent biodiversity action and management plans (Sutherland *et al.*, 2004).

Another challenge to evidence-based conservation arises from disproportionate research effort across species and aspects of their ecology (Fleming & Bateman, 2016). This can lead to replication of research findings, which may divert research efforts from exploring other important aspects of a given species' ecology, while strengthening the evidence base and conclusions (Fleming & Bateman, 2016). Furthermore, taxonomic debates, uncertainty, and revisions can complicate species-specific conservation actions. Species once managed as a single species may be part of species complexes containing multiple species, each with potentially different needs (Silva *et al.*, 2020). This has important implications given conservation management and planning for threatened taxa depends on recognition and definition of individual conservation units that may have differing management requirements (Mace, 2004; Dussex *et al.*, 2018; Stronen *et al.*, 2022).

Australia has experienced one of the highest rates of species extinction globally over the last 500 years (Woinarski *et al.*, 2019; Legge *et al.*, 2023). This rate is predicted to increase unless conservation and management actions improve (Geyle *et al.*, 2018). Australia's mammals have been disproportionately affected as a group, with 39 species considered extinct and over 112 species at risk of extinction (Department of Climate Change, Energy, the Environment and Water, 2025). Included in these threatened mammals are greater gliders. These folivorous, arboreal marsupials include the largest gliding marsupial species and the second largest gliding mammal in the world (the southern greater glider). Once considered a single species (*Petauroides volans*), recent genetic evidence supports their classification as three distinct species: the northern (*P. minor*), central (*P. armillatus*), and southern greater glider (*P. volans*) (McGregor *et al.*, 2020). This separation agrees with earlier morphological assessments (Jackson & Groves, 2015).

Greater gliders are distributed along Australia's east coast, with the northern species found near Cairns and Townsville in the far north of Queensland, the central species' range extends from south of Townsville to the Queensland and New South Wales border, while the southern species ranges from this border to southern Victoria. They were once considered common across their range but have suffered significant population declines (Lindenmayer *et al.*, 2011b), leading to the recent conservation listing of 'Endangered' for the southern and central species, which the listing inaccurately refers to both as *P . volans*, (Department of Climate Change, Energy, the Environment and Water, 2022a), while the northern species is listed as 'Vulnerable'(Department of Climate Change, Energy, the Environment and Water, 2022b).

There has been an increase in research and public interest in greater gliders in recent years, driven by their rapidly declining populations exacerbated by climate change (Smith & Smith, 2018; Wagner *et al.*, 2020), logging (typically clearfelling in Australia), and land-clearing (Ashman *et al.*, 2021; Lindenmayer *et al.*, 2021, 2022) and concerns about the impacts of the 2019-2020 large-scale fires (Smith & Smith, 2022; Driscoll *et al.*, 2024). Their threatened conservation status has significantly elevated their profile, with the species' becoming a high priority conservation target for researchers and environmental community groups. This has put pressure on governments to develop and enforce policies that will reduce the impact of key threatening processes such as logging, land clearing, habitat fragmentation, and the impacts of climate change (Ward *et al.*, 2024). However, without adequate ecological knowledge and relevant research across the range of all three species, developing and implementing tailored, informed, and practical conservation policies is challenging.

Given the importance of reviews for informing evidence-based conservation, we conducted the first comprehensive systematic review of greater glider research. Specifically, we synthesised the existing ecological knowledge base, which for most of this period, treated greater gliders as a single species, and reclassified studies according to the revised taxonomy recognising three distinct species: *Petauroides volans*, *P. armillatus*, and *P. minor*. To achieve this, we assigned each study to one or more species based on its geographic location relative to the best-available delineations of each species' distribution. We then quantified research effort per species and per ecological topic, identified core research themes, and summarised current ecological understanding, threats, management and policy recommendations. We highlight critical knowledge gaps and under-researched areas necessary for informing species-specific conservation and recovery efforts. This synthesis is intended to guide researchers, conservation practitioners, and policymakers by providing a consolidated evidence base to support the development of targeted and effective recovery plans, which as of 2025, have yet to be published.

II. MATERIALS AND METHODS

(1) Literature searches and database compilation

Our literature review followed best-practice recommendations from the ROSES (RepOrting standards for Systematic Evidence Syntheses) framework (Haddaway *et al.*, 2018). We developed a review protocol and transparent inclusion and exclusion criteria (Haddaway *et al.*, 2015; see Supporting Information) prior to conducting our review. Articles returned by bibliographic and citation searches were screened and reviewed according to the predefined review protocol (see Supporting Information). We searched five bibliographic databases—Web of Science, Zoological Record, Scopus, ProQuest Dissertation and Theses Global, and Google Scholar—using the search string ("greater glider" OR "*Schoinobates volans*" OR "*Petauroides volans*" OR "*Petauroides armillatus*" OR "*Petauroides minor*"). Greater gliders have a complex and often confusing taxonomic history, having been classified under multiple genera and binomial names. Notably, they were referred to as *Schoinobates volans* for an extended period in the scientific literature (Maloney & Harris, 2008); accordingly, we included this genus in our search terms.

Searches targeted terms located in the publication title, abstract, keywords, and main text. Relevant literature included peer-reviewed journal articles, theses, and government reports. In addition, we conducted citation searches systematically on included studies using a targeted set of key terms (see Supporting Information for details). We considered only articles written in English; however, we identified only one article in another language, which was subsequently excluded.

(2) Data extraction & synthesis

For each article included in the final synthesis, we recorded the title, authors, year of publication, article type, and study location and coordinates, where possible. Following a similar approach to previous systematic literature reviews (Ashman, Watchorn & Whisson, 2019; Moore *et al.*, 2021), we conducted a content analysis (Krippendorff, 2018) by categorising the focus of each study relative to 22 topics (Data S1). Individual studies could be categorised as multiple topics simultaneously.

To assess research effort per greater glider species, we assigned each article to a species based on its geographic location, relative to the known or inferred species distribution, as described by Arbogast *et al.* (2011), Jackson & Groves (2015), McGregor *et al.* (2020), and Youngentob (personal communication; see Supporting Information). We assigned each study to one or more species, depending on whether its location overlapped with the inferred range of a single species or multiple species. This information was used to descriptively synthesise the research effort per research topic per species.

III. GREATER GLIDER STUDIES

Our systematic literature searches identified 891 unique articles, of which 178 met our inclusion criteria and contained unique information that was subsequently summarised (see Supporting Information; Data S1). There has been a substantial increase in the number of greater glider studies published from the 1980s onwards (8% (*n* = 15) pre-1980 vs 92% (*n* = 163) post-1980), with the first five and a half years of the current decade (2020-2025) being the most prolific decade with nearly one third of studies published (*n* = 52, 29%; Fig. 1). This increase in greater glider research is likely a result of the threatened conservation listing for greater gliders in 2016. The earliest study that met our search criteria was published in 1923 and investigated the meiotic phase in male greater gliders, at an unreported location (Agar, 1923).

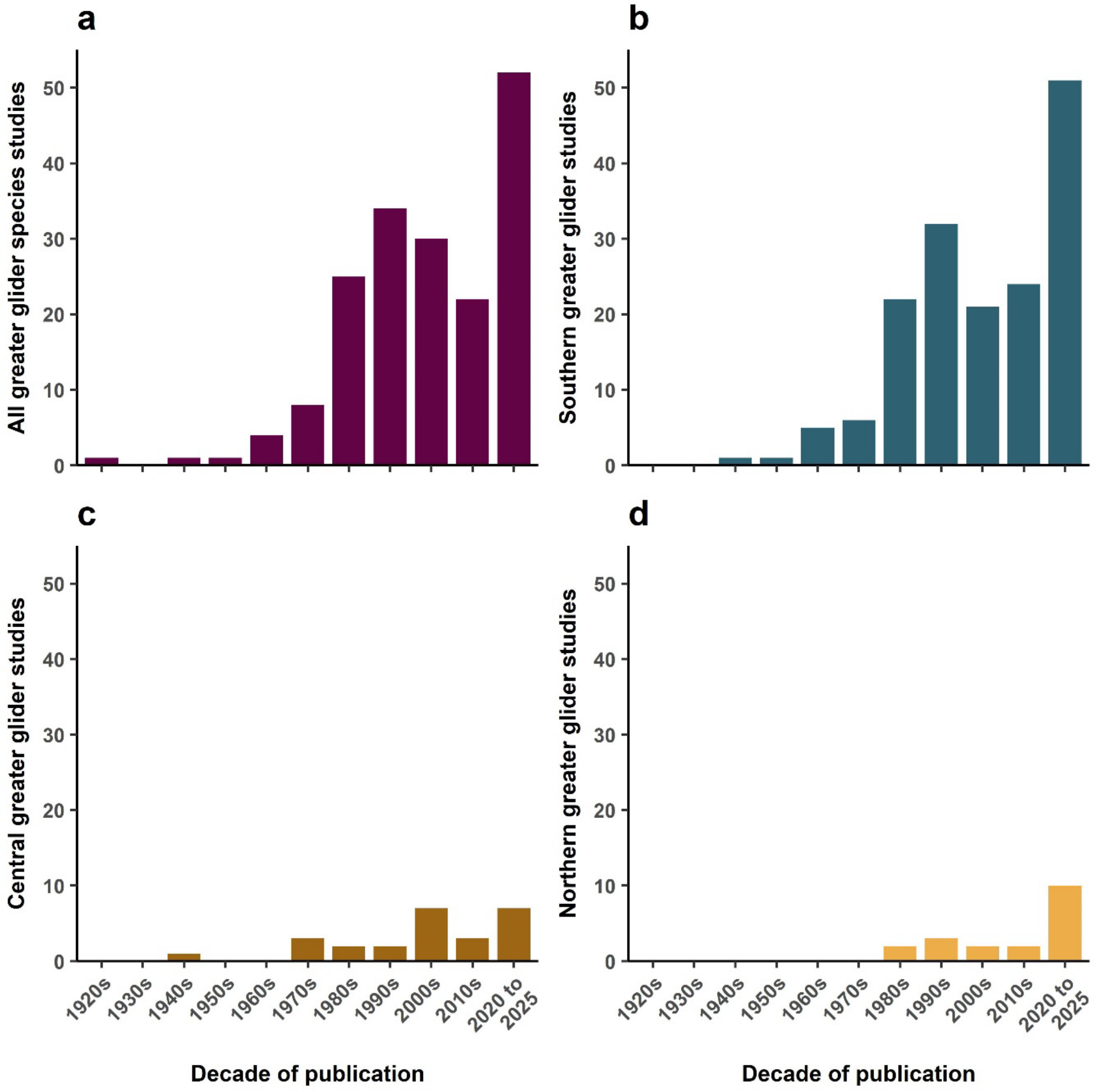


Figure 1. (a) Number of unique greater glider articles/studies per decade of publication for all species. This includes seven articles where the species could not be determined because of

a lack of reported location data. Number of unique greater glider articles/studies per decade of publication is shown for (b) southern (*Petauroides volans*), (c) central (*P. armillatus*), and (d) northern (*P. minor*) greater gliders.

(1) Geographic distribution of greater glider studies

Most studies have been conducted within the southern extent of the greater glider distribution (Fig. 2). The highest proportion of greater glider studies has been conducted in New South Wales and the Australian Capital Territory (*n* = 102), followed by Victoria (*n* = 60), and then Queensland (*n* = 33). There were 20 studies that were conducted across more than one state (Data S1).

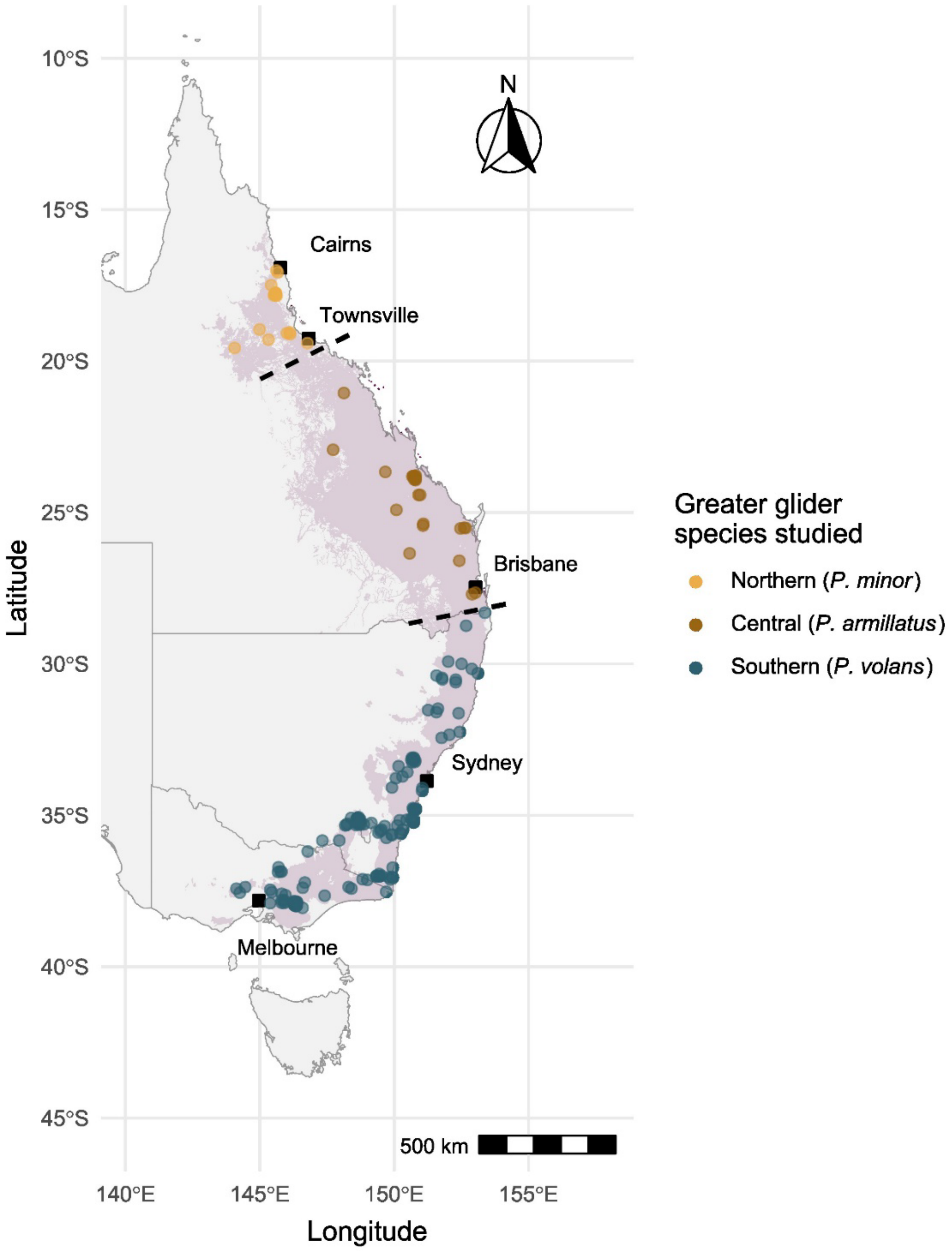


Figure 2. Geographic distribution of studies for northern (*Petauroides minor*), central (*P. armillatus*), and southern greater gliders (*P. volans*). Species distributions and approximate species boundaries (black dashed lines) are based on findings by Arbogast *et al.* (2011), Jackson & Groves (2015), McGregor *et al.* (2020), and Youngentob (personal communication). The pink shaded area shows the predicted geographic distribution of the three greater glider species in Australia (Species Profile and Threats Database; Department of Climate Change, Energy, the Environment and Water, 2023).

The southern greater glider was the subject of the highest proportion of studies (85%, *n* = 151), followed by 14% (*n* = 25) of studies for the central species, and 11% (*n* = 19) for the northern species (Fig. 3). A species could not be determined for 4% (*n* = 7) of studies because the research was conducted in a laboratory, or the study location could not be reliably determined (Fig. 3). There 15 studies (8%) that reported information for more than one species, hence the combined proportions sum to greater than 100%.

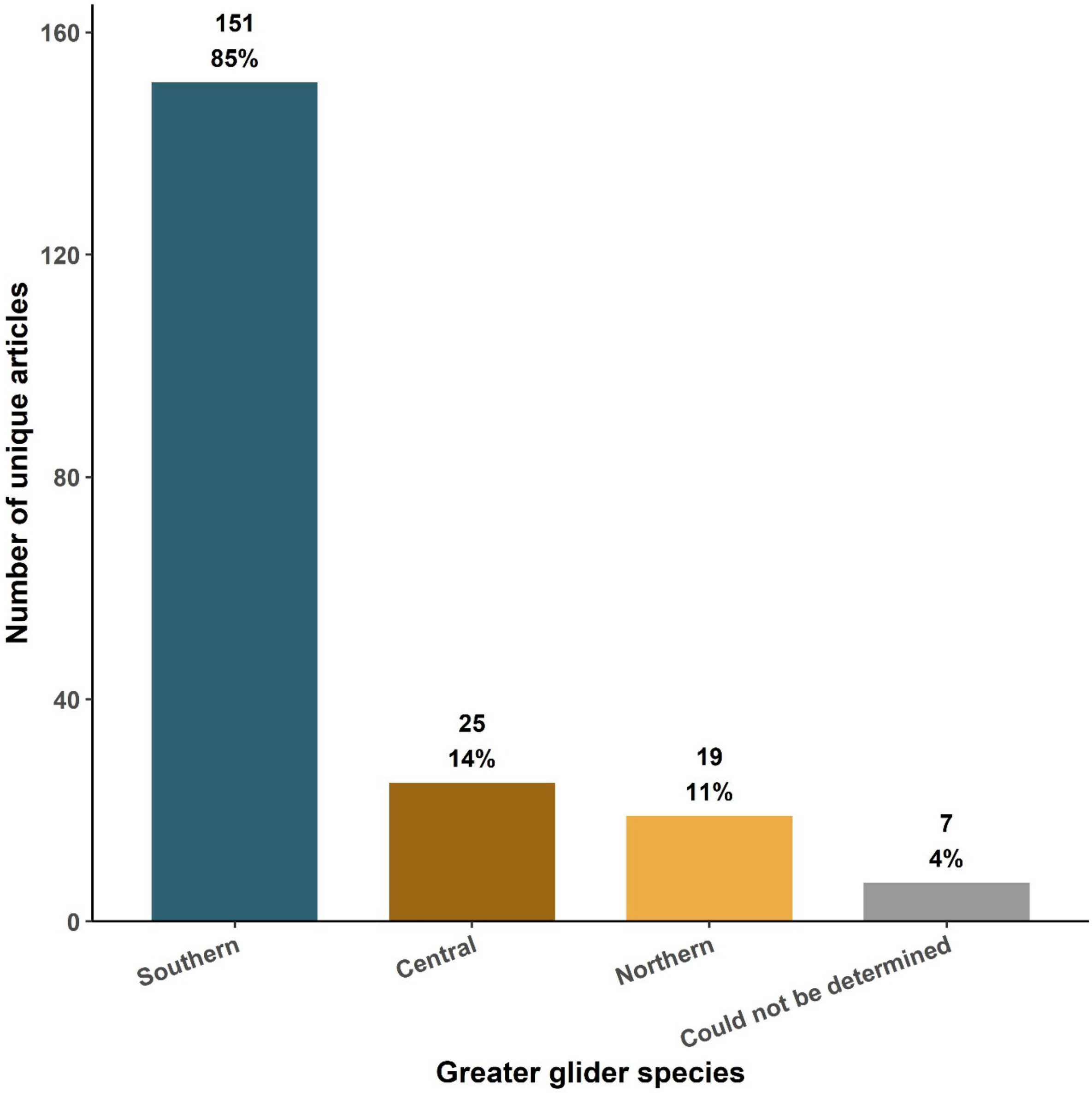
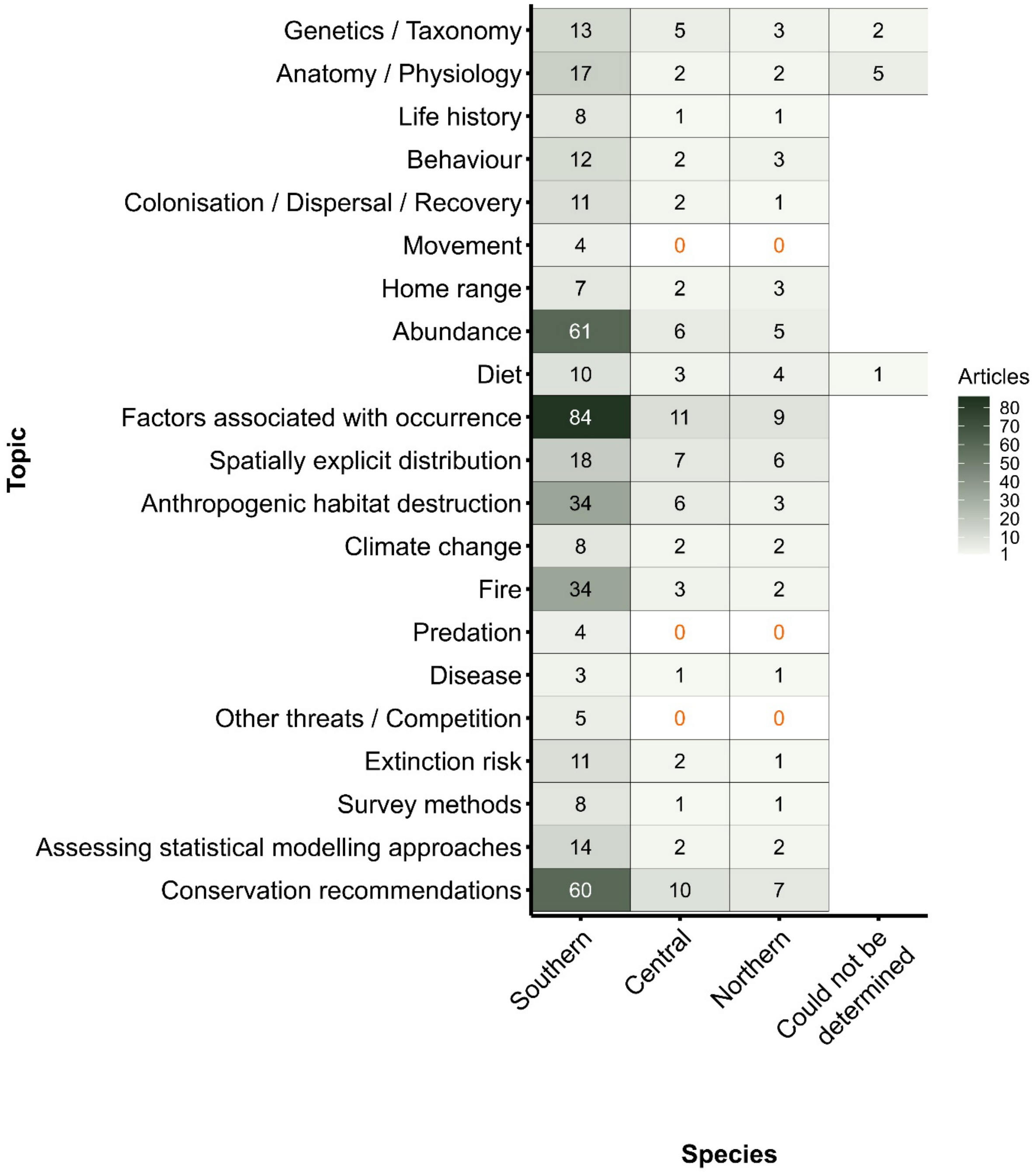


Figure 3. Number of unique articles per greater glider species. Information for multiple greater glider species could be reported in the same article, thus the total number of unique

articles ($N = 178$) does not equal the sum of all articles per species, and combined proportions sum to greater than 100%.

(2) Distribution of research across greater glider species per research topic

Research effort was not evenly distributed across topics or species (Fig. 4). The most frequently researched topics were factors associated with occurrence, abundance, anthropogenic habitat destruction, fire, and spatially explicit distribution (Fig. 4). There was a lack of research investigating life history, movement, predation and disease, and for the central and northern greater glider generally (Fig. 4). Numerous articles provided management and policy recommendations (Fig. 4) for improving the conservation of greater gliders, with the earliest of these published in 1987 by Kavanagh (1987) and Lunney (1987).



Topic	Southern	Central	Northern	Could not be determined
Genetics / Taxonomy	13	5	3	2
Anatomy / Physiology	17	2	2	5
Life history	8	1	1	
Behaviour	12	2	3	
Colonisation / Dispersal / Recovery	11	2	1	
Movement	4	0	0	
Home range	7	2	3	
Abundance	61	6	5	
Diet	10	3	4	1
Factors associated with occurrence	84	11	9	
Spatially explicit distribution	18	7	6	
Anthropogenic habitat destruction	34	6	3	
Climate change	8	2	2	
Fire	34	3	2	
Predation	4	0	0	
Disease	3	1	1	
Other threats / Competition	5	0	0	
Extinction risk	11	2	1	
Survey methods	8	1	1	
Assessing statistical modelling approaches	14	2	2	
Conservation recommendations	60	10	7	

Figure 4. Number of unique greater glider studies categorised by species and topic, indicating considerably greater research effort across most topics for the southern species (*Petauroides volans*) compared to the central (*P. armillatus*) and northern species (*P. minor*).

IV. TAXONOMY & GENETICS

(1) Taxonomy

A phylogenetic study into possums and gliders estimated that the divergence of *P. volans* occurred from a common ancestor of other possums approximately 39 million years ago (Edwards & Westerman, 1995). More recently, *Petauroides volans*, traditionally considered the only gliding member of the family Pseudocheiridae, was recognised as two subspecies by the Australian government: *Petauroides volans volans* and *Petauroides volans minor*. These subspecies differed in morphology, colour, and distribution (Comport, Ward & Foley, 1996; McKay, 2008). Recently it was proposed to split *P. volans* into three distinct species: *P. volans, P. minor*, and *P. armillatus* (Jackson, 2015; Jackson & Groves, 2015), based on geographical and morphological distinctions. The first test on a three species designation using molecular sequence data was performed by McGregor et al. (2020), which indicated three distinct species.

However, the adoption a three species classification is not universal. Currently, only two species are formally recognised under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act; Department of the Environment, 2025a, 2025b), while only one species is now recognised under Queensland's *Nature Conservation Act 1999* (Queensland Government, 2025), following the Australasian Mammal Taxonomy Consortium which currently recognises two subspecies (i.e. *P. volans volans* and *P. volans minor;* (AMTC, 2024). Only one species is currently recognised by the IUCN Redlist (Burbidge & Woinarski, 2020). These discrepancies have implications for population and conservation assessments, and targeted management actions, particularly our review indicates that each of the three species have smaller distributions than that previously attributed to just *P. volans*. However, the genetic samples underpinning this classification have primarily utilised samples from Victoria and Queensland, leaving a significant gap in New South Wales

(NSW) for taxonomic delegation. Further genetic sampling across the NSW distribution of greater gliders is of high importance for taxonomic work to identify the exact range, potential overlap and hybridisation between species.

(2) Genetics

Early genetic work for *Petauroides* species involved understanding the cytological characteristics contributing to the understanding of their meiotic processes, which was performed on southern greater gliders (Agar, 1923). Some of the first observations of *B* chromosomes in mammals was found in southern greater gliders (Hayman & Martin, 1965). Further chromosome work in southern and central greater gliders have investigated the composition of *B* chromosomes (Mcquade, Hill & Francis, 1994; McQuade, 1995) and the structure of sex chromosomes, chromosomal elimination and intrapopulation variation of chromosomal inactivation (Murray, McKay & Sharman, 1979; Murray & McKay, 1979, 1982).

There is an absence of conservation genetic research for most of the distribution of all greater glider species. Early work on southern greater glider conservation genetics used microsatellite data from southern greater gliders in a fragmented *Eucalyptus* forest surrounded by extensive stands of exotic *Pinus radiata* (Taylor, Tyndale-Biscoe & Lindenmayer, 2007). The study found that while the *Pinus radiata* plantation did not support populations, the southern greater glider could have potentially moved through the “soft matrix” of these exotic tree stands, maintaining some connectivity between isolated patches of remnant *Eucalyptus* forest (Taylor, Kraaijeveld & Lindenmayer, 2002; Taylor *et al.*, 2007). Only one other study into conservation genomics has occurred and this was for southern greater gliders on the south coast of NSW (Knipler, Gracanin & Mikac, 2023). Across fourteen locations spanning an area of approximately 15,000 km^2, the authors found most populations had low genetic diversity, evidence of inbreeding, and low effective population size, raising concerns over increasing localised population extinctions in the future (Knipler *et al.*, 2023). Given the recent uplisting of the southern greater glider to 'Endangered' under the EPBC Act, understanding the baseline genetic structure of populations across the distribution of all three species is critical to inform conservation management actions and identify stronghold populations.

V. DISTRIBUTION

Greater gliders are distributed along the east coast of Australia with a range extending over 3000 km north to south and up to ~400 km inland from the coast (Fig. 2). They occur across an elevational gradient of 0-1400 m above sea level (Lindenmayer *et al.*, 2018; Emerson, Ballard & Vernes, 2019) but are more likely to occur at higher elevations (Bennett *et al.*, 1991; Kavanagh & Bamkin, 1995; Kavanagh, 2000; Smith & Smith, 2020; Ridley *et al.*, 2024). Greater glider distribution is broadly driven by availability of woodland and open eucalypt forest containing suitable food species (Eyre, 2006; Lindenmayer *et al.*, 2022), hollow-bearing trees (Lindenmayer *et al.*, 1990a; Eyre, 2006; Lindenmayer *et al.*, 2021, 2024a), and suitable climatic conditions (Kearney, Wintle & Porter, 2010; Smith & Smith, 2020; Wagner *et al.*, 2020). Numerous habitat characteristics are associated with greater glider occupancy (e.g. McCarthy & Lindenmayer, 1999b; Youngentob *et al.*, 2012; Smith & Smith, 2018) and are discussed later in the manuscript.

Across the distribution of all three greater glider species, annual average rainfall ranges from ~400 to over 3000 mm and annual average temperatures range from ~6°C to 27°C (Bureau of Meteorology, 2024). However, species distribution modelling suggests that greater gliders in general are most likely to occur where temperatures peak at ~18°C during the warmest part of the year and annual rainfall is ~1500 mm, although this may not accurately describe the northern species' tolerances due to a lack of data to inform such modelling (Torres, 2020). Within this broad climatic envelope, conditions vary for each species: northern greater gliders persist in the warmest environments and span both the driest and wettest parts of the range (~18–27°C; ~400–3000 mm annual averages), central greater gliders occur in intermediate conditions (~15–27°C; ~400–1500 mm), and southern greater gliders are largely restricted to cooler and wetter habitats (~6–21°C; ~600–2000 mm; Bureau of Meteorology, 2024).

Since European invasion, the extent of occurrence has been contracting for all greater glider species and is estimated to be 43 655 to 48 946 km^2 for the northern species (Woinarski, Burbidge & Harrison, 2014; Department of Climate Change, Energy, the Environment and Water, 2022b) and 752 962 to 1 066 146 km^2 for the central and southern species combined (Woinarski *et al.*, 2014; Department of Climate Change, Energy, the Environment and Water, 2022a). Additionally, the area of occupancy has significantly decreased for all three species since European arrival, primarily due to habitat destruction (Woinarski *et al.*, 2014), with further contraction being driven by forestry activities and fire (McLean *et al.*, 2018; Lindenmayer & Sato, 2018; Ashman *et al.*, 2021), habitat fragmentation and edge effects (Youngentob *et al.*, 2012), and climate change (Smith & Smith, 2018; Wagner *et al.*, 2020). Area of occupancy has been estimated at 500 to < 2000 km^2 for the northern species (Woinarski *et al.*, 2014; Department of Climate Change, Energy, the Environment and Water, 2022b) and 15 244 to > 20 000 km^2 for the central and southern species combined (Woinarski *et al.*, 2014; Department of Climate Change, Energy, the Environment and Water, 2022a). However, this is likely a substantial underestimate because of limited sampling across the occupied range (Woinarski *et al.*, 2014). Recorded dramatic declines and extirpation of some greater glider subpopulations (Woinarski *et al.*, 2006; Smith & Smith, 2018; Lindenmayer *et* *al.*, 2018), as well as continuing negative impacts of habitat destruction, fire (McLean *et al.*, 2018; Lindenmayer & Sato, 2018; Ashman *et al.*, 2021; Campbell-Jones *et al.*, 2022; Lindenmayer *et al.*, 2022; Smith & Smith, 2022), and climate change (Kearney *et al.*, 2010; Smith & Smith, 2020), strongly suggests that many unmonitored subpopulations of greater gliders are also declining (Department of Climate Change, Energy, the Environment and Water, 2022a).

Northern greater gliders have the most restricted distribution of the three species occurring in the tropical region of north-eastern Australia from the Windsor Tablelands north of Cairns (~16°S; Fig. 2), to just south of Townsville (~19.5°S; Fig. 2). Their distribution likely overlaps with the northern extent of the central species, given hybridisation between the two species has been documented (McGregor *et al.*, 2020). Two isolated subpopulations have also been recorded at Blackbraes National Park (Vanderduys, Kutt & Kemp, 2012) and the Gregory Range, at the western limit of the species' distribution (~19.5°S & 143.5°E; Fig. 2), (Winter *et al.*, 2004; Woinarski *et al.*, 2014). This isolation, exacerbated by habitat destruction, could have conservation implications for these subpopulations (Winter *et al.*, 2004). Furthermore, the apparent lack of studies examining the distribution of northern and central greater gliders (Fig. 4) raises additional concerns regarding our understanding of their ecology and our subsequent ability to conserve and manage these threatened species.

The exact distribution of the central and southern greater glider species remains unresolved (McGregor *et al.*, 2020). Genetic work indicates that the central species' range extends from near Townsville (~19.5°S; Fig. 2) in the north to at least the Queensland and NSW border in the south (~28°S; Fig. 2) (McGregor *et al.*, 2020). Similarly, the southern species' range extends from Wombat State Forest in central Victoria (~37.5°S & 144.5°E) to at least the Victorian and NSW border (Fig. 2; Arbogast *et al.*, 2011; Jackson & Groves, 2015;

McGregor *et al.*, 2020; Youngentob (personal communication)). Further genetic assessments are required to determine the range extents of these two species because it remains unclear how far south the central greater glider's distribution extends, or how far north the southern species is distributed (McGregor *et al.*, 2020). This uncertainty could inhibit species-specific monitoring and conservation actions, thus more surveys across the distribution of each species need to be conducted to determine accurate areas of occupancy.

VI. ANATOMY & PHYSIOLOGY

Greater gliders are the largest of the Australian marsupial gliders. Adults of the southern species generally weigh between 1000 g and 1700 g (Norton, 1988; Viggers & Lindenmayer, 2001; Cunningham, Pope & Lindenmayer, 2004), with a head-body length of 35-40 cm and a tail length of around 50 cm (Viggers & Lindenmayer, 2001; McGregor *et al.*, 2020). The central and northern species are smaller; adults of the central species weigh about 900 g on average, while northern greater gliders are 600 g to 800 g (Foley *et al.*, 1990; Comport *et al.*, 1996; McGregor *et al.*, 2020). In all three species, males and females are similar in size (Norton, 1988; McGregor *et al.*, 2020).

Southern greater gliders are heavily furred with variable coat colour, ranging from white to mottled grey to dark brown, usually with a white belly and chest (Comport *et al.*, 1996; McGregor *et al.*, 2020). The central and northern species are less variable in colour and have dark brown dorsal hair with silvery or grey subterminal bands (Comport *et al.*, 1996; McGregor *et al.*, 2020). All three species have a patagium (gliding membrane) that connects the elbow on the forelimb to the ankle on the hind limb (Johnson-Murray, 1987). This differs from all other marsupial gliders, in which the gliding membrane predominantly connects the wrist to ankle (Johnson-Murray, 1987). When gliding, greater gliders extend their hindlimbs and keep their forelimbs flexed with the digits adjacent to the chin (Johnson-Murray, 1987).

The gliding membrane also helps to insulate against heat dissipation at cooler temperatures (Rübsamen *et al.*, 1984). At warmer temperatures, southern greater gliders can become hyperthermic at temperatures above 20-22°C and must expend significant energy and water for cooling (Rübsamen *et al.*, 1984). This sensitivity to heat may explain why greater gliders are often found at higher elevations, where it is generally cooler (Moore *et al.*, 2004; Lindenmayer *et al.*, 2022). Less is known about the thermal physiology of northern and central greater gliders. This information could assist with understanding their current distribution and future implications of heat waves and climate change (Kearney *et al.*, 2010).

Captive southern greater gliders have a resting metabolic rate of around 210 kJ $kg^{-0.75}$ d^{-1} (Foley, 1987), while field metabolic rates of 520 kJ d^{-1} have been measured in central greater gliders (Foley *et al.*, 1990). Higher field metabolic rates reflect the increased energy demands of activity, thermoregulation and locomotion in free living animals (Foley *et al.*, 1990). In both studies, calculated values were similar to the predicted rates for marsupials of their size. The maintenance energy requirements of captive southern greater gliders fed *Eucalyptus radiata* foliage were 0.35 MJ of metabolizable energy $kg^{-0.75}$ d^{-1}, but this value may be somewhat dependent on the specific diet and the cost of metabolising and eliminating associated plant secondary metabolites (PSMs) (Foley, 1987).

Large herbivores (greater than 1 kg) can survive on plant diets by eating large volumes of food and having slow gut passage rates that allow time for synergistic microbes to break down plant cell walls and maximise nutrient extraction (Tyndale-Biscoe, 2005). For smaller herbivores, however, food intake is constrained by gut fill (Crowe & Hume, 1997). Because greater gliders are close to the minimum size for a herbivore with a strictly folivorous diet, they have several anatomical and physiological adaptations that allow them to meet their nutritional requirements on a highly specialised diet of eucalypt leaves. These adaptations include shearing teeth that reduce leaves to small particles to increase surface area, and a large and complex caecum for microbial fermentation (Foley, Hume & Cork, 1989; Hume, 1999). Microbial digestion facilitates the extraction of nutrients from food and also provides products from microbial digestion and potential detoxification of PSMs (Moore *et al.*, 2004).

The digestive physiology of greater gliders has predominantly been studied in the southern species. Like other arboreal folivores, southern greater gliders have long mean retention times for digesta (Foley & Hume, 1987). The gut-filling effect of eating fibrous leaves is reduced by excreting coarse particles more rapidly, while fine particles are selectively retained in the caecum (Foley & Hume, 1987). Although short chain fatty acids (SCFA) produced by fermentation in the caecum can be absorbed from all regions of the hindgut (Rübsamen *et al.*, 1983), they contribute relatively little (approx. 7%) to the digestible energy intake of southern greater gliders (Foley *et al.*, 1989). Thus, the bulk of energy requirements come from cell contents (Foley *et al.*, 1989). There is no evidence that southern greater gliders practice caecotrophy to improve nitrogen (N) assimilation as observed in the closely related eastern ring-tailed possum (*Pseudocheirus peregrinus*; Crowe & Hume, 1997).

Southern greater gliders have an estimated truly digestible maintenance N requirement of 0.56 g $kg^{-0.75}$ d^{-1} when feeding on *E. radiata* foliage (Foley & Hume, 1987). This requirement is higher than other captive folivores eating *Eucalyptus* foliage, but it could be related to N loss in response to PSM detoxification on the specific diet offered (Foley & Hume, 1987). This is supported by field measurements in which free living central greater gliders maintained bodyweight when feeding on diets that were substantially lower in N than those fed to captive animals (Foley *et al.*, 1990).

One important physiological adaptation for a diet of eucalypt leaves is the capacity to metabolise PSMs, which are often found in high concentrations in these leaves. Terpenes (essential oils), for example, are readily absorbed and disappear from the stomach and small intestine before reaching the hindgut (Foley, Lassak & Brophy, 1987). In northern greater gliders, the process for metabolising monoterpenes involves extensive oxidation (Boyle *et al.*, 1999). There is minimal conjugation with glucuronic acid (derived from glucose), which is likely an adaptation to conserve nutrients on their low energy diet (Boyle *et al.*, 1999). Nevertheless, the costs and limitations on the rate at which they can detoxify eucalypt PSMs relative to acquiring nutrients probably dictates feeding preferences and feeding rates (Moore *et al.*, 2004; Marsh *et al.*, 2006).

VII. LIFE HISTORY

(1) Reproduction

Empirical data on the life history of greater gliders, including reproductive traits, are limited to the southern species (*P. volans*), with no studies conducted on the central or northern species. This represents a substantial knowledge gap with important implications for conservation and management (Kearney *et al.*, 2010).

Southern greater gliders are highly seasonal, monoestrous breeders (Tyndale-Biscoe, 2005). Reproductive activity occurs in a narrow window, with mating typically observed between March and May and births occurring from April to May (Smith, 1969; Henry, 1985; Norton, 1988). Sperm production in males is restricted to autumn and early winter (Smith, 1969; Baldwin, Temple-Smith & Tidemann, 1974), and social interactions between adult males and females peak in late summer and early autumn (Henry, 1985). Males maintain exclusive access to their associated female through den sharing or visiting them at night (Henry, 1985; Norton, 1988).

Southern greater gliders are monovular, with only one offspring conceived at a time (Smith, 1969) and breeding occurring annually, resulting in one young per year (Smith, 1969; Tyndale-Biscoe & Smith, 1969). Not all females breed annually, with proposed explanations including limitations on the number of available males and variation in habitat quality (Bancroft, 1970; Henry, 1985; Norton, 1988). Breeding is typically restricted to females weighing over 1 kg, suggesting sexual maturity is reached in the second year of life, where annually >80% of individuals were observed to be either pregnant or with a pouch young (Smith, 1969; Tyndale-Biscoe & Smith, 1969; Bancroft, 1970). However, in Victoria, natality rates of 50% or less were reported (Henry, 1985).

Young are born in an underdeveloped state and continue development in the pouch, which opens forward and is well developed (Smith, 1969). Lactation is prolonged, helping females avoid peak nutritional demands (Moore *et al.*, 2004). Pouch emergence occurs around October when the juvenile weighs ~150 g, after which they may ride on the mother's back until reaching ~300 g, or remain in tree hollows while the mother is foraging (Henry, 1985; Norton, 1988). Juveniles remain with the mother until they are about 10 months of age and weigh ~500–600 g around January of their first year (Smith, 1969; Bancroft, 1970; Henry, 1985; Norton, 1988). Dispersal behaviour and survival rates of juveniles remain poorly understood (Henry, 1985; Norton, 1988). Male reproductive anatomy in greater gliders is similar to other marsupials (Smith, 1969).

Mechanistic modelling indicated that the environmental drivers limiting reproduction (milk production) in greater gliders vary geographically (Kearney *et al.*, 2010). At the northern and inland extremities of the northern species' range, reproduction is primarily constrained by water availability and balance during September, when rainfall is typically low (Kearney *et al.*, 2010). In contrast, protein is the major limiter of reproduction for the central and southern species, while energy availability also constrains reproduction in highland areas of the southern species range (Kearney *et al.*, 2010).

(2) Sex ratio

Sex ratios have been reported exclusively for the southern greater glider. At birth, the sex ratio is approximately 1:1 (Smith, 1969; Henry, 1985), however, as offspring mature, a female-biased sex ratio emerges, with males comprising less than 40% of the population (Smith, 1965; Tyndale-Biscoe & Smith, 1969). Other studies in southeastern Australia similarly report female-biased sex ratios (Kehl & Borsboom, 1984; Henry, 1985), with only one study reporting near parity near Armidale, NSW (Griffith, 1973). Although not specifically tested for greater gliders, the local-resource-competition hypothesis, observed in other arboreal mammals such as common brushtail possums (*Trichosurus vulpecula*), may also apply, whereby sex ratios are biased towards the dispersing sex when philopatric offspring compete with their mothers for resources, such as food or dens (Johnson *et al.*, 2001).

(3) Life expectancy

In southeastern NSW, life spans of greater gliders were theoretically estimated to be between five and ten years with annual mortality rates of ~20% of adult individuals (Smith, 1965). In the absence of a sound method for age determination in adult individuals, calculations of life expectancy are problematic and include assumptions of some animals being able to live for

15 years (Tyndale-Biscoe & Smith, 1969). Differential mortalities about 20% in favour of females were hypothesised prenatally or in pouch life, which may also be a factor in driving the unequal sex-ratio in the southern species (Smith, 1965). In southeastern NSW, juvenile mortality averaged 15.8%, with no evidence of juvenile mortality within the studied population in some years (Tyndale-Biscoe & Smith, 1969). The greatest mortality occurs when juveniles become >300 g, which coincides with the observed decline in the proportion of male individuals (Smith, 1965; Tyndale-Biscoe & Smith, 1969).

VIII. BEHAVIOUR & MOVEMENT

(1) Social Behaviours

Greater gliders spend most of their time either stationary (resting), or feeding on foliage (Norton, 1988; Comport *et al.*, 1996; Cunningham *et al.*, 2004; Starr *et al.*, 2021). All three species are generally solitary during the night, with the majority of spotlighting observations identifying gliders as alone in a tree, rarely sharing trees with conspecifics (Kavanagh & Lambert, 1990; Comport *et al.*, 1996; Cunningham *et al.*, 2004). Den sharing has been observed among male-female pairs in all species (Norton, 1988; Lindenmayer *et al.*, 1991c; Comport *et al.*, 1996), although it is considered rare for both the southern (Kehl & Borsboom, 1984; Lindenmayer, Pope & Cunningham, 2004) and northern species (Comport *et al.*, 1996). More recently however, high rates of den sharing by southern greater gliders has been observed in Tallaganda NSW (Gracanin, A., unpublished data).

Patterns of den use vary among the species, reflecting resource availability. Central greater gliders were found to use between four and 20 dens, sometimes sharing dens either concurrently or sequentially in landscapes where hollow-bearing trees were limited (Smith, Mathieson & Hogan, 2007). Southern greater gliders utilised between one and 13 dens (Norton, 1988; Kavanagh & Wheeler, 2004; Lindenmayer *et al.*, 2004), while the northern species used between one and six (Comport *et al.*, 1996; Starr *et al.*, 2021; McGregor *et al.*, 2023).

Social interactions between females and male southern greater gliders include behaviours such as nasaling, mutual sniffing, climbing over the top of another, and sitting beside a consort (Henry, 1985; Norton, 1988). Similar behaviours have been reported for northern greater gliders (Comport *et al.*, 1996). Antagonistic interactions have been observed between females, and between males and females in the southern species (Henry, 1985; Norton, 1988), while both neutral and antagonistic interactions have been observed between males for the northern species (Comport *et al.*, 1996). Soft vocalisations between females and their young at den entrances have been described for southern greater gliders (Henry, 1985).

Scent-marking is common for both sexes and appears to guide movements (Kehl & Borsboom, 1984; Henry, 1985; Norton, 1988). It typically involves rubbing of the cloacal region on tree branches and trunks; in one instance a male was observed dribbling urine while scent marking (Henry, 1985). These behaviours likely play a role in territory delineation and individual recognition.

Methodological variation and differences in survey effort between behavioural studies—most of which were conducted during the late 20th century—highlight the need for updated research on social and individual behaviours. The application of advanced technologies (e.g. motion-activated cameras; (Gracanin *et al.*, 2025) thermal and infrared imaging; (Vinson, Johnson & Mikac, 2020)) offers promising opportunities to refine and expand our understanding of greater glider behaviour.

(2) Mating systems

Only four copulation events have been observed in the wild for the southern greater glider (Henry, 1985; Ritchie, 2025). For each event, the same sequence was observed. Before mating, the male chased the female. The female engaged in scent-marking using her cloacal region, prompting the male to sniff the area and mark it with his own cloaca. The male also sniffed the female's cloaca before attempting to mount her. The female initially evaded his attempts, but after several tries, the male succeeded. On one occasion, this pursuit phase lasted 30 minutes (Henry, 1985). The act of copulation itself was brief, lasting less than a minute. Afterward, the male showed a decrease in persistent following behaviour, although he continued to share her den and maintain nightly associations with her in the following months.

Monogamous and polygynous mating systems have been observed in greater gliders (inferred from home range size, overlap, den sharing and direct social behaviours), with some of this plasticity attributed to differences in population density (Norton, 1988; Comport *et al.*, 1996; Pope, Lindenmayer & Cunningham, 2004). Social monogamy has been associated with lower population densities (Norton, 1988), whereas evidence suggesting polygamous individuals has been documented in higher-density populations, such as in a study of northern greater gliders (Comport *et al.*, 1996). In southern greater gliders, both mating strategies have been reported. Henry (1985) observed evidence of both monogamy and polygyny, while Norton (1988) found that all individuals studied were socially monogamous, except for a single bigamous male. Further support for polygynous behaviour in southern gliders was provided by Pope *et al*. (2004), who documented males mating with multiple females.

Studies on the mountain brushtail possum (*Trichosurus cunninghami*) show that shifts between monogamy and polygyny can arise from variation in resource distribution (Martin, Handasyde & Taylor, 2007; Martin & Handasyde, 2007; Martin & Martin, 2007). In this species, evenly distributed and abundant food and den trees promote smaller, overlapping female ranges and polygyny in roadside populations, whereas patchier resources in contiguous forests result in larger, more dispersed female ranges and social monogamy (Martin & Martin, 2007). These findings indicate that resource distribution shapes female home range size, which in turn determines the degree of male–female range overlap and thus the prevailing mating system. Similar mechanisms may underlie mating system variation in greater gliders, where habitat quality and hollow availability likely influence female spacing and, consequently, male mating opportunities.

(2) Dispersal, colonisation & recovery

Research on dispersal, colonisation, and recovery in greater gliders has primarily focused on the southern species. However, all three species exhibit specialised habitat requirements and strong site fidelity (Tyndale-Biscoe & Smith, 1969; Kavanagh & Wheeler, 2004), which likely limit their capacity to colonise new or distant habitat patches. Empirical data on dispersal, colonisation, and inter-subpopulation movements is scarce across all species (Norton, 1988; Lindenmayer & Lacy, 1995; McCarthy & Lindenmayer, 1999a). To address these knowledge gaps, several studies have used population modelling to assess the role of dispersal and colonisation in metapopulation viability and recovery for southern greater gliders (Lindenmayer & Lacy, 1995;

Lindenmayer, McCarthy & Pope, 1999c; McCarthy & Lindenmayer, 1999a; Lindenmayer, Lacy & Pope, 2000) .

Dispersal typically occurs when juveniles leave their mothers at 10–11 months of age (Kerle, 2001). Modelling for southern greater gliders has demonstrated that although dispersal can facilitate colonisation, it does not ensure recovery unless subpopulations are large enough and habitat patches are of sufficient quality to support viable populations (Lindenmayer & Lacy, 1995). Dispersal can lead to biased sex ratios (Norton, 1988; Lindenmayer & Lacy, 1995), and elevated dispersal can destabilise small subpopulations and increase extinction risk (Lindenmayer & Lacy, 1995). Accordingly, simulations suggest that a single large habitat patch may provide better prospects for population persistence than several smaller patches of equivalent total area (Lindenmayer & Lacy, 1995; McCarthy & Lindenmayer, 1999a; Wagner, Baker & Nitschke, 2021b). However, in highly fragmented landscapes, even modest rates of dispersal—particularly if aided by connectivity-enhancing interventions such as habitat corridors or crossing structures—can substantially reduce extinction risk for small subpopulations (Taylor & Goldingay, 2009). Additionally, modelling by Goldingay, McHugh and Parkyn (2022) found that colonisation increases with rainforest cover, even though rainforest trees do not provide food for greater gliders. This finding was potentially due to the favourable thermal buffering and productivity of habitats containing rainforest patches, though this requires further investigation.

Empirical studies investigating greater glider dispersal and colonisation have predominantly examined responses to habitat disturbance events, particularly logging. Southern greater gliders respond negatively to intense logging, which can cause direct mortality or a reduction in their home range size, with little evidence of individuals dispersing into nearby unlogged areas (Kavanagh & Wheeler, 2004). This limited dispersal response may not only be influenced by their strong home range fidelity (Tyndale-Biscoe & Smith, 1969), but also by physiological and ecological constraints that hinder movement following habitat disturbance (McCarthy & Lindenmayer, 1999a). Additionally, greater gliders possess low body fat reserves and rely on a low-energy folivorous diet, both of which can lead to rapid declines in body condition under energetically demanding conditions, such as those experienced during dispersal (Hume, 1999).

(3) Movement

Similar to research on dispersal, colonisation and recovery, studies on movement have focused on the southern species. No key differences have been identified between the movement behaviour of the southern and central species. The movement of greater gliders is almost exclusively arboreal, involving gliding between trees or walking along interlocking branches (Smith, 1969; Kavanagh & Wheeler, 2004). Greater gliders use their tail as a rudder to change direction when gliding (Kerle, 2001; Van Dyck & Strahan, 2008). Greater gliders are frequently cited as capable of gliding up to 100m in a single glide (Troughton, 1941, cited in Wakefield, 1970), although the evidence for this claim is limited and is not reliable as the species observed gliding was clearly a yellow-bellied glider (*Petaurus australis*) misidentified as a greater glider. A maximum glide angle of 40° below the horizontal was estimated (Wakefield, 1970) and this indicates a steeper descent. Calculating the glide angle of greater gliders is critical for informing the design of roads and mitigation structures that may potentially allow safe gliding across gaps in forest cover, thereby helping to reduce habitat fragmentation and the risk of vehicle collisions (Taylor & Goldingay, 2009). However, the use of such structures by greater gliders has not been evaluated. Further field-based research is needed to accurately determine the gliding angle and distance for greater gliders. Gliding enables greater gliders to move between trees in their forest habitats, which is essential for foraging and avoiding ground-based predators, particularly as they are slow and clumsy when on the ground (Kerle, 2001). However, greater gliders typically avoid unnecessary gliding, often choosing to walk or jump between the tree canopy where possible (Norton, 1988; Kavanagh & Wheeler, 2004). This avoidance of gliding may be related to energy conservation or predator avoidance. Gliding results in considerable height loss, with gliders usually landing low on the trunk of their target tree. Climbing back up to the canopy requires substantial energy and can increase exposure to predators (Norton, 1988).

A comparison of emergence times among hollow-dependent marsupials, showed that larger bodied animals like southern greater gliders are among the last to emerge from their dens (Lindenmayer *et al.*, 1991c). Southern greater gliders typically emerge from their dens an average of 100 minutes after sunset and return approximately 165 minutes before sunrise (Kavanagh & Wheeler, 2004). Emergence timing varies seasonally, occurring earlier in summer when nights are shorter (~72 minutes after sunset) and later in winter (~161 minutes after sunset), with individuals spending the longest periods outside their dens in late winter and early spring (~507 minutes; Kavanagh & Wheeler, 2004). Greater gliders spend long periods (~40–60%) of their nightly emergence period stationary to conserve energy and aid digestion, with peak periods of activity occurring at the start and end of the night (Norton, 1988; Kavanagh & Wheeler, 2004; Miritis *et al.*, 2025).

Nightly movements of greater gliders are influenced by home range size and the distribution of resources following disturbance events such as fire (Norton, 1988; Miritis *et al.*, 2025). Research using GPS telemetry showed that southern greater gliders undertook longer and more direct movements in habitat that had experienced severe fire (average 513 m moved per night) compared to unburnt forest (average 462 m moved per night; Miritis *et al.*, 2025). Similarly, Norton (1988) found southern greater gliders increased their travel distances in low-quality habitats, concluding that these movements were a response to reduced food availability.

(4) Home range

Home range sizes of greater gliders vary both within and between species (Table 1), but comparisons are limited by the small number of studies and variation in methodologies employed. Most studies report small home ranges across each species (Table 1). However, larger home ranges have been observed where resources, particularly food and tree hollows, are more spatially dispersed (Norton, 1988; Pope *et al.*, 2004; Smith *et al.*, 2007; McGregor *et al.*, 2023). Resource availability appears to influence not only home range size but also population densities and mating systems of greater gliders (Henry, 1985; Norton, 1988; Smith *et al.*, 2007). High quality habitats can result in smaller and overlapping home ranges and facilitate facultative polygyny (Henry, 1985; Norton, 1988). Males often maintain larger home ranges than females (Table 1), particularly where males exhibit polygynous mating behaviour, allowing them to encompass the ranges of multiple females and increase mating opportunities (Henry, 1985; Comport *et al.*, 1996).

Notably, northern greater gliders, despite their smaller body size, tend to have larger home ranges than their southern counterparts (Table 1), likely reflecting lower resource density in tropical sclerophyll forests (McGregor *et al.*, 2023). Similarly, central greater gliders were found to have substantially larger home ranges and lower population densities in areas with low hollow availability (0.8 den trees ha^{-1}; Smith *et al.*, 2007) compared to areas with higher hollow densities (7.7 den trees ha^{-1}; (Kehl & Borsboom, 1984); Table 1).

To date, ten studies have investigated home range sizes of greater gliders, limiting our ability to generalise across species and habitats, or understand the ecological drivers of observed differences. Further research is needed to clarify how resource distribution, population density, and social organisation interact to shape greater glider space use. This knowledge is crucial for estimating population sizes and carrying capacities throughout the range of each species, and for guiding conservation and management strategies focussed on habitat retention and restoration.

Table 1. Comparison of home range area estimates (ha) for three species of greater glider. Geometric home range estimates are shown as either Minimum Convex Polygon (MCP) or Modified Minimum Area Method (MMAM). Kernel Home Range Areas are shown as either Kernel Utilisation Distribution (KUD) or Kernel Density Estimate (KDE), the latter either using a fixed or adaptive approach.

Species	**Study**	**Tracking Method**	**Mean geometric home range ± S.D**	**Mean Kernel Home Range Area ± S.D**	**Population density (ha-1)**	**Habitat type**	**Factors investigated**
Southern greater glider	Miritis *et al*., 2025	GPS collars	Females: 1.61 ± 0.78 Males: 3.63 ± 1.68 Range: 0.64–6.43 Method: 100% MCP	Females: 1.58 ± 0.99 Males: 3.29 ± 1.32 Range: 0.71 – 5.47 Method: 95% KDE		Wet sclerophyll forest	Burnt versus unburnt, sex
	McGregor *et al*., 2023	GPS and radio-tracking collars	Females: 0.91 ± 0.44 Males: 0.85 ± 0.21 Range: 0.4–1.6 Method: 95% MCP	Females: 1.99 ± 0.39 Males: 2.10 ± 0.71 Range: 1.5 - 2.6 Method: 95% KUD	0.61–2.49	Open sclerophyll forest and woodland	Resource availability, sex
	Kavanagh & Wheeler, 2004	Collared radio-tracking	Females: 0.8 ± 0.21 Males: 2.0 ± 0.69 Range: 0.47–2.91 Method: 100% MCP	Females: 0.8 ± 0.25 Males: 1.9 ± 0.83 Range: 0.46–3.11 Method: 95% adaptive KDE		Wet sclerophyll forest	Before-After Logging, sex
	Pope *et al*., 2004	Collared radio-tracking		Females: 2.0 ± 0.6 Males: 2.6 ± 0.8 Range: 1.26 – 4.10 Method: 95% fixed KDE	0.24–1.66	Remnant patches of eucalyptus forest in a matrix of radiata pine	Patch size, population density, sex
	Norton, 1988	Tagged or unique individuals re-	Population 1 Females: 1.5 ± 0.2 Males: 1.8 ± 0.1		Population 1: 0.88	Dry sclerophyll forest	Forest type, population density, sex

		sighted repeatedly via spotlighting	Range: 0.8–1.9 Population 2 Females: 1.5 ± 0.1 Males: 1.4 ± 0.1 Range: 0.9–1.6 Method: MMAM		Population 2: 0.89–1.67		
	Henry, 1985	Tagged or unique individuals re-sighted repeatedly via spotlighting	Females: 1.25 ± 0.46 M. Males: 1.36 ± 0.19 P. Males: 2.08 ± 0.66 Range: 0.7–2.94 Method: MMAM		0.56	Wet sclerophyll forest	Breeding system, sex
Central greater glider	Smith *et al*., 2007	Collared radio-tracking	Females: 3.3 ± 2.1 Males: 11.5 ± 7.2 Range: 1.4–19.3 Method: 100% MCP	Females: 4.1 ± 2.3 Males: 10.8 ± 6.7 Range: 1.8–17.8 Method: 95% Fixed KDE	0.1–0.36	Dry sclerophyll forest	Hollow-availability, sex
	Kehl & Borsboom, 1984	Collared radio-tracking	Females: 2.5 ± 1.2 Males: 2.6 ± 1.7 Method: 100% MCP		1.2–2.3	Coastal lowland forest	Sex
Northern greater glider	McGregor *et al*., 2023	GPS and radio-tracking collars	Females: 3.13 ± 1.11 Males: 3.16 ± 1.14 Range: 2.0–4.7 Method: 95% MCP	Females: 5.00 ± 1.41 Males: 4.66 ± 0.77 Range: 3.7 – 6.5 Method: 95% KUD	0.96–1.92	Dry sclerophyll forest	Resource availability, sex
	Starr *et al*. 2021	Collared radio-tracking	NA	Females: 4.14 ± 2.67 Males: 6.74 ± 3.18 Range: 1.03 -11.45 Method: 95% fixed KDE	0.24 (in wet forest) 0.38 (in dry forest)	Wet and dry sclerophyll forest	Sex

	Comport *et al*., 1996	Collared radio-tracking	Females: 1.02 ± 0.29 Males: 2.32 ± 1.31 Range: 0.8 - 4.1 Method: 95% MCP	Females: 1.30 ± 0.33 Males: 2.48 ± 1.10 Range: 0.9 - 4.2 Method: 95% adaptive KDE	3.3–3.8	Wet-dry tropics open sclerophyll forest	Sex

IX. DIET

All three greater glider species are considered strict herbivores that specialise on eating eucalypt leaves from the related tree genera *Eucalyptus*, *Corymbia* and *Angophora*, although they will also occasionally eat eucalypt buds and flowers or leaves from non-eucalypts (Marples, 1973; Kehl & Borsboom, 1984; Henry, 1985; Kavanagh, 1987; Norton, 1988; Foley *et al.*, 1990; Comport *et al.*, 1996; Cunningham *et al.*, 2004; Kavanagh & Wheeler, 2004). Greater gliders are nocturnal and spend around 2.3 hours feeding each night, approximately one quarter of their active time (Kehl & Borsboom, 1984; Norton, 1988).

Across their distribution, greater gliders are known to feed on a variety of eucalypt species (see Data S2). A synthesis of available studies identified greater glider associations with 66 tree species, of which 51 have been observed to be fed on and 21 are considered highly preferred, although preferences for particular tree species appear to vary regionally (Data S2). Feeding preferences remain poorly understood in many areas. Characterising feeding preferences in the wild requires extensive periods of night-time observation. In some cases, tree use by wild individuals is used as a surrogate for feeding observations (e.g. Kavanagh, 1987), but trees that are not suitable for feeding may be used for other purposes, such as denning or social interactions (Comport *et al.*, 1996; Eyre, 2006), making it difficult to discern which are critical browse species. More research is needed to address knowledge gaps surrounding diet to ensure that appropriate habitat can be identified and conserved and that revegetation activities target eucalypt species that provide high quality food for greater gliders in restored habitat.

The availability of eucalypt species and variations in nutritional quality within and between tree species are thought to be important drivers of the patchy distribution of greater gliders in eucalypt forests (Braithwaite, Dudzihski & Turner, 1983; Braithwaite, Turner & Kelly, 1984;

Tyndale-Biscoe, 2005; Youngentob *et al.*, 2011). Animals need to obtain sufficient nutrients from their food to survive, and, to sustain populations, there must also be enough nutrients to support the growth and development of young (Tyndale-Biscoe, 2005). Although eucalypt leaves are widespread and abundant, they are low in protein and energy, high in fibre, and contain high concentrations of deterrent, toxic, or nutrient-binding plant secondary metabolites (PSMs) (Kavanagh & Lambert, 1990; Comport *et al.*, 1996). This makes them a relatively poor-quality food source.

To meet their nutritional requirements, greater gliders actively select eucalypt species, individual trees, or leaf types that are higher in nutritional quality or lower in deterrent PSMs (Kavanagh & Lambert, 1990; Youngentob *et al.*, 2011; Jensen *et al.*, 2014; Jensen, Wallis & Foley, 2015). Each night, they feed in multiple trees, often of different eucalypt species (Kehl & Borsboom, 1984; Henry, 1985; Norton, 1988; Foley *et al.*, 1990; Kavanagh & Wheeler, 2004). Many studies have also noted that all greater glider species preferentially eat young foliage from some (but not all) eucalypt species when it is available, likely increasing their intake of digestible nutrients (Kavanagh, 1987; Norton, 1988; Kavanagh & Lambert, 1990; Comport *et al.*, 1996). This can lead to seasonal differences in diet composition depending on which species are producing young leaves (Henry, 1985; Kavanagh, 1987; Norton, 1988). Within eucalypt species of the subgenus *Symphyomyrtus*, greater gliders also prefer individual trees with lower concentrations of a PSM known as sideroxylonal (Youngentob *et al.*, 2011; Jensen *et al.*, 2014, 2015). Because of their apparent preference for young leaves, some studies have suggested that high quality habitat for greater gliders should contain a diversity of tree species to facilitate access to young leaves for a large portion of the year (Moore *et al.*, 2004). Additionally, in times of nutritional stress, greater gliders may favour *Symphyomyrtus* species which offer more digestible forms of nitrogen (Youngentob *et al.*, 2011; Jensen *et al.*, 2014).

Foliar nutritional quality and PSM concentrations can vary between trees and sites (Norton, 1988; Youngentob *et al.*, 2015), but these variables are not influenced by soil composition or fertility in a straightforward manner (McIlwee, 2001). Because nutrition underpins many physiological processes, the nutritional quality of available eucalypts can influence the distribution and abundance of southern greater gliders (Braithwaite *et al.*, 1983, 1984; Norton, 1988; Youngentob *et al.*, 2015). Work on central and northern greater glider populations suggest that these types of relationships cannot be determined using simple measures such as total nitrogen (N; Comport *et al.*, 1996). It is likely that there is a nutrient threshold below which populations of greater gliders cannot be sustained, but densities are highly variable above this threshold in response to other environmental and social factors (Braithwaite *et al.*, 1983, 1984; Moore *et al.*, 2004).

The eucalypt species preferences of greater gliders differ from other eucalypt folivores, likely reducing competition with co-occurring species such as eastern ring-tailed possums (Henry, 1985; Moore *et al.*, 2004; Jensen *et al.*, 2014). This may be driven partly by different nutrient requirements and partly by differences in tolerance for particular PSMs. For example, southern greater gliders from Tumut, NSW, tolerated higher concentrations of formylated phloroglucinol compounds (FPCs – a class of deterrent PSMs) in leaves than did eastern ring-tailed possums (Jensen *et al.*, 2014), while ring-tailed possums are highly tolerant of tannins and have low N requirements compared to greater gliders (Foley & Hume, 1987; Marsh *et al.*, 2003). Similarly, greater gliders appear to be more tolerant of PSMs in species from the *Eucalyptus* subgenus (common name, Monocalypt) than koalas, and therefore may utilise these species to a greater extent (Moore *et al.*, 2004; Marsh *et al.*, 2021; Gopalan, 2022).

X. HABITAT ASSOCIATIONS

(1) Tree species associations

Greater glider occurrence and density are strongly influenced by the availability of both food and denning resources (McCarthy & Lindenmayer, 1999a; Eyre, 2006; Kearney *et al.*, 2010; Lindenmayer *et al.*, 2021, 2024a), which are in turn shaped by the species composition, stand age, and structural attributes of eucalypt-dominated forests (Braithwaite *et al.*, 1983; Lindenmayer *et al.*, 1991c; Wagner *et al.*, 2021b). Although greater gliders consume leaves from a variety of eucalypt species (see above and Data S2), their presence and abundance are often associated with specific tree species that provide both suitable foliage for foraging and hollows for shelter (Braithwaite *et al.*, 1983, 1984; Youngentob *et al.*, 2011). Many of these preferred species occur predominantly in wetter, higher-elevation forests (Kavanagh & Lambert, 1990; Smith *et al.*, 2007; McLean *et al.*, 2015; Wagner *et al.*, 2021b).

Greater gliders use a variety of tree species for shelter (Kehl & Borsboom, 1984; Comport *et al.*, 1996; Kavanagh & Wheeler, 2004; Smith *et al.*, 2007; Starr *et al.*, 2021; Eyre *et al.*, 2022; Hofman, Gracanin & Mikac, 2022), but southern greater gliders may favour smooth-barked eucalypts as den trees, possibly because they form large hollows more readily than rough-barked species (Kavanagh & Wheeler, 2004). While species such as *E. fibrosa*, *E. latisinensis*, *E. moluccana*, and *E. tereticornis*, along with dead trees, have been noted as important for denning for central and northern greater gliders (Kehl & Borsboom, 1984; Comport *et al.*, 1996; Smith *et al.*, 2007; Starr *et al.*, 2021; Eyre *et al.*, 2022), evidence suggests tree size rather than tree species is the more influential determinant of den tree selection, particularly as tree hollow availability is primarily determined by tree age and size (Lindenmayer *et al.*, 1991b; Gibbons *et al.*, 2000).

The use of tree species by greater gliders for foraging is predominantly driven by foliar chemistry (see diet section). Greater gliders show localised preferences for particular eucalypt species (Data S2) within their home ranges, likely driven by complex interactions between nutrient content and the presence of PSMs (Cork & Foley, 1991; Cork & Catling, 1996; Youngentob *et al.*, 2011; Jensen *et al.*, 2015), as well as physical characteristics of the trees (Kavanagh & Wheeler, 2004; Hofman *et al.*, 2022).

The detoxification limitation hypothesis (Marsh *et al.*, 2006) provides a potential mechanism for some observed feeding patterns and tree species associations. Greater gliders may forage preferentially on species from one eucalypt subgenus until detoxification constraints necessitate a switch to the other subgenus (Marsh *et al.*, 2006; Youngentob *et al.*, 2011; Jensen *et al.*, 2015). Thus, stands containing eucalypts from both major subgenera, should allow less restricted feeding by greater gliders and may enhance as a critical indicator of habitat quality for such folivorous marsupials (Au *et al.*, 2019; Wagner *et al.*, 2021a). However, more research is needed to determine the effects of stand composition on foraging quality for greater glider populations.

Tree species which support populations of greater gliders in the southern extent of their distribution, include *Eucalyptus regnans*, *E. radiata, E. viminalis, E. cypellocarpa, E.fastigata, E. obliqua* and *E. pilularis* (Lindenmayer *et al.*, 1999b; Youngentob *et al.*, 2011; Vinson *et al.*, 2020; Wagner *et al.*, 2021b); Data S2). Further north (northern NSW and throughout Queensland), commonly occupied forests consist of *Corymbia citriodora, C. intermedia, E. acmenoides, E. latisinensis* and *E. tereticornis* (Eyre, 2006; Eyre *et al.*, 2022; Data S2). Within Queensland, additional species including *E. fibrosa*, *E. moluccana*, *E. portuensis,* and *C. dallachiana* have also been identified as important and preferred species for foraging (Kehl & Borsboom, 1984; Wormington *et al.*, 2002; Eyre, 2006; Smith *et al.*, 2007; McGregor *et al.*, 2023; Data S2).

Stand composition, particularly the mix and structural characteristics of dominant eucalypt species, represents a key determinant of habitat suitability for greater gliders (Braithwaite *et al.*, 1983, 1984; McLean *et al.*, 2015; Wagner *et al.*, 2021a; Lindenmayer *et al.*, 2024a). Forest stands that support both high-quality foraging and denning resources are likely to be especially favourable (McCarthy & Lindenmayer, 1999a; Eyre, 2006; Smith *et al.*, 2007). However, further research is required to quantify how specific combinations of tree species, tree sizes, and stand ages influence foraging efficiency and habitat quality for greater gliders at multiple scales.

(2) Habitat associations other than tree species

Greater gliders are hollow-dependent and hence their distribution and abundance is associated with older forest stands that are more likely to contain hollow-bearing trees with suitability large hollows essential for denning (Kehl & Borsboom, 1984; Lindenmayer *et al.*, 1991c; Eyre, 2006; McLean *et al.*, 2018; Lindenmayer *et al.*, 2024a). For example, southern greater gliders at Seven Mile Beach National Park in NSW preferred trees with a mean diameter at breast height (DBH) of 114 cm for denning, most commonly selecting branch-end hollows, and hollows with a mean depth of 2.5 m, a mean minimum entrance of 18 cm, and cavity walls a mean minimum thickness of ~8 cm, features likely important for temperature buffering (Hofman *et al.*, 2022). The preference for large trees may also extend to foraging, as greater gliders have been found to preferentially select trees >50-70 cm DBH while avoiding trees ≤ 30cm DBH (Smith *et al.*, 2007; McGregor *et al.*, 2023), although data on this remains limited.

Although trees provide both food and shelter for greater gliders, several other environmental factors also influence the ability of landscapes to support populations of these species. Climatic conditions such as temperature, rainfall and humidity play a substantial role in determining habitat suitability for greater gliders, with multiple studies reporting a positive association between the presence of greater gliders and wetter, cooler forest environments (e.g., (Goldingay & Daly, 1997; Smith & Smith, 2020; Wagner *et al.*, 2020). In support of this, the Normalised Difference Vegetation Index (NDVI), a remotely sensed measure of vegetation productivity, is strongly correlated with temperature and rainfall, and has been found to have a positive association with greater glider occurrence and abundance in some forest types (Youngentob *et al.*, 2015).

The persistence of southern greater glider populations at higher elevations, and their decline or disappearance in similar forest types at lower elevations, has also been attributed to the cooler and wetter conditions characteristic of these environments (Smith & Smith, 2020; Lindenmayer *et al.*, 2022). This has led to the suggestion that future climate refugia for greater gliders, and in particular the southern species, are likely to be in areas of higher elevation with cooler microclimates (Wagner *et al.*, 2020). However, additional research is urgently needed to better understand the bounds of this assumption, as other studies have found that some higher elevation areas also lack critical foliar nutrients, like sodium, which could limit upward range expansions for some leaf eating animals (Au *et al.*, 2017). In the far north, it appears that water balance limits greater glider distribution (Kearney *et al.*, 2010). More research is needed to understand how climate and climate change affects habitat suitability for the central and northern greater glider species and how particular genetic variations found in some populations of the southern species may help them persist in warmer, lowland coastal conditions (Knipler *et al.*, 2023).

The importance of temperature and moisture in determining greater glider habitat suitability is likely driven by their relatively low thermal tolerance and reliance on leaf moisture and condensation to obtain water for evaporative cooling (Rübsamen *et al.*, 1984; Foley *et al.*, 1990). Most of the research in this area has focused on the southern species; however, Eyre (2006) also reported an association between the central species and taller, more productive forest types that are typically associated with higher rainfall and cooler temperatures. Hotter, drier temperatures can also increase fire occurrence and severity, which negatively affect greater glider populations and habitat quality, although the magnitude and duration of impacts are influenced by the forest type and the intensity and frequency of fire (Berry *et al.*, 2015; McLean *et al.*, 2018; May-Stubbles, Gracanin & Mikac, 2022).

While greater gliders are reliant on mature eucalypt forest or woodlands and absent from heathland and shrub dominated landscapes, most studies have not found a relationship between understorey vegetation density or type, and greater glider occurrence (e.g., (Eyre, 2006; Youngentob, Wood & Lindenmayer, 2013). However, a dense understorey may obscure ground-based observations and lower survey counts, making it unclear how native, or invasive understorey species affect greater glider habitat quality and abundance when the availability of suitable overstorey trees remains unchanged. Research suggests that trees in exposed landscape positions are more vulnerable to loss from windthrow or decay, which could contribute to lower glider densities in these areas due to limited hollow availability for denning (Lindenmayer, Cunningham & Donnelly, 1997). For the southern species in particular, there is some evidence that they may be more abundant on slopes with north and westerly aspects than south and easterly aspects (Lindenmayer *et al.*, 2013). Notably, other studies have found no association between aspect or slope and the presence or abundance of greater gliders (Lindenmayer, Cunningham & McCarthy, 1999a).

A few studies have reported relationships between the occurrence of greater gliders and soil types associated with higher "productivity" or particular soil nutrients for both the southern species (Braithwaite *et al.*, 1984; Wagner *et al.*, 2020) and the northern species (Starr *et al.*, 2021). It is often thought that soils with higher nutrient levels may result in foliage that also has higher nutritional value for Eucalyptus leaf eating animals; however, the evidence for this is equivocal (Kavanagh, 1987; McIlwee, 2001). While some eucalypt species grown under controlled glasshouse conditions have shown increased palatability of their foliage for some species, such as common brushtail possums, in response to higher soil fertility (e.g., McArthur *et al.*, 2003), other studies have reported that eucalypts growing in more fertile soils produce leaves that are less palatable to various arboreal marsupials due to higher concentrations of herbivore-deterrent PSMs (e.g., Gleadow & Woodrow, 2002; Moore *et al.*, 2004). While increased soil fertility has been linked with rates of tree growth and hollow formation (Forrester *et al.*, 2007; Wagner, 2021; Wagner, Baker & Nitschke, 2024), several studies have also found no relationships between key indicators of soil fertility (e.g., soil nitrogen) and leaf nitrogen, as a proxy for protein (e.g., (de la Fuente *et al.*, 2024), which is thought to be a key limiting nutrient for greater gliders (Foley & Hume, 1987). Phenotypic variation within and between tree species, which can influence the production of foliar chemicals, coupled with local adaptation, creates a more complex relationship between soil fertility and eucalypt foliar chemistry than what might be observed in agricultural crops or wild species adapted to highly fertile soils (Youngentob *et al.*, 2011; Youngentob, Marsh & Skewes, 2021; Marsh *et al.*, 2018). More research is needed to understand potential relationships between soil chemistry and habitat quality for greater gliders before soil types or geology are used as an indicator of habitat suitability for these widely distributed species.

XI. ABUNDANCE

Numerous studies have attempted to quantify greater glider abundance across a range of habitat types and geographic regions (Fig. 4; Table 2). However, most of these have focussed on the southern greater glider, with few abundance estimates for the central and northern species (Fig. 4; Table 2). Most reported estimates are indices or measures of relative abundance, such as individuals per spotlight hour or kilometre, rather than standardised and ecologically meaningful metrics like density (individuals ha^{-1}; Table 2). Even when densities are reported, cross-study comparisons remain challenging due to methodological inconsistencies. These can include the use of raw counts, strip transects, and circular plots that do not account for detection probability, in contrast to more robust approaches such as single- or double-observer line transect distance sampling, which explicitly account for detectability and yield more reliable estimates (Buckland *et al.*, 2001; Emerson *et al.*, 2019; Cripps *et al.*, 2021).

Densities for southern greater gliders are highly variable across studies, ranging from as low as 0.01 individuals ha^{-1} (Braithwaite, 1983; Davey, 1989) to as high as 2.77 individuals ha^{-1} ((Downes, Handasyde & Elgar, 1997; Table 2). Most studies using robust methods that account for detection probability report mean densities for southern greater gliders between 0.3 and 2.5 individuals ha^{-1} (e.g., McGregor *et al.*, 2023; Cally *et al.*, 2025; Table 2). Habitat disturbance events such as severe fire or storms resulted in southern greater glider densities below 0.3 individuals ha^{-1} (e.g., May-Stubbles *et al.*, 2022; Cally *et al.*, 2025; Table 2).

Density estimates for central greater gliders are generally lower and less variable compared to those reported for the southern species, with mean values ranging from 0.10 to 2.3 individuals ha^{-1} (Kehl & Borsboom, 1984; Smith *et al.*, 2007; Table 2). Higher density estimates for central greater gliders (>1.5 individuals ha^{-1}) have been recorded in coastal woodlands (Kehl & Borsboom, 1984; Table 2). However, none of the studies estimating central greater glider densities have accounted for detection probability, limiting the reliability and comparability of these estimates (Table 2).

Densities for northern greater gliders vary substantially, with estimates ranging from 0 to 3.8 individuals ha^{-1} (McIlwee, 2001; Ward cited in Comport *et al.*, 1996; Table 2). The highest densities of northern greater gliders are from unpublished data (Ward cited in Comport *et al.*, 1996), although the methods for these estimates are unclear (Table 2).

Table 2. Comparative density, method and habitat data for three species of greater glider (table adapted and updated from Emerson *et al*. 2019).

Species	**Study**	**Survey method**	**Density (individuals ha^{-1})**	**Accounts for detection probability**	**Habitat**
Southern greater glider	Cally *et al*. (2025)	Spotlight – line transect mark–recapture distance sampling	Pre-storm: 0.37 (mean) Post-storm: 0.28 (mean) Fire past 40 years: 0.027 (mean), 0.009–0.061 (90% CI) Unburnt: 0.352 (mean), 0.241–0.507 (90% CI)	Yes	Open eucalypt forest, central Victoria
	Mulley, Gracanin & Mikac, 2024	Spotlight – line transect mark–recapture distance sampling	0.46 (mean), 0.21-0.84 (95% CI)	Yes	Dry sclerophyll forest with sections of littoral rainforest, south-east New South Wales
	McGregor *et al.* (2023)	Spotlight – line transect distance sampling (road-driven transects)	Eastern site: 0.61 (mean), 0.51–0.73 (95% CI) Western site: 2.49 (mean), 1.89–3.28 (95% CI)	Yes	Tall-open eucalypt forest, central and eastern Victoria

	May-Stubbles *et al*. (2022)	Spotlight – line transect multi-covariate distance sampling (off track)	0.456 (mean), 0.256–0.654 (95% CI) Low fire severity: 0.779 (mean), 0.358–1.692 (95% CI) Moderate fire severity: 0.472 (mean), 0.262–0.848 (95% CI) High fire severity: 0.077 (mean), 0.014–0.414 (95% CI)	Yes	Wet and dry eucalypt forest, south-east New South Wales
	Cripps *et al*. (2021)	Spotlight – line transect mark–recapture distance sampling	0.96 (mean), 0.60–1.50 (95% CI)	Yes	Open eucalypt forest, north-east Victoria
	Vinson, Johnson & Mikac, 2021	Spotlight – strip transect (total width 50 m)	0.41 (mean)	No	Open eucalypt forest, south-east New South Wales
	Emerson *et al.* (2019)	Spotlight – line transect distance sampling (off track)	1.36 (mean), 1.07–1.72 (95% CI)	Yes	Open eucalypt forest, north-east New South Wales
	Smith and Smith (2018)	Spotlight – strip transect (total width 120 m)	>500m elevation: 0.349 (mean) <500m elevation: 0.053 (mean)	No	Tall eucalypt forest, Blue Mountains, eastern New South Wales

	Pope *et al*. (2004)	Animal capture	0.24–1.66 (means)	Assumes 100% detection	Dry to wet, open eucalypt forest, south-east New South Wales
	Downes *et al*. (1997)	Spotlight – transects (on and off track)	1.90–2.77 (means)	No	Open, wet, eucalypt forest, north-east Victoria
	Davey (1989)	Spotlight – circular plot (55-m radius)	0.01–2.00 (means)	No	Wet and dry eucalypt forest with temperate rainforest patches, south-east New South Wales
	Norton (1988)	Spotlight – transects (information lacking)	0.88–1.67 (means)	No	Open eucalypt forest, south-east New South Wales
	Shields (unpublished) cited in Norton (1988)	Unknown	0.08–1.36	Unknown	Riparian eucalypt forest corridors within pine plantation, south-east New South Wales
	Henry (1984)	Tagging and spotlight (information lacking)	0.56 (mean)	Assumes 100% detection	Dry and wet open eucalypt forest, south-east Victoria

	Kavanagh (1984)	Spotlight – line transect distance sampling (off track) and strip transect (total width 20 m)	Distance sampling: 0.3–1.2 (means) Strip transect: 0.5–1.3 (means)	Yes (distance sampling) No (strip transect)	Wet eucalypt forest, south-east New South Wales
	Braithwaite (1983)	Sightings (dead or alive) during clear felling operations	0.01–0.60 (means)	Assumes 100% detection	Open dry and wet eucalypt forest, south-east New South Wales
	Griffith (1973)	Spotlight and shooting – road strip transect (total width 50 m)	0.24 (mean)	Assumes 100% detection	Dry and wet eucalypt forest, north-east New South Wales
	Tyndale-Biscoe and Smith (1969)	Sightings (dead or alive) during clear felling operations and shootings	0.83 (mean)	Assumes 100% detection	Wet eucalypt forest, south-east New South Wales
	Smith (unpublished)	Spotlight (information lacking)	0.31–0.98 (mean)	Unknown	Open eucalypt forest, north-east New South Wales
Central greater glider	Ferguson, Laidlaw & Eyre, 2018	Spotlight – strip transect (total width 50 m)	0.3 (mean)	No	Dry to wet, eucalypt forest, south-east Queensland
	Taylor & Goldingay 2009	Spotlight – strip transect (total width 80 m)	0.36 mean	Assumes 100% detection	Dry sclerophyll open forest and woodland, south-east Queensland

	Smith *et al*. (2007)	Spotlight – transects (off track)	0.10–0.36 (means)	Information lacking	Dry sclerophyll forest, Southern Queensland
	Eyre (2006)	Spotlight – strip transect (total width 100 m)	0.14–0.53 (mean) 0.33–0.60 (range)	No	Tall moist and dry mixed eucalypt forest, south-east Queensland
	Kehl and Borsboom (1984)	Tagging and spotlight (information lacking)	1.6–2.3 (range)	Assumes 100% detection	Coastal woodland, south-east Queensland
Northern greater glider	McGregor *et al*. (2023)	Spotlight – line transect distance sampling (road-driven transects)	Eastern site: 0.96 (mean), 0.77–1.19 (95% CI) Western site: 1.92 (mean), 1.52–2.43 (95% CI)	Yes	Open eucalypt forest and woodland, north Queensland
	Starr *et al*. (2021)	Spotlight – strip transect (total width 50 m)	Dry sclerophyll: 0.38 (mean) Wet sclerophyll: 0.24 (mean)	No	Wet and dry sclerophyll forest, north Queensland
	McIlwee 2001	Spotlight – line transect distance sampling	0.00–1.85 (range)	Yes	Tropical eucalypt forest, north Queensland

	Ward (unpublished) cited in Comport *et al*. (1996)	Unknown	3.3–3.8	Unknown	Tropical eucalypt forest, north Queensland

XII. THREATS

Greater glider populations are subject to a range of direct and indirect threats (Fig. 5). Direct threats include climate change, habitat destruction and modification, logging, fire, predation, competition, disease, genetic isolation, and artificial materials and structures such as ropes and fencing (Kavanagh, 1988; van der Ree, 1999; McCarthy & Lindenmayer, 1999a; Youngentob *et al.*, 2012; Wagner *et al.*, 2020; Lindenmayer *et al.*, 2022; Green *et al.*, 2024; Mulley *et al.*, 2024). Concerningly, some of these direct threats may be compounded by indirect drivers such as ongoing habitat degradation, increasing climatic extremes (Smith & Smith, 2020; Mulley *et al.*, 2024), and the predatory habits of invasive predators that may indirectly lead to increased predation pressure on greater gliders from native predators (Tyndale-Biscoe & Smith, 1969; Bilney, Cooke & White, 2006) (Fig. 5).

Figure 5. Summary of direct (inner ring) and indirect (outer ring) threats to greater glider populations.

(1) Climate change

Climatic conditions are major determinants of greater glider habitat suitability and distribution at the landscape scale. Southern greater gliders becoming hyperthermic at ambient temperatures above 20˚C (Rübsamen *et al.*, 1984). This limited thermoregulatory capacity, coupled with poor water-use efficiency, due to low foliar moisture, restricted water access, and evaporative cooling, renders greater gliders particularly vulnerable to heat stress if hot conditions persist over extended periods (Rübsamen *et al.*, 1984). Consequently, their occurrence in cooler, high-elevation forests likely reflects their thermal constraints (Wagner *et al.*, 2020).

The range contraction of southern greater gliders over the last 40 years has been attributed to increasing temperatures and extended periods of severe drought (Wagner *et al.*, 2020). Studies across the southern distribution of greater gliders support climate-driven declines (Smith & Smith, 2020; Lindenmayer *et al.*, 2024a), including local extirpations that appear unrelated to habitat disturbance (Smith & Smith, 2020). Empirical observations link southern greater glider density in the Blue Mountains of NSW to climatic factors such as high mean annual temperatures, low precipitation, and increased fire frequency (Smith & Smith, 2020), while in Victoria, habitat suitability and species occurrence correlates with aridity and the frequency of night-time temperatures exceeding 20˚C (Wagner *et al.*, 2020). Furthermore, species distribution models predict a range contraction of 76.3 to 98.4% and possible extinction of the northern species under a 3˚C increase in warming scenario (Kearney *et al.*, 2010).

Given the geographic range that the three greater glider species occupy, there are likely species-specific and local adaptations to elevated ambient temperatures (Kearney *et al.*, 2010; Knipler *et al.*, 2023), however climatic and physiological thresholds for the central and northern species remain unknown. Nonetheless, climatic warming and an increase in extreme heatwaves pose serious threats to arboreal mammals across northern Australia (Handayani *et* *al.*, 2018; de la Fuente & Williams, 2023). Projected increases in temperature and aridity across the distribution of all greater glider species are also expected to elevate fire frequency and severity, plus the frequency of severe storm events, further reducing habitat suitability by reducing foraging and denning resources (Green *et al.*, 2024; Ridley *et al.*, 2024; Wagner *et al.*, 2024; Cally *et al.*, 2025).

(2) Fire

Wildfires can dramatically alter habitat structure and composition for greater gliders, with both direct and indirect consequences. Extensive high-severity fires have been widely associated with southern greater glider population declines due to direct mortality and reduced resource availability (e.g. Lindenmayer *et al.*, 2013; Chia *et al.*, 2015; McLean *et al.*, 2018; Campbell-Jones *et al.*, 2022; May-Stubbles *et al.*, 2022; Smith & Smith, 2022, 2025; Green *et al.*, 2024). Although we found no empirical studies reporting the impacts of severe fire on northern or central greater gliders, similar responses to southern greater gliders are likely given their ecological similarities (Department of Climate Change, Energy, the Environment and Water, 2022c).

Southern greater gliders are less likely to occupy sites in landscapes with increasing fire extent (Lindenmayer *et al.*, 2021). Although the rates of direct mortality according to different fire severities are unknown, the absence of greater gliders from many high-severity burn sites strongly suggests that resident individuals are killed during such events (Lindenmayer *et al.*, 2013; Chia *et al.*, 2015; McLean *et al.*, 2018; Ridley *et al.*, 2024; Smith & Smith, 2025). As obligate folivores, even those that survive high-severity fires may face acute food shortages due to loss of live foliage (Lindenmayer *et al.*, 2013; Chia *et al.*, 2015; McLean *et al.*, 2018; Smith & Smith, 2022, 2025), while reduced canopy cover may elevate predation risk (Smith & Smith, 2020), as observed in eastern ring-tailed possums (Russell, Smith & Augee, 2003).

Wildfires can significantly reduce the abundance of hollow-bearing trees, resulting in a loss of shelter and breeding sites for greater gliders (Lindenmayer *et al.*, 2013; Gibbons *et al.*, 2024). Severe wildfires may lead to the depletion of suitable hollows when damaged trees collapse, are removed post-fire for public safety, or because they become unsuitable for occupancy (Andrew *et al.*, 2014; Berry *et al.*, 2015; McLean *et al.*, 2018; Lindenmayer *et al.*, 2021; Smith & Smith, 2022; Green *et al.*, 2024; Wagner *et al.*, 2024). Declines in hollow-bearing trees are strongly linked to reduced abundance and site occupancy of southern greater gliders (Lindenmayer *et al.*, 2013, 2024a). Recovery from high-severity burns is slow, with gliders often absent or present in low numbers for more than a decade post-fire (Braithwaite *et al.*, 1983; Lunney, 1987; Andrew *et al.*, 2014; Campbell-Jones *et al.*, 2022; Lindenmayer *et al.*, 2024a; Smith & Smith, 2025). Low- and moderate-severity fires generally have less severe impacts on greater gliders, with southern greater gliders more frequently detected in habitats where the canopy is only partially burnt or remains intact, compared to completely scorched areas (Chia *et al.*, 2015; Campbell-Jones *et al.*, 2022; May-Stubbles *et al.*, 2022; Smith & Smith, 2022, 2025; Green *et al.*, 2024). Gliders also persist in unburnt patches within fire affected areas, although at significantly lower abundance compared to outside the burn area (Lunney, 1987; Lindenmayer *et al.*, 2013; Berry *et al.*, 2015; Green *et al.*, 2024). However, small, isolated patches of refugia within the fire boundary may support populations in the short term but with reduced genetic diversity (Knipler *et al.*, 2023) and low long-term viability (Possingham *et al.*, 1994; Mulley *et al.*, 2024). Post-fire population recovery is likely facilitated by the availability of unburnt habitat and habitat burnt at lower severities where mortality has been lower and where some canopy cover has remained (Chia *et al.*, 2015; Smith & Smith, 2020, 2025; Campbell-Jones *et al.*, 2022; Lothian, Denny & Tong, 2022; May-Stubbles *et al.*, 2022). Low-severity burns may also facilitate the formation of new tree hollows, enhancing habitat suitability for recovering populations (Wagner *et al.*, 2024).

Planned burning, which aims to reduce fuel loads and limit wildfire severity, may pose additional risks to greater gliders (Smith & Smith, 2018). If burns are more intense than intended, they can cause extensive foliage scorching, loss of hollow-bearing trees (Smith & Smith, 2018), and may result in significant high mortality rates of arboreal mammals, as observed for a population of the critically endangered ngwayir (*Pseudocheirus occidentalis*) in Western Australia (Zylstra, 2023). Hollow-bearing trees may also be removed before planned burns for safety (Bluff, 2016), which may further reduce habitat resources for greater gliders.

While no studies have directly examined the impacts of planned burning on greater gliders, limited observations suggest that low-intensity, small-scale burns may be tolerated. For example, a radio-collared northern greater glider temporarily left its home range during a cool patch burn and returned a week later (Starr *et al.*, 2021). However, vulnerable individuals, such as females with pouch young, may be particularly sensitive (Starr *et al.*, 2021), and short-term displacement may disrupt population dynamics. Concerningly, some studies suggest planned burns could increase the risk of severe fire in some forest types, which would be detrimental to greater glider populations (Lindenmayer & Zylstra, 2024). The paucity of empirical data highlights the need for further research into both the direct and indirect effects of planned burning on greater glider populations and habitat (McLean *et al.*, 2018).

(3) Anthropogenic habitat disturbance and destruction

All three greater glider species depend on forested environments containing hollow-bearing trees and are threatened by human activities that degrade or destroy their habitat. Most research exploring the impact of human caused habitat disturbance has focused on southern greater gliders, while this review indicates that the impacts on the central and northern species remain underexplored (Fig. 4), although similar outcomes are likely.

Southern and central greater gliders are highly sensitive to habitat destruction and fragmentation, leading to direct mortality, increased predation (Tyndale-Biscoe & Smith, 1969), lower occurrence and abundance (Eyre, 2006; Lindenmayer *et al.*, 2022), decreased dispersal ability, and elevated extinction risk (Taylor & Goldingay, 2009). Logging was previously considered the major form of habitat destruction for southern greater gliders in Victoria. Although industrial scale native forest logging on public land in Victoria ceased in 2024, logging of some areas of private land continues. Further north in NSW and Queensland, habitat destruction is attributed to deforestation for agriculture, mining, logging, and urbanisation (Tyndale-Biscoe & Smith, 1969; Lindenmayer *et al.*, 1990b; Eyre, 2006; Ashman *et al.*, 2021).

Logging significantly reduces the availability of hollow-bearing trees essential for greater glider denning (Lindenmayer *et al.*, 2016). This was particularly critical in the montane ash forests of Victoria's Central Highlands, where typical logging intervals (40–120 years) were shorter than the time needed for new hollows to form (typically greater than >170 years; Lindenmayer *et al.*, 2017). Consequently, southern greater gliders are less common in young regrowth than in long-undisturbed forests (Lindenmayer *et al.*, 2022). Alarmingly, high conservation value forests where greater gliders are most likely to occur are also among the most frequently logged, both in NSW (Ward *et al.*, 2024), and until recently, in Victoria (Taylor & Lindenmayer, 2019).

Even on unlogged sites, increasing amounts of logging in the surrounding landscape (6.25 km^2) has been shown to have a negative effect on long-term levels of site occupancy of southern greater gliders (Lindenmayer *et al.*, 2021). Central greater gliders appear to be similarly sensitive to the proportion of cleared habitat in the surrounding landscape (3.14 km^2) with density predicted to decline to less than one glider per three hectares if more than 15% of habitat is cleared (Eyre, 2006). Logging can also alter forest composition and reduce habitat suitability for greater gliders. For example, logging operations in southern NSW have resulted in forests that are now dominated by tree species such as silver-top ash (*Eucalyptus sieberi*) which represent less preferred or suboptimal food species for southern greater gliders (Au *et al.*, 2019; Gopalan, 2022). This is a widespread problem in landscapes that have been subject to recurrent logging and fire-related disturbances for many decades (Au *et al.*, 2019; Lutze *et al.*, 2025). Additionally, logging operations following disturbance events such as fire or logging (i.e., salvage logging) removes large numbers of remaining hollow-bearing trees (Lindenmayer & Ough, 2006), with likely compounding negative impacts on cavity-dependent species such as greater gliders.

Replacement of native eucalypt forests with exotic species such as radiata pine (*Pinus radiata*) represents an additional threat. These exotic stands create unsuitable habitat for gliders, although research has shown that southern greater gliders can persist in adjacent native forest patches (Lindenmayer *et al.*, 1999b; Youngentob *et al.*, 2013). Moreover, animals appear to be able to move between patches, even though the surrounding pine matrix is unsuitable habitat for them (Taylor *et al.*, 2007).

Interactions between different types of disturbances may magnify impacts on greater glider habitat. For example, young forests regenerating after logging can increase the risk of high-severity wildfire relative to intact or long unburnt forest (Taylor, McCarthy & Lindenmayer, 2014), or support fewer hollow-bearing trees (Lindenmayer *et al.*, 2016; Ferguson *et al.*, 2018), therefore increasing the time required for forests to recover, mature and support greater glider populations.

Given the strong relationship between central and southern greater gliders and long undisturbed forest containing hollow-bearing trees (Lindenmayer *et al.*, 1990a, 2022; Ferguson *et al.*, 2018), disturbances that lead to a loss of trees with suitable cavities (such as logging and fire) will likely have major negative impacts on populations of greater gliders (Possingham *et al.*, 1994; Lindenmayer & Lacy, 1995; McCarthy & Lindenmayer, 1999a; Eyre, 2006; Lindenmayer & McCarthy, 2006; Taylor & Goldingay, 2009). Notably, whilst both logging and wildfire have detrimental impacts on greater gliders, logging can have more severe impact on key habitat resources such as hollow-bearing trees (McLean *et al.*, 2015).

(4) Predation

Research examining the role of predation in shaping greater glider populations or the importance of gliders as a prey species is limited, particularly for the central and northern species, where no predation studies have been conducted (Fig. 4). Among avian predators, the powerful owl (*Ninox strenua*) is considered an important predator capable of substantially reducing the local abundance of southern greater glider populations (Kavanagh, 1988). The greater sooty owl (*Tyto tenebricosa*) also preys on greater gliders and appears to have increased its reliance on arboreal marsupials since European colonisation (Bilney *et al.*, 2006). This shift may be linked to habitat modification and the introduction of red foxes (*Vulpes vulpes*) and cats (*Felis catus*), which primarily prey on small terrestrial mammals (Bilney *et al.*, 2006). As a result, competition between sooty owls and powerful owls for shared prey, including greater gliders, may have intensified (Bilney *et al.*, 2006; Bilney, Cooke & White, 2010, 2011). However, a study in the Blue Mountains, NSW, found no significant relationship between greater glider abundance and the presence of either owl species (Smith & Smith, 2018). Predation of southern greater gliders by wedge-tailed eagles (*Aquila audax*) has been recorded following logging operations, however greater gliders are not considered regular prey of diurnal hunting eagles outside of these disturbance events, given greater gliders are nocturnal (Tyndale-Biscoe & Smith, 1969).

Southern greater gliders are also prey for the near-threatened spotted-tailed quoll (*Dasyurus maculatus*), representing the dominant prey species in some regions (Glen & Dickman, 2006; Belcher, Nelson & Darrant, 2007). However, the potential impact of quoll predation on greater glider populations, as well as the relationship between quoll and glider abundance, remains unknown. Logging operations can displace gliders to lower strata or even to the ground, rendering them vulnerable to predation by powerful owls and introduced red foxes (Tyndale-Biscoe & Smith, 1969). However, due to their largely arboreal habits, greater gliders are not generally considered common prey for red foxes, feral cats, or wild dogs/dingoes (*Canis familiaris*/*C. Dingo*; Triggs, Brunner & Cullen, 1984; Lunney, 1987). Reptilian predators such as large pythons and lace monitors (*Varanus varius*) also pose a predation risk to greater gliders (Smith *et al.*, 2007). It is possible that predation risk from reptiles could increase following disturbance events such as fire, as was found for eastern ring-tailed possums (Russell *et al.*, 2003).

Despite the extensive distribution of greater glider species, their ecological importance as prey species, pollinators, or players in nutrient cycling within forest ecosystems remains understudied. This lack of understanding may pose a risk to forest ecosystems given the decline of greater gliders and other arboreal marsupials in Australia.

(5) Disease

There is limited information on diseases and parasites known to affect greater gliders. The only known disease found to be present in the greater glider is Chlamydia, with evidence of the disease in southern greater gliders (Lindenmayer, 2002; Bodetti *et al.*, 2003; Burnard & Polkinghorne, 2016). The greater glider harbours several types of ectoparasites, including mites (Domrow, 1974; Domrow & Lester, 1985), fleas and ticks (Lindenmayer, 2002). Endoparasites are also known to occur, including species from the class Cestoda and Nematoda phylum (Lindenmayer, 2002). Given the severity of impacts of Chlamydia and mange (as caused by sarcoptic mites) on wildlife populations throughout Australia (Bodetti *et al.*, 2003; Burnard & Polkinghorne, 2016; Fraser *et al.*, 2016; Kasimov *et al.*, 2022), further research is warranted on the identity, distribution, and epidemiology of Chlamydia and mites affecting greater glider populations. There is limited information on diseases and parasites known to affect greater gliders. Recent work in gut microbiome profiling in southern gliders have detected potential evidence of mycobacterial infection in the form of a *M. tuberculosis* complex (Clough, Schwab & Mikac, 2023); understanding the risk posed by this pathogen warrants further screening of gliders for Mycobacterium.

(6) Other threats and competition

The delicate gliding membrane of greater gliders, known as the patagium, makes them vulnerable to entanglement in fencing, especially barbed wire, when attempting to cross gaps that exceed their gliding capacity (van der Ree, 1999). There has also been a documented case of a greater glider which died after becoming entangled in a rope left in a tree, and they have been observed to snag their long nails on enclosure structures when kept in captivity, requiring intervention to free themselves (K. Youngentob, *et al.*, unpublished data). These observations underscore the need for careful design and placement of artificial structures in their habitat, including nest boxes, to minimize the risk of unintended harm to greater gliders.

Greater gliders depend on large, old trees with suitable hollows for shelter, but competition for these limited resources can be intense (Gibbons & Lindenmayer, 2002). Larger, hollow-dependent arboreal marsupials, including the common brushtail possum and mountain brushtail possum (*Trichosurus cunninghami*), have been observed displacing greater gliders from hollows (Lindenmayer *et al.*, 2011a; Youngentob *et al.*, 2012). These more generalist, hollow-dependent species can utilise mid- and understorey vegetation and often occur at higher densities in disturbed landscapes and along forest edges, where such vegetation is more abundant, placing additional pressure on greater gliders (Youngentob *et al.*, 2012). Predator control, particularly of red foxes, may exacerbate this competition by reducing predation pressure on brushtail possums, thereby indirectly contributing to declines in greater gliders (Dexter *et al.*, 2012) Additional competition can arise from other taxa that use hollows, including birds such as the sulfur-crested cockatoo (*Cacatua galerita*) and insects like the European honeybee (*Apis mellifera*), which have been observed usurping nesting hollows used by other arboreal marsupial species (Wood & Wallis, 1998; Smith & Smith, 2018).

(7) Extinction risk

Exploration of population viability and extinction risk has predominantly focussed on the southern greater glider (Fig. 4). Local extinctions have already occurred, including within protected areas such as Booderee National Park in the Jervis Bay Territory, where other arboreal marsupials like the yellow-bellied glider (*Petaurus australis*) have also disappeared, and species such as the eastern ring-tailed possum have undergone steep declines

(Lindenmayer *et al.*, 2018). Although the specific causes of these population declines remain unclear, multiple concurrent threats are likely contributing factors (Lindenmayer *et al.*, 2018). For example, a population viability analysis (PVA) of a declining southern greater glider population in Seven Mile Beach National Park, NSW, revealed a 99% probability of extinction over 50 years, primarily due to fire, followed by low effective population size and inbreeding (Mulley *et al.*, 2024).

PVA studies for southern greater gliders have also indicated elevated extinction risk with decreasing patch size and declining resource availability (McCarthy & Lindenmayer, 1999a; Lindenmayer & McCarthy, 2006). Small, isolated patches of suitable habitat have limited capacity to support long-term occupancy of southern greater gliders (Possingham *et al.*, 1994), while contiguous areas of old-growth forest and reductions in the extent of timber harvesting appear critical for maintaining viable populations (McCarthy & Lindenmayer, 1999a). Furthermore, declines in effective population sizes, genetic diversity, and habitat quality, along with increased frequency of high-intensity wildfire, are predicted to have significant negative impacts on the persistence of southern greater glider populations (Possingham *et al.*, 1994; Lindenmayer & Lacy, 1995).

PVA modelling for the central greater glider indicates that habitat fragmentation, wildfire, and barriers to movement such as roads pose significant threats to population viability (Taylor & Goldingay, 2009). Although extinction risk may be reduced with relatively low levels of dispersal between habitat patches, frequent fires remain a major threat to the survival of fragmented glider populations, reinforcing the importance of habitat connectivity for population persistence (Taylor & Goldingay, 2009).

We found no species-specific PVA studies for northern greater glider populations. This highlights a critical knowledge gap, and underscores the need for comprehensive, species-specific assessments of extinction risk for all greater glider populations to determine the most at-risk populations and to inform threat mitigation actions.

XIII. SURVEY METHODS

As a large gliding possum, the greater glider is relatively conspicuous during nocturnal surveys due to its bright reflective eyeshine (Harris & Maloney, 2010) and tendency to remain stationary for prolonged periods. Greater gliders are generally non-vocal, so they are most often detected visually using methods aimed at detecting their eye-shine, silhouettes, or body heat. We identified 10 studies that examined the effectiveness of different survey methods for greater gliders, with the majority focussed on the southern species (Fig. 4).

Three main survey methods were identified: spotlighting, stag watching, and more recently, thermal imaging. During the late 1980s and 1990s, stag watching of den trees (Smith *et al.*, 1989) and ground-based spotlighting (Davey, 1990) were considered the most effective methods for detecting greater gliders. However, both methods are subject to imperfect detection, influenced by environmental conditions such as fog, rainfall, high temperature, moon phase, time after dusk, habitat quality, and time of year (Smith *et al.*, 1989; Davey, 1990; Eyre, 2004; Wintle *et al.*, 2005).

Spotlighting remains the most widely used technique for detecting greater gliders, however indicates that spotlighting surveys may significantly underestimate the number of greater gliders seen (Lindenmayer *et al.*, 2001). As a result, most monitoring programs have used relative abundance indices rather than absolute counts, particularly in large forest patches. In response, recent literature advocates for more sophisticated spotlighting protocols that explicitly account for imperfect detection (Emerson *et al.*, 2019; Cripps *et al.*, 2021). Distance sampling techniques improve population estimates by accounting for declining detection probability with increasing distance from the transect line (Buckland *et al.*, 2001). Research has shown that using two independent observers on a transect can yield abundance and density estimates with good precision (Cripps *et al.*, 2021), although assumptions underpinning distance sampling protocols for greater gliders warrant further investigation. Decisions around which survey method to use will depend on the research question and the type of habitat surveyed.

The use of emerging technologies, such as thermal imaging cameras, for conducting greater glider surveys, have shown promise but remain understudied. Published evaluations of their effectiveness for surveys of southern greater gliders are mixed, with Vinson *et al.* (2020), finding no significant improvement over traditional spotlighting methods, particularly at ambient temperatures above 24ºC. However, (Wagner *et al.*, 2025) recently showed that thermal drone surveys achieved high detection rates for arboreal mammals, including southern greater gliders, particularly in dense vegetation or low-density populations. The use of thermal imaging technologies warrants further exploration across a variety of habitat types.

Only one study has examined the effectiveness of survey methods for each of the central and northern greater glider species (Fig. 4). Although survey methods suitable for southern greater gliders should be effective for all greater glider species, differences in vegetation density and ambient temperatures could influence detection efficacy across regions. Traditional methods such as spotlighting and stag watching remain valuable for locating individuals and den trees (Hofman *et al.*, 2022), facilitating capture (Gracanin *et al.*, 2021), and tracking long-term population trends (Lindenmayer *et al.*, 2024a). However, the validation and standardisation of both traditional and emerging survey methods are critical to ensure comparability and accuracy across the range of all three species. Establishing robust, standardised protocols will be essential for effective long-term monitoring and management.

XIV. POLICY & CONSERVATION MANAGEMENT RECOMMENDATIONS

(1) Policy recommendations

Policy reform is urgently required to address inconsistencies between state and federal environmental laws that currently permit the continued degradation and destruction of greater glider habitat. Existing regulatory frameworks are failing to prevent ongoing species declines (Lindenmayer *et al.*, 2011b; Ashman *et al.*, 2021) and do not adequately account for the cumulative impacts of forest destruction and degradation since European invasion (Ward *et al.*, 2024), indirect impacts (Khaine & and Woo, 2015), and interacting effects of logging (Lindenmayer *et al.*, 2021), fire (Campbell-Jones *et al.*, 2022), and climate change on greater gliders (Smith & Smith, 2018; Lindenmayer & Sato, 2018). For example, under current policy arrangements, logging in part of the range of greater gliders is exempt from assessment under the EPBC Act due to Regional Forest Agreements (RFAs) between state and federal governments (Samuel, 2020), thus undermining conservation efforts for these threatened species (Ashman *et al.*, 2021).

RFAs are now outdated instruments that fail to reflect contemporary ecological knowledge, do not account for compounding effects of climate change and increasingly frequent wildfires, and are inadequate for protecting threatened species (Lindenmayer, 2018; Samuel, 2020). Logging operations permitted under RFAs continue to contribute to the destruction and degradation of native forest habitat of greater gliders, resulting in ongoing population declines of the species (McLean *et al.*, 2018; Lindenmayer *et al.*, 2021; Wardell-Johnson & Robinson, 2022), which is inconsistent with the conservation objectives of the EPBC Act.. These issues are unlikely to be resolved by simply amending Regional Forest Agreements, or by amending the EPBC Act to allow greater oversight over these agreements. Rather than amending RFAs or modifying the EPBC Act to allow greater oversight, a more effective and precautionary approach would be to remove exemptions altogether. Destructive practices likely to impact greater gliders and other threatened species should be subject to consistent, robust, enforceable, and independent national environmental regulation (Environmental Defenders Office, 2020; Samuel, 2020).

Immediate formal protection of native forest habitats from further destruction and degradation is essential if Australia is to meet its global commitments (Ritchie & Nimmo, 2025) and will facilitate threatened species persistence and recovery (Legge *et al.*, 2023), and respond to the global biodiversity and climate crises. In particular, the prevention of further logging and clearing of mature native forests is critical to the persistence of greater gliders and other threatened species (Ashman *et al.*, 2021; Lindenmayer & Taylor, 2023; Ward *et al.*, 2024).

Greater glider conservation cannot be achieved in isolation from climate action. Climate change is a major and intensifying driver of habitat degradation, altered fire regimes, and physiological stress in arboreal marsupials (Wagner *et al.*, 2020; Nitschke *et al.*, 2020; Bergstrom *et al.*, 2021). Accordingly, national climate and emissions policies must be aligned with biodiversity conservation goals to mitigate direct and indirect climate-related threats. Policies aimed at reducing emissions and limiting warming will contribute substantially to the protection of climate-sensitive species such as greater gliders (Kearney *et al.*, 2010; Smith & Smith, 2022).

(2) Management recommendations

Management recommendations for greater gliders in the reviewed literature emphasise four key strategies for their conservation: 1) habitat protection and restoration, 2) appropriate fire management, 3) ongoing monitoring and research, and 4) community engagement and education (Lindenmayer *et al.*, 2013; Ashman *et al.*, 2021; Campbell-Jones *et al.*, 2022; Smith & Smith, 2022; Wardell-Johnson & Robinson, 2022; Knipler *et al.*, 2023). Central to effective conservation management and legislation is the formal recognition of the three distinct species of greater glider (*Petauroides* spp.; (McGregor *et al.*, 2020)), along with consistency in species recognition and listings across state and national jurisdictions (Smith & Smith, 2022). Effective conservation also requires the separate management of populations, given the unique genetic structures, ecological contexts, and threatening processes influencing each (Knipler *et al.*, 2023). Furthermore, the management of greater gliders and associated biodiversity must occur at a landscape scale to enhance resilience to disturbance events (Smith & Smith, 2022). The following recommendations are intended to guide land managers and policy makers to take actions that address the primary threats facing greater gliders and their habitats to support their long-term survival.

Habitat protection and restoration

Protection of areas from logging, land clearing, development, firewood collection, hazardous tree removal, fence line clearing, and other land-use changes that could further degrade greater glider habitat availability, quality, and connectivity are key priorities (Lunney, 1987; Ashman *et al.*, 2021; Vinson *et al.*, 2021; Wardell-Johnson & Robinson, 2022; Lindenmayer *et al.*, 2024a). The trees and hollows that greater gliders depend upon can take long timeframes to form (Lindenmayer *et al.*, 1991a). Consequently, in many regions, suitable habitat is limited or continuing to decline, and extinction debts (older trees dying but not being replaced) will compound this issue (Kuussaari *et al.*, 2009).

At the policy and planning level, stronger vegetation preservation laws are required, including in roadside areas that often contain remnants with limited formal protection (Ashman *et al.*, 2021; Wardell-Johnson & Robinson, 2022; Lindenmayer & Taylor, 2023).

Roadside corridors can provide important habitat for a variety of wildlife, including greater gliders (Downes *et al.*, 1997; Martin & Martin, 2004; Tingate, 2021). At broader scales, spatial conservation planning supported by species distribution modelling, which incorporates current and projected greater glider distributions under climate change (Kearney *et al.*, 2010) and the degree of protection across land tenures (Norman & Mackey, 2023), would enable targeted conservation acquisitions (Lindenmayer & Taylor, 2023). Such modelling also helps to identify large-scale climate refugia (areas that are climatically stable or becoming more suitable in the future) that need to be conserved or restored to maintain connectivity between greater glider populations and support viable meta-populations (Taylor & Goldingay, 2009).

Where natural connectivity is disrupted, engineered solutions may provide interim support and ensure population viability. Artificial structures such as gliding poles may facilitate movement across fragmented landscapes, including urban infrastructure or areas affected by disturbance events such as fire, thereby supporting gene flow (Taylor & Goldingay, 2009).

In addition to maintaining connectivity, conservation strategies have been proposed to mitigate extinction risk through interventions such as genetic reinforcement via translocation and the installation of nest boxes to supplement hollow availability (Mulley *et al.*, 2024). However, conserving and connecting forest fragments should remain the priority, as this reduces reliance on translocations and minimises the risk of outbreeding depression (Knipler *et al.*, 2023). Ultimately, suitably large areas of intact habitat are required to sustain viable populations of greater gliders. For example, theoretical long-term viable breeding populations of southern greater gliders have been estimated at between 2 375 and 5 000 individuals (Davey, 1989).

Beyond these broad-scale strategies, the protection of fine-scale habitat features, and local refuges is also critical. Habitat containing preferred feeding trees (Eyre, 2006; McGregor *et* *al.*, 2023), microrefugia such as sheltered gullies or patches that buffer against disturbance events like fire, storm damage, or heat extremes, and areas that remain within suitable climate windows at local scales are particularly important (Lunney, 1987; Kearney *et al.*, 2010; Wagner *et al.*, 2020; Smith & Smith, 2022; Cally *et al.*, 2025). Retention of large old trees that are more likely to contain hollows is especially vital for protecting greater gliders (Davey, 1989; Lindenmayer *et al.*, 1991a, 2022). Trees >80 cm DBH are of greatest importance, with over 80% of denning trees for southern greater gliders occurring in this size class, while no denning occurred in trees <40 cm DBH (Davey, 1989). Southern greater gliders were more likely to occur where there were more than 20 hollow-bearing trees (HBTs) >80 cm DBH per hectare (Lindenmayer *et al.*, 2022). For central greater gliders, retention of trees >60 cm DBH in logged areas has also been recommended, regardless of whether they currently contain hollows (Eyre, 2006). Modelling indicated that approximately three HBTs per hectare were required to maintain one central greater glider per three hectares (Eyre, 2006). To protect HBTs used by wildlife, logging operations should occur at low intensity where greater gliders are present (Lunney, 1987), and adequate densities of HBTs should be retained to support greater gliders and other hollow-dependent species (Lindenmayer *et al.*, 1991a, 2022). The importance of drainage lines and protection of all trees in these areas have also been emphasised for greater gliders (Lunney, 1987).

Appropriate fire management

Fire management is also central to greater glider conservation (Ridley *et al.*, 2024). Frequent and severe fires risk direct impacts on greater gliders, as well as indirectly affecting the species by removing hollow-bearing trees (Lunney, 1987; Lindenmayer *et al.*, 2013; Chia *et al.*, 2015; Smith & Smith, 2022). The risk of large, severe and frequent fires needs to be minimised. Identifying key areas of greater glider habitat that are at risk of fire will aid prioritising attempts at any fire suppression (where this is practical) prior to any fire occurring. Hazard reduction burning needs to consider the cumulative impacts of fires on tree health and potential loss of hollows. A planned fire that overlaps with large, old trees has the capacity to destroy key habitat, and this can compound through time given gliders require multiple den trees through which they cycle their use (Kavanagh & Wheeler, 2004). Raking around and protecting such trees prior to any prescribed fire should be prioritised. Where planned burning is employed, low-intensity burns that avoid canopy scorch are recommended to minimise potential impacts (Chia *et al.*, 2015; Ridley *et al.*, 2024).

Monitoring and research

Ongoing monitoring and research is vital to assess population health (Lindenmayer *et al.*, 2013; Knipler *et al.*, 2023), habitat conditions, and the effectiveness of management actions, enabling adaptive strategies based on up-to-date information. Research on genetic structuring, diversity, and taxonomy remains critical to ensure that conservation actions are appropriately targeted, prevent the masking of declines within distinct taxa, and allow monitoring programs to detect species- or population-specific responses to threats and management interventions. Central to this should be the establishment of a network of systematic monitoring sites to assess changes in greater glider distribution and abundance through time and across their range (Lindenmayer *et al.*, 2025).

Greater gliders can co-occur with other arboreal marsupials (Lindenmayer & Cunningham, 1997; Emerson *et al.*, 2019), which could interest in using biodiversity indicators or surrogates (Landres, Verner & Thomas, 1988; Lindenmayer *et al.*, 2024b). However, co-occurrence patterns are generally weak, inconsistent, or site-specific (Lindenmayer & Cunningham, 1997; Lindenmayer *et al.*, 2024b). Although some associations with species from other trophic groups have been observed—for example, the occurrence of southern greater gliders were positively correlated with sooty owls (*Tyto tenebricosa*) (Hogg, Wang & Stone, 2021), a known predator of greater gliders (Bilney *et al.*, 2006)— these correlations are context-specific and do not provide a reliable basis for surrogate monitoring. Targeted conservation and monitoring efforts are therefore recommended to ensure effective management outcomes (Lindenmayer *et al.*, 2024b).

Commitments to long-term funding are essential to support ongoing monitoring, active forest management, and conservation efforts. Sustained investment enables the consistent application of monitoring protocols, the maintenance of systematic sites over time, and the capacity to respond adaptively to emerging threats, ensuring that management actions are evidence-based and effective (Smith & Smith, 2022).

Community engagement and education

Engaging with local communities and raising awareness about the importance of conservation, including species' habitat requirements, can foster support for wildlife conservation efforts (Ikin *et al.*, 2015). Central to this is engagement with and decision making by First Nations peoples and rural communities where greater glider populations occur (Norman & Mackey, 2023). Large areas of greater glider habitat are outside of formal conservation protection, on private land (Wagner *et al.*, 2020; Norman & Mackey, 2023). Market-based initiatives such as conservation covenants (Ashman *et al.*, 2021) offer opportunities to greatly enhance the area of greater glider habitat that is protected and connected.

XV. CONCLUSIONS

(1) This review demonstrates the value of reassessing existing literature following recent species reclassifications. We have shown that such analyses can highlight strengths and gaps in the species-specific ecological and conservation evidence base that may have otherwise been overlooked, thereby guiding future research and informing species-specific conservation, management, and policy. Similar reviews for other taxa would be valuable as genetic studies increasingly uncover cryptic species (e.g., *Petaurus* spp.; Cremona *et al.*, 2021).

(2) Further genetic sampling across all greater glider species—particularly in northern NSW and geographic isolates such as Blackbraes National Park in northern Queensland—is essential to clarify species boundaries, evolutionary significant units, detect potential hybridisation, and guide targeted conservation. Establishing baseline genetic structure will also enable assessment of the genetic impacts of climate change, habitat fragmentation, and other disturbances, and underpin robust population viability analyses.

(3) Current ecological knowledge is disproportionately concentrated on the southern greater glider, leaving the central and northern species understudied and potentially vulnerable to poor conservation outcomes. Research across all three species is needed to understand key drivers of population dynamics, including the roles of climate change, life history traits, genetics, physiology, predation, competition, disease, habitat quality, prescribed burning, and spatial ecology. This information is essential for accurate extinction risk assessments and effective threat mitigation.

(4) The long-term persistence of all three greater glider species and the habitats they occupy requires coordinated actions encompassing habitat protection and restoration, community engagement and education, urgent legislative reform, and expanded, robust, and ongoing research and monitoring. Monitoring programs should

incorporate fine-scale habitat–density analyses, standardised protocols, and remote sensing technologies to enable rapid, landscape-scale assessment. Strengthening environmental protections and implementing large-scale restoration and climate change mitigation are critical to addressing cumulative threats across the species' distribution.

(5) Central to effective conservation of greater gliders is the formal recognition of the three distinct species and the consistent application of this taxonomy across state and national legislation. Development of species- and population-specific recovery plans will provide a legally binding framework for coordinating research and management actions, mitigating threats, and supporting the long-term survival of all greater glider species.

(6) To facilitate ongoing synthesis and support future research, we have developed an interactive online database and visualisation tool available at https://lukedanielemerson.shinyapps.io/greaterglidershinyapp/. We encourage researchers studying greater gliders to engage with this resource to prioritise research efforts and to notify us of newly published papers, datasets, or reports, so this resource remains current and guides future research across all species.

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XVII. CONFLICT OF INTEREST

A potential conflict exists for government employees and constraints on their ability to comment on current government policy. Therefore, while all authors support the scientific evidence presented in this paper, opinions provided on the interpretation of this information may not reflect the views of all co-authors and the views of their employers.

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XVIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. (separate file) Included studies and study themes for each greater glider species

Data S2. (separate file) Tree species associations and feeding preferences

Supporting Information for

Taxonomic revisions, strategic decisions: research and management priorities for the threatened greater glider complex

Luke D. Emerson *et al.*

*Corresponding author. Email: lukedanielemerson@hotmail.com

TABLE OF CONTENTS

I. STUDY DESIGN

1.1 Systematic literature review and data synthesis protocol

1.1.1 Aims and objectives

Our aim was to conduct a systematic literature review following the recommendations from the ROSES approach (Haddaway *et al.*, 2018), according to transparent criteria (Haddaway *et al.*, 2015), and a content analysis (Krippendorff, 2018) to determine the extent of species-specific research for each of the three greater glider species as described by Arbogast *et al.*

(2011), Jackson & Groves (2015), and McGregor *et al.*(2020). The core objectives of our review were to:

- (i) identify and collate relevant greater glider literature
- (ii) evaluate geographic patterns in research effort for each species
- (iii) conduct a content analysis (Krippendorff, 2018) and descriptive synthesis to determine the distribution of research effort across different research topics and to identify research deficiencies for each species (gap analysis)
- (iv) summarise and synthesise key research findings for each greater glider species
- (v) summarise explicit management and policy recommendations
- (vi) provide a list of recommendations to inform future species-specific research, policies and conservation actions.

1.1.2 Approach to bibliographic database searches

We conducted bibliographic database searches in English only using Web of Science Core Collection, Zoological Record, Scopus, ProQuest Dissertations & Theses Global, and Google Scholar. We conducted initial database searches on 29th November 2022, and conducted an additional search of all databases on the 5th September 2023 to capture any new articles that were published during the intervening time (Fig. S1.1). We conducted additional Google Scholar searches on the 12th October 2024 and 2nd April 2025 to identify any other articles published since the last search of all databases (Fig. S1.1). The final Google scholar search was a rapid screen of recently published literature and contributed to articles returned ad hoc, resulting in just 14 additional relevant articles (Fig. S1.1). All returned articles were imported into Zotero reference manager, where duplicate articles were identified and removed, and open-source articles imported.

1.1.3 Search string used for all bibliographic database searches

"greater glider" OR "schoinobates volans" OR "petauroides volans" OR "petauroides armillatus" OR "petauroides minor"

1.1.4 Search syntax

Web of Science-Core Collection, and Zoological Record:
TS=()

Scopus:
TITLE-ABS-KEY()

ProQuest Dissertations & Theses Global:
NOFT()

Limits applied to *ProQuest Dissertations & Theses Global* database searches:

- Manuscript type: Master’s theses and Doctoral dissertations
- Language: English
- Spelling variants and form variants of search terms deselected

- All dates
- Exclude duplicate documents

Google Scholar:
() OR ()

Note: Just the first 400 articles were exported from Google Scholar in the first round of searches.

1.1.5 Title and abstract screening process

Owing to limited human resources, a single reviewer (K.N.K) independently screened the title and abstracts of each article returned by the first two rounds of bibliographic database searches. The last round of searches was solely conducted by the primary investigator (L.D.E.). The chance of incorrectly omitting potentially relevant articles at this stage was negligible given we erred on the side of inclusion. For articles to be considered for the full-text review stage, they had to meet all the inclusion criteria and none of the exclusion criteria.

Inclusion criteria:

- Aspect of greater glider ecology, management, impacts or policy appear to be focus of study
- Greater glider, arboreal marsupial, folivorous marsupial, gliding marsupial, arboreal mammal mentioned but is unclear if relevant or not

Exclusion criteria:

- Not in English
- Does not refer to greater gliders or arboreal marsupials
- Simple biodiversity survey that may or may not mention greater glider

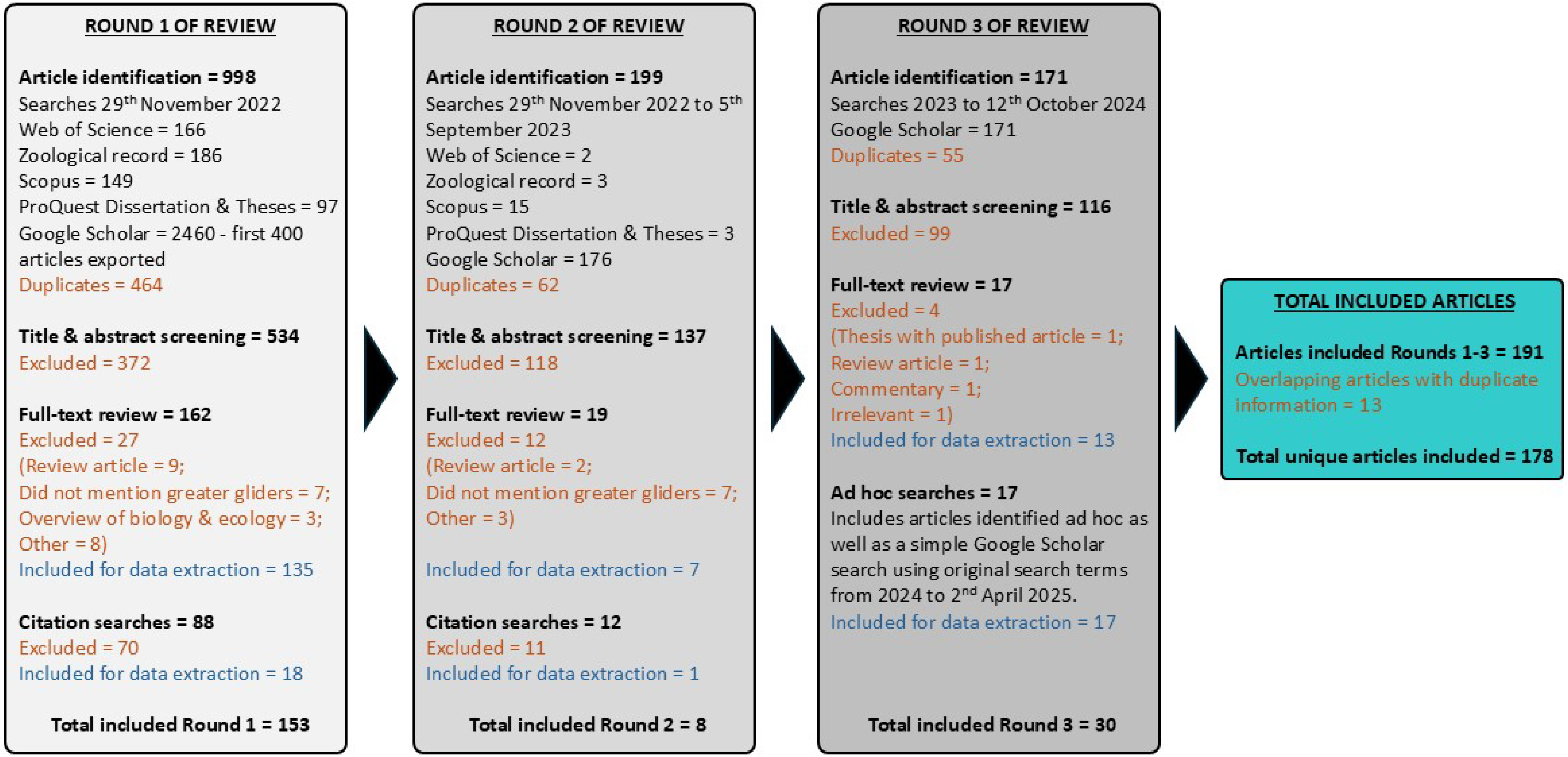

Figure S1. Summary of data sources, and the number of studies identified, screened/reviewed, excluded, and included at each stage of each round of the systematic review process.

1.1.6 Full-text review process

Two people were involved in the full-text review process. K.N.K independently performed the full-text review for the first two rounds of searches and L.D.E. resolved any uncertainties that were flagged by K.N.K., thereby the chance of incorrectly omitting a relevant article at this stage was negligible. L.D.E independently conducted the full-text review of the last round of searches. To be considered for inclusion, an article had to meet all the inclusion criteria and none of the exclusion criteria.

Inclusion criteria:

- An aspect of greater glider ecology, genetics, anatomy & physiology, impacts & threats, survey methods, habitat, conservation history or management, associated indigenous knowledge, or policy/management recommendations is the focus of the study/article

Exclusion criteria:

- Does not refer to greater gliders
- Statistical analysis or results are not specific to greater gliders
- Review article that does not reanalyse original data or contribute any new findings
- Blog, news article, website
- Simple biodiversity survey that does not mention greater gliders or if mentioned, does not attempt to calculate standardised abundance estimates or assess detections/abundance relative to potentially influencing variables

1.1.7 Systematic citation searches

The titles of articles in the reference lists of included articles or any relevant excluded articles, such as reviews, were screened for the following terms. If any one of the following were observed in the title, that article was also located and reviewed. The search terms included ‘glider’ (determine if ambiguous or relevant based on other terms e.g. greater, sugar, etc.), ‘Schoinobates’, ‘Petauroides’, ‘arboreal marsupial’, ‘folivorous marsupial’, ‘gliding marsupial’, and ‘arboreal mammal’.

1.1.8 Data extraction

We developed a data extraction tool in the form of a Microsoft Excel spreadsheet (Data S1). We extracted important article information including title, authors, year of publication, article type, and study location/s.

We conducted a content analysis (Krippendorff, 2018) by developing the following list of pre-defined research / topic areas and coding studies relative to each code. This information was used to descriptively synthesise the research effort per research topic per species.

Pre-defined research / topic areas for content analysis:

- Genetics & taxonomy
- Anatomy & physiology
- Life history

- Behaviour
- Colonisation, dispersal, recovery
- Movement
- Home range
- Abundance
- Diet
- Factors associated with occurrence
- Spatially explicit distribution
- Anthropogenic habitat destruction
- Climate change
- Fire
- Predation
- Disease
- Other threats or competition
- Extinction risk
- Survey methods
- Assessing statistical modelling approaches
- Management recommendations
- Explicit policy recommendations

1.1.9 Determining unique studies

We identified unique studies to avoid pseudo-replication when summarising research effort per species. If the same information was reported across multiple articles and no new information was presented, we kept the article reporting the most comprehensive information and excluded the other articles with overlapping information.

1.1.10 Determining research effort per topic per species

To assess research effort by greater glider species, we assigned each study to a species based on its geographic location relative to the known or inferred distribution of each species, as described by Arbogast *et al.* (2011), Jackson & Groves (2015), McGregor *et al.* (2020), and Youngentob (personal communication).

Studies conducted in Victoria or New South Wales were assigned to the southern greater glider (*Petauroides volans*). The central greater glider (*P. armillatus*) was considered to occur from the New South Wales–Queensland border northward to just south of Townsville. The northern greater glider (*P. minor*) was considered to occur from just south of Townsville and further north to the Windsor Tablelands north of Cairns.

Using the aforementioned sources, we delineated the approximate distributional extents of each species in ArcGIS Pro (Esri Inc. 2024) and spatially mapped the locations of all included studies. Based on this mapping, we assigned each study to one or more species, depending on whether its location overlapped with the inferred range of a single species or multiple species.

It is important to note that species boundaries remain uncertain. The precise northern extent of *P. volans* and the southern extent of *P. armillatus* are not clearly defined, though the New South Wales–Queensland border is considered to mark an approximate transition between these species. Similarly, the boundary between *P. armillatus* and *P. minor* is imprecise but is assumed to lie near Townsville (Arbogast *et al.*, 2011; Jackson & Groves, 2015; McGregor *et al.*, 2020; Youngentob (personal communication).

Where studies encompassed locations spanning the inferred distribution of multiple species, we considered those studies to contribute to the research effort of each relevant species. Research effort per species and per topic was synthesised and visualised using the ggplot2 R package (v3.3.6; Wickham, 2016) in R Statistical Software (v4.1.1; R Core Team, 2021).

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III. LIST OF GREATER GLIDER STUDIES MEETING INCLUSION CRITERIA AND INCLUDED IN REVIEW AND SYNTHESIS

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