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Diving into spring biodiversity: A natural heritage assessment of Australia's Great Artesian Basin discharge wetlands

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Abstract

The Great Artesian Basin (GAB) is Australia's largest groundwater resource and feeds thousands of springs in the country’s arid centre. GAB springs are globally important “time capsules” that support relictual species not found elsewhere on Earth, yet they are considerably threatened by ongoing water abstraction for pastoral, agricultural, and industrial practices. Biomonitoring and robust management plans are needed to prevent further extirpations of GAB-dependent taxa, but there remains a paucity of biodiversity and ecological knowledge in the literature. We conducted a comprehensive review of GAB spring biota for South Australia, the state containing the majority of springs. Almost 500 taxa are recorded from GAB springs and surrounding wetlands. Invertebrates represent the largest proportion of GAB endemics and biota overall, yet they are highly threatened and have not received adequate conservation attention. Community composition differs considerably among spring clusters, highlighting their intrinsic value as refugia for both endemics and cosmopolitan taxa. Further, several potential biodiversity hotspots have been overlooked in the literature and the true extent of GAB spring biodiversity is likely far greater than currently known. Our findings underscore the importance of freshwater sources in arid regions and the need for fundamental research in the face of ongoing human impacts.

Key words: Great Artesian Basin, groundwater-dependent ecosystems, aquifers, springs, biodiversity, biogeography

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1 Introduction

The Great Artesian Basin (GAB) is Australia's largest groundwater resource, spanning over one fifth of the continent's area or almost 2 million km^2 (Habermehl, 2020). As the Basin is a confined aquifer mostly sealed off from the Earth's surface by impermeable rock, water is only accessible via fissures or artificially drilled boreholes. At the outer margins of the GAB where the confining layer is thinner, water is often forced to the surface to form springs and associated wetlands. Thousands of such springs are found throughout Central Australia, with >5,000 individual spring vents (discrete discharge points of water) in South Australia (hereafter SA) (Arabana Aboriginal Corporation, 2021; Government of South Australia, 2023), >2,000 in Queensland (Queensland Department of Regional Development, Manufacturing and Water, 2023), and >400 in New South Wales (New South Wales Department of Planning, Industry and Environment, 2021). Springs fed by the GAB therefore represent a widespread and permanent potable water source that has supported humans, flora, and fauna in Australia's arid and semi-arid zones for thousands of years (Priestley et al., 2018). From an ecological and evolutionary standpoint, GAB-fed springs also support wetlands that represent "museums of biodiversity", supporting plant and animal species not found elsewhere on Earth (Murphy et al., 2015). As relicts of the continent's mesic past, species endemic to GAB springs can have exceptionally small distributions and it is not uncommon for taxa to be restricted to a single cluster of springs, also termed *ultra-short range endemics* (Harvey, 1990; Gotch et al., 2008; King, 2009; Murphy et al., 2009, 2012; Guzik et al., 2012, 2019; King et al., 2014).

The conservation and management of groundwater resources are generally inadequate worldwide (Famiglietti, 2014). Springs fed by the Great Artesian Basin are no exception and are, generally speaking, considerably threatened by a range of industrial and pastoral practices (Mudd, 2000; Fairfax & Fensham, 2002; Lewis & Harris, 2020). Substantial reductions in artesian pressure (hereafter drawdown) and spring flow have occurred as a result of the sinking of over 50,000 artificial boreholes and the direct abstraction of Basin water, both historically and in the present day (Mudd, 2000; Gotch et al., 2016; Great Artesian Basin Coordinating Committee, 2019; Beasley-Hall et al., 2023). Indeed, a complete cessation of flow has occurred for an estimated 800 springs across Australia (Andersen et al., 2016; Fensham et al., 2016). Concomitant declines in observations of endemic fauna have also been documented, many of which have occurred as a result of reduction in size and/or complete extinction of their corresponding spring habitat (Kinhill-Stearns, 1984; McLaren et al., 1986; Zeidler & Ponder, 1989; Kinhill, 1997; Fatchen, 2000; NSW National Parks and Wildlife Service, 2002; Fensham & Fairfax, 2003; Kodric-Brown et al., 2007; Rossini et al., 2018). Initiatives such as the Great Artesian Basin Sustainability Initiative (hereafter GABSI), a basin-wide bore capping program to curb the uncontrollable flow of drilled bores, has "saved" over 250 gigalitres of water (Great Artesian Basin Coordinating Committee, 2019). The work of GABSI combined with the implementation of the Great Artesian Basin Strategic Management Plan, a longer-term framework related to GAB natural resource management, appears to have improved artesian pressure (Habermehl, 2020). However, net water flows in GAB springs nonetheless appear to be reducing across certain regions of the Basin, and understandings of the relationship between artesian pressure and spring flow remain poorly understood (Green & Berens, 2013). While drawdown represents the major cause of spring extinction, grazing, trampling, and soiling of wetlands by livestock (Fatchen, 2000), overabundant invasive (Noack, 1994; Kerezsy, 2015) and native (Davies et al., 2010; Lewis & Packer, 2020) species, climate change (Ordens et al., 2020), and tourist activity (Witjira National Park Co-management Board, 2022) pose threats to both spring health and the ecological communities dependent on springs themselves.

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Wetlands supported by GAB springs have high biodiversity value and, correspondingly, their ecological communities are protected under the *Environment Protection and Biodiversity Conservation Act 1999* (Cth) (hereafter EPBC Act), a key piece of Australian federal environmental legislation. However, it is recognised that in many cases, the extinction of GAB spring endemic species represents a permanent loss of Australia's genetic diversity and unique evolutionary lineages that have persisted over millions of years in isolation (Murphy et al., 2015). Basic taxonomic and biological information is still largely unknown, inaccessible, or disparate, making it difficult to accurately assess and monitor all species present at springs in the face of rapid, human-driven change. This lack of taxonomic information is particularly the case for endemic spring invertebrates (Rossini, 2020). Similarly, the relationship between environmental characteristics of springs and biodiversity is also not well understood. Metrics commonly used by industry to measure the robustness of springs, such as increased spring flow rate and aquifer pressure, are associated with formation of wetland areas (White & Lewis, 2011; BHP, 2018, 2021; Fensham & Laffineur, 2022) and biodiversity is thought to increase with the number of active springs in a region (Harris, 1992; Rossini et al., 2018). Conversely, drawdown can lead to the extinction of springs and their corresponding biota (Kinhill, 1997: 199; Fensham et al., 2010). However, more precise interactions among spring characteristics are not known and these trends have not been observed for all springs (Green & Berens, 2013). As such, the vulnerability of GAB spring taxa therein is almost impossible to gauge based on spring traits alone, complicating conservation management and planning. Thus, there is a clear need to compile baseline information on these taxa in a centralised, accessible resource to facilitate future conservation work on this community.

Data are crucial to decision-making capabilities in the context of biodiversity assessment, monitoring, and developing an understanding of ecosystem health (Vaughan et al., 2001; Stall et al., 2019). For industry partners, policymakers, and not-for-profit stakeholders, effective data sharing is essential for future progress and predictions in operations, products, and services (e.g., in the geosciences, (Hanson et al., 2017)). Guiding principles for scientific data management and stewardship have been developed by a global consortium of stakeholders to ensure digital assets are *findable*, *accessible*, *interoperable*, and *reusable* (FAIR) (Wilkinson et al., 2016) to promote the open sharing and reuse of research data, promote reproducibility, increase transparency, and ultimately accelerate scientific discovery. FAIR practices recommend data storage on open-access platforms, using persistent identifiers and built-in metadata in standard formats and vocabularies widely adopted by the research community. Currently, data on GAB springs, particularly biodiversity and hydrogeological information, has been collected and maintained in a sequestered and diffuse manner (38,39,44). No single centralised and public database or inventory that collates data for all fauna, flora, and funga—a term seeking to more accurately encapsulate biodiversity in conservation policy frameworks (Kuhar et al., 2018)—associated with the GAB springs exists. The closest resource is a publicly accessible dataset established by the Queensland Government which combines information on metrics such as water quality, chemistry, flow rate, biodiversity, and spring condition (Queensland Government, 2018) (absent for SA and New South Wales). The development of a biotic inventory has been identified as an urgent action to recover the community of native species dependent on GAB springs (Fensham et al., 2010). Such data can help to inform future management plans and early warning systems that detect changes in these ecosystems of high biodiversity value (Vaughan et al., 2001; Brack et al., 2015; Obura et al., 2019) and so improving their accessibility is a clear priority.

The first published sampling efforts began in the 1980s, which largely concerned small areas of the GAB and/or specific taxa, such as filamentous algae and the crustaceans (Kinhill-Stearns, 1984; Symon, 1984; Badman, 1985;

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Greenslade, 1985; McLaren et al., 1985; Mitchell, 1985; Thompson, 1985; Mollemans, 1989; Skinner, 1989; Zeidler, 1989). The majority of these checklists concern SA. In 2010, Fensham (Fensham et al., 2010) undertook one of the first robust scoping exercises of spring endemics and documented 30 taxa associated with SA GAB springs. Rossini *et al*. (Rossini et al., 2018) subsequently increased this number to 52 across 154 SA spring groups in a synthesis on GAB spring endemics. These checklists have been supplemented by genetic studies of the taxa found in SA GAB springs such as crustaceans (Murphy et al., 2009, 2013, 2015; Guzik et al., 2012, 2019; Guzik & Murphy, 2013; Stringer et al., 2019), snails (Ponder et al., 1995; Murphy et al., 2012), beetles (DeBoo et al., 2019), spiders (Gotch et al., 2008), and microbes (Byers et al., 1998). Collating fundamental biodiversity information such as this and ensuring the data are accessible and usable is a first step towards future science-based decision making (i.e., FAIR). Here, we collated all published information on the occurrence extents of fauna, flora, and funga associated with GAB springs in SA. This state was selected for its high number of GAB springs (>60% of Australia's springs) and the comparatively well-studied nature of their biodiversity from taxonomic and phylogenetic standpoints (Ponder et al., 1989; King, 2009; Guzik et al., 2012, 2019; Guzik & Murphy, 2013; Murphy et al., 2013, 2015; King et al., 2014), allowing for a more accurate reflection of the true number of taxa in these ecosystems. We also collated metadata associated with the conservation status, extent of occurrence, and taxonomic status of spring biota, and used these to calculate biodiversity metrics for springs, in keeping with existing checklists (Fensham & Price, 2004; Rossini et al., 2018). Further, we explored connectivity of these communities, allowing us to put forward preliminary conservation priorities for GAB-fed wetlands.

2 Materials and Methods

2.1 Literature review and database construction

A non-systematic review of all available information relevant to the biodiversity of GAB springs in SA was undertaken in the present study. A formal systematic searching strategy was not possible as a large proportion of information on springs is present in unpublished or grey literature such as government reports, internal publications from mining companies, and museum records. We therefore relied heavily on repositories such as the Government of South Australia's WaterConnect portal (South Australian Department for Environment and Water, 2023) and The Atlas of Living Australia (Belbin et al., 2021). We were specifically interested in data indicating the presence or absence of species in or around spring wetlands as well as their occurrence extents, if available, to gauge where taxa occurred and their degree of endemicity. The scope of this review spanned the three spring supergroups in SA: Kati Thanda–Lake Eyre, Munda / Lake Frome, and Dalhousie (Figure 1). **Supergroups** are clusters of **spring complexes**, which themselves contain **spring groups** composed of individual **springs**. Spring complexes share similar geomorphological characteristics and water chemistry, whereas groups are clusters of springs sourcing from the same fault of structure (Lewis et al., 2013). Individual springs are composed of permanent wetland vegetation with at least one **vent**, a discrete discharge point of water (Gotch, 2013). Within these three supergroups, we focused on 23 spring complexes containing 170 spring groups (Supplementary File S1, available publicly via FigShare: https://doi.org/10.25909/24457105). Whilst the number of these spring clusters, as well as their naming conventions, have previously not been standardised (Gotch et al., 2016), we selected these locations due to their widespread use in the literature and Australian Government publications (Lewis & White, 2013; Murphy et al., 2013; Rossini et al., 2018; Department of the Environment, 2022).

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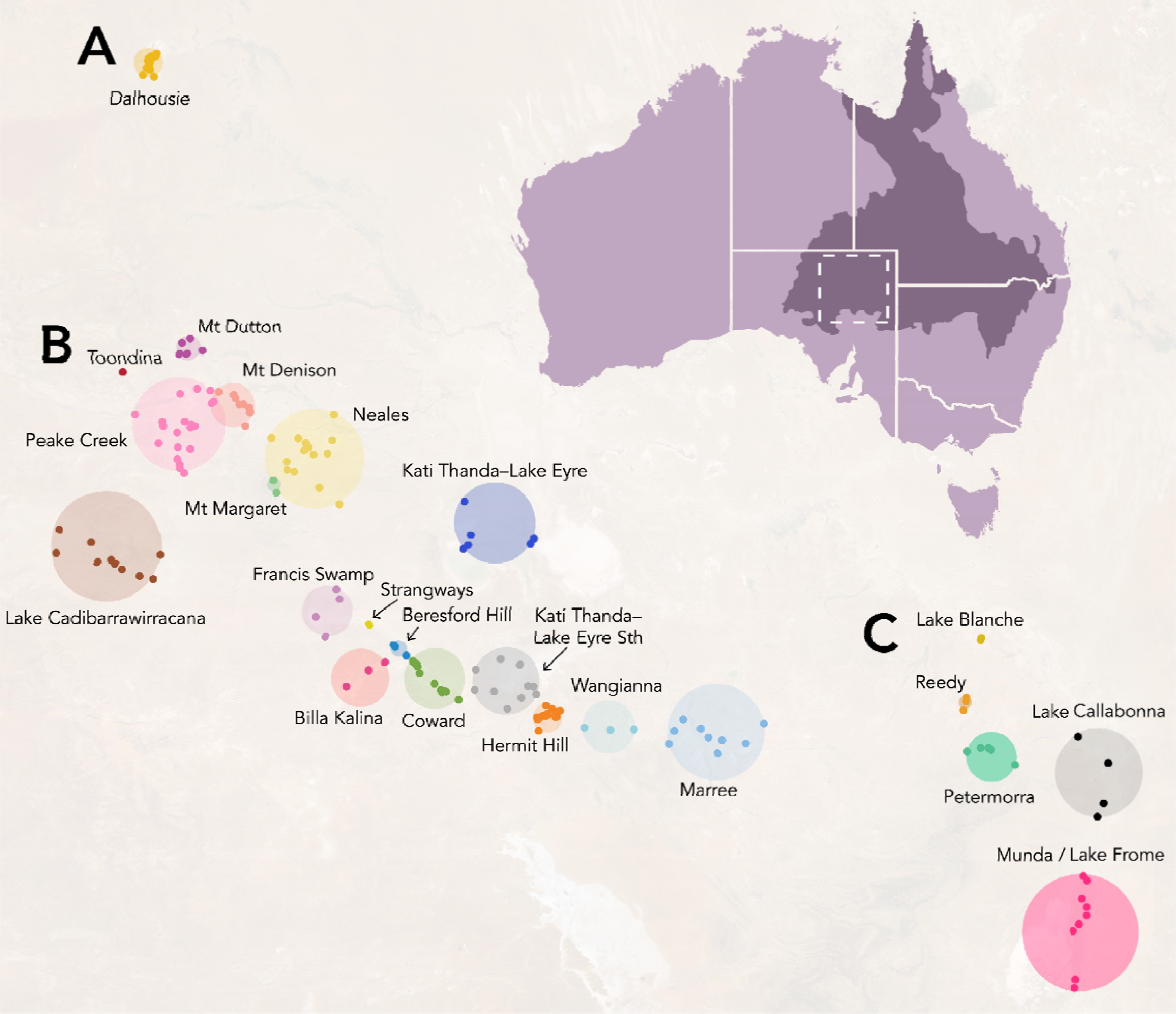

Fig. 1: Springs fed by the Great Artesian Basin (GAB) in South Australia. Springs are classified hierarchically as supergroups, the broadest classification (A, Dalhousie; B, Kati Thanda–Lake Eyre; C, Munda / Lake Frome); complexes (labelled coloured circles); groups (coloured points); springs; and finally vents, discrete water discharge points. The approximate area of the GAB is shown in dark purple and the location of the SA GAB springs is indicated by the dashed square.

We retrieved Aboriginal names for spring groups from a key anthropological study (Hercus & Sutton, 1985) to ensure locations were referred to by a dual naming convention whenever possible. The validity of these names were

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confirmed by The Arabana Aboriginal Corporation in a personal communication to the authors. In South Australia, the GAB springs can be found on the country of the Antakarinja, Arabana, Dhirari, Dieri, Karangura, Kokatha, Kuyani, Ngamini, Pirlatapa, Southern Aranda, Southern Arrente, Thirrari, Wangkangurru, and Yandruwandha peoples (Hercus & Sutton, 1985). The springs are the focus of cultural activities and oral histories for many of these peoples and almost all spring groups are documented as having mythological significance, historical significance, or both (Hercus & Sutton, 1985; Nursey-Bray & Arabana Aboriginal Corporation, 2015; Nursey-Bray et al., 2020). For locations with dual names, but lacking "official" formatting (e.g., not used by federal/state government legislation or publications), we followed the Australian Government's style manual (Australian Government, 2023). While Kati Thanda–Lake Eyre has an official name in government legislation, the formatting of the dual naming of Munda / Lake Frome is not standardised and we default to the style manual mentioned above in this case. We chose not to standardise names across springs, groups, or complexes as they refer to specific locations with distinct associated mythologies and histories (Hercus & Sutton, 1985). As a result, we do not refer to e.g. the Coward complex as Pitha Kalti-kalti / Coward (corresponding to a spring group), nor have we generalised the names of individual springs to the group level (e.g., Ngalpangkardanha and Pangki Warrunha refer to different locations within the Strangways group, but not the entire group itself). Alternative names and identifying codes for all locations were also recorded where present, e.g. for spring groups with several English or Aboriginal names or spelling variants. Records below the spring group level, where present, were standardised to the group level due to the rarity of such records and the inconsistency of spring vent naming conventions. As GAB spring fauna are often morphologically cryptic yet genetically distinct, we recorded species as separate taxa if explicitly indicated by their species authorities based on genetic data following Rossini *et al.* (Rossini et al., 2018).

To supplement presence/absence records of spring taxa, we also gathered metadata related to taxonomic status, conservation status, common names, synonyms, and endemicity where available. Taxonomic status was coded into three categories: taxa for which there is a corresponding formal taxonomic description ("described"), taxa awaiting taxonomic description ("undescribed"), or those for which species-level occurrence records were not available (e.g., a family-only record; "unidentified"). For taxa with species-level identifications, conservation status information was retrieved from the Species Profile and Threats Database to capture listings under the IUCN Red List of Threatened Species and Australian federal and state environmental legislation (Department of Climate Change, Energy, the Environment and Water, 2023). Finally, for each endemic taxon we noted whether it occupied only one spring group, complex, or supergroup. With the exception of undescribed species with well-established occurrence records, endemicity was not recorded for taxa without a species-level identification.

2.2 Biodiversity metrics

For each spring group, we first transformed presence/absence records to weight them by whether they were at the resolution of the spring group level (hereafter confident records) or those which referred to a taxon's presence within a certain complex, but did not supply spring group information (hereafter coarse records). To assess the inclusion of uncertain occurrence information, we calculated metrics for our entire dataset and a subset of the data only considering confident records. As the dataset included only presence/absence records, we were limited in our choice of biodiversity metrics and focused on species richness and endemicity. We calculated species richness values (hereafter taxon richness) by the number of putative taxa in each spring. Spring groups were ranked by the degree of endemicity of their biota using a modification of the scoring system developed by Fensham and Price (Fensham & Price, 2004). Originally applied to

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GAB flora in spring complexes in Queensland, the ranking has since been expanded to fauna across Australia (Rossini et al., 2018) and relies on the number of populations corresponding to the most widespread taxon in a spring dataset. The desert goby *Chlamydogobius eremius* (Zietz, 1896) is the most widespread SA GAB spring endemic, occurring across 24 known groups (Gotch et al., 2016; Rossini et al., 2018); we used this value as a proxy for the taxon's number of populations, although we acknowledge this may be an underestimate as spring groups do not necessarily share permanent wetlands. Rankings for each endemic taxon were first calculated by dividing 24 by the number of groups the taxon occurred in such that *C. eremius* (24/24) would receive the lowest ranking due to its comparably widespread distribution. As all endemic taxa assessed here do not occur beyond their respective supergroups, each taxon was then scored by whether it was further restricted to a single spring complex (+1) or group (+2). These scores, hereafter *endemicity rankings*, were summed for each spring group. We visualised these metrics using QGIS (QGIS Association, 2023). Spring groups were first mapped using latitude and longitude information corresponding to vents retrieved from the Government of South Australia's WaterConnect portal (Government of South Australia, 2023); for groups containing multiple vents, centroids were calculated to approximate their location. Circles corresponding to the above metrics per group were then scaled using the Flannery method and an exponent method of 0.57. To assess differences in community composition among spring groups, we calculated pairwise Jaccard distances using a binary matrix of presence/absence records using the *proxy* package in R v.4.3.0 (Meyer & Buchta, 2022; R Core Team, 2023). Principal components analysis was performed using the native R *stats* package and visualised using *ggplot2* (Wickham, 2016; R Core Team, 2023). Springs without occurrence records were excluded from the analysis, as were taxa known to occur in SA GAB springs generally but without specific location information. Finally, we produced rarefaction curves using the R package iNEXT (Hsieh & Chao, 2022) from our entire dataset and a subset of the data considering only confident records. Rarefaction was performed using the rarefaction and extrapolation models for species richness ($q = 0$), 95% confidence intervals, and 100 replications.

3 Results

3.1 Biodiversity of the SA GAB

The database we compiled based on our comprehensive literature review captured 3,463 occurrence records corresponding to 495 putatively distinct taxa (De Deckker, 1979; Greenslade, 1985; Thompson, 1985; Sluys, 1986; Sokol, 1987; Ling et al., 1989; Mollemans, 1989; Ponder et al., 1989, 1995, 1996; Zeidler & Ponder, 1989; Harvey, 1990, 1998; Zeidler, 1991, 1997; Fatchen & Fatchen, 1993; Morton et al., 1995; Ponder, 1995, 1996a, 1996b, 1996c, 1996d; Clark et al., 2003; Perkins, 2005; Framenau et al., 2006; Furler & Willing, 2006; Kodric-Brown et al., 2007; Page et al., 2007; Gotch et al., 2008, 2016; Clark, 2009; King, 2009; Murphy et al., 2009, 2013, 2015; Fensham et al., 2010; Unmack & Dowling, 2010; Guzik et al., 2012, 2019; King et al., 2014; Rossini et al., 2018; DeBoo et al., 2019; Stringer et al., 2019; Belbin et al., 2021; Department of the Environment, 2022; Witjira National Park Co-management Board, 2022; Froese & Pauly, 2023). Of these records, 2,300 were considered coarse—i.e., corresponding to the supergroup or complex level, but not informing the presence of taxa at a specific spring group. Invertebrates were by far the most speciose group in the dataset (42%, 206 taxa) followed by vascular plants (22%, 111 taxa), vertebrates (21%, 102 taxa), algae (14%, 68 taxa), non-vascular plants (1%, 5 taxa), and fungi (0.4%, 2 taxa) (Figure 2). Sixty-five taxa (13%) are known only from SA GAB springs, almost all of which are invertebrates. Despite this, invertebrates are also the most poorly known in the system from a taxonomic standpoint. Just over one-third of invertebrate taxa in the database have

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formal taxonomic names, whereas the remainder of the fauna are either undescribed (15%) or have an unknown taxonomic status due to a lack of species-level occurrence records (49%). For other taxonomic groups, these values range from 50–100% (described), 0–1.5% (undescribed), and 0–50% (unidentified). Further, apart from the Gastropoda no invertebrate taxon has had its conservation status assessed at the global, federal, or state level (Figure 2). Fifty-eight of the 170 spring groups assessed in this study had no corresponding occurrence records in the literature. A rarefaction curve derived from the dataset suggests the artesian wetlands of SA as a whole have not been adequately surveyed, and if additional locations were examined with equal sampling intensity, dozens of additional taxa would likely be documented (Figure 3).

In addition to occurrence records in the dataset, we also identified several records of potential local extinctions in the literature (Table 1). In all, we retrieved absence records corresponding to one isopod taxon, which may represent multiple species (*Phreatomerus latipes* (Chilton, 1922) Central, North, South haplotypes) (Kinhill-Stearns, 1984; Kinhill, 1997; Fensham et al., 2010; Guzik et al., 2012), one ostracod (*Ngarawa dirga* De Deckker, 1979) (McLaren et al., 1985; Kinhill, 1997; Fensham et al., 2010), 15 snail taxa (*Fonscochlea accepta*, members of *F. aquatica*, *F. billakalina*, *F. variabilis*, *Trochidrobia punicea*, *T. smithii* species complexes [all Ponder, Hershler & Jenkins, 1989], *Sinumelon pedasum* Iredale, 1937) (Zeidler & Ponder, 1989; Ponder et al., 1995; Fensham et al., 2010; Rossini et al., 2018; Department of the Environment, 2022), and four fishes (the Dalhousie goby *Chlamydogobius gloveri* Larson, 1995, Lake Eyre hardyhead *Craterocephalus eyresii* (Steindachner, 1883), spangled perch *Leiopotherapon unicolor* (Günther, 1859), Dalhousie gudgeon *Mogurnda thermophila* Allen & Jenkins, 1999) (Zeidler & Ponder, 1989; Kodric-Brown et al., 2007; Gotch et al., 2016; Rossini et al., 2018; Department of the Environment, 2022; Froese & Pauly, 2023). To the best of our knowledge, all of these records corresponded to local extinctions as opposed to complete species extinctions (i.e., relevant taxa were present in at least one additional location). These extirpations have occurred across 13 spring groups in the Dalhousie and Kati Thanda–Lake Eyre supergroups (Table 1).

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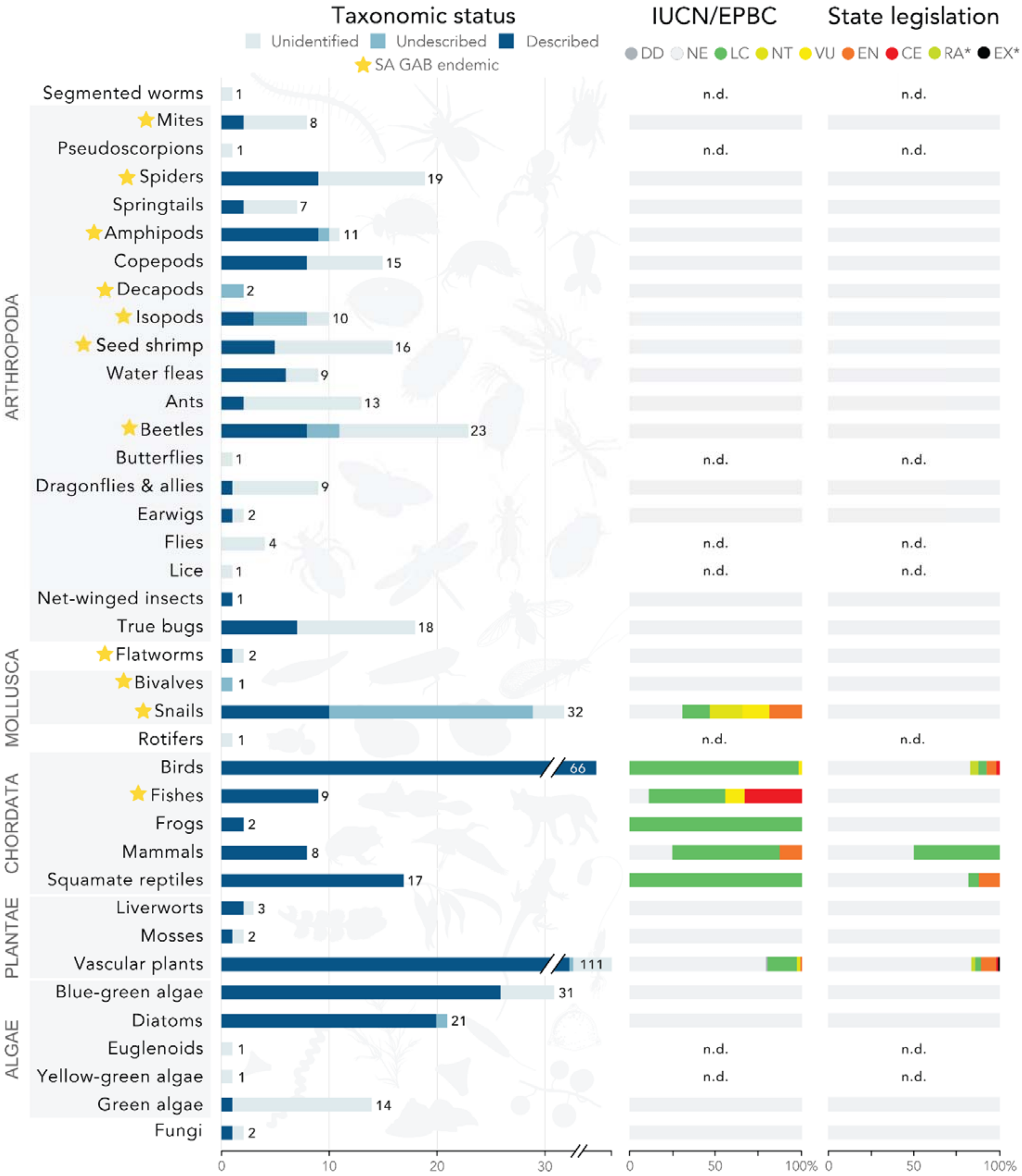

Figure 2: Fauna, flora, and funga associated with SA GAB spring wetlands, with major organismal groups indicated by grey boxes. Groups lacking species-level records have an unknown conservation status and are indicated with n.d. (no data). * Rare (RA) and extinct (EX) conservation statuses here are specific to SA/TAS and NSW legislation, respectively, and only refer to populations/taxa within those states. Silhouette credits Maxime Dahirel, Armelle Ansart, Mathieu Pélissié, and Lafage via PhyloPic.

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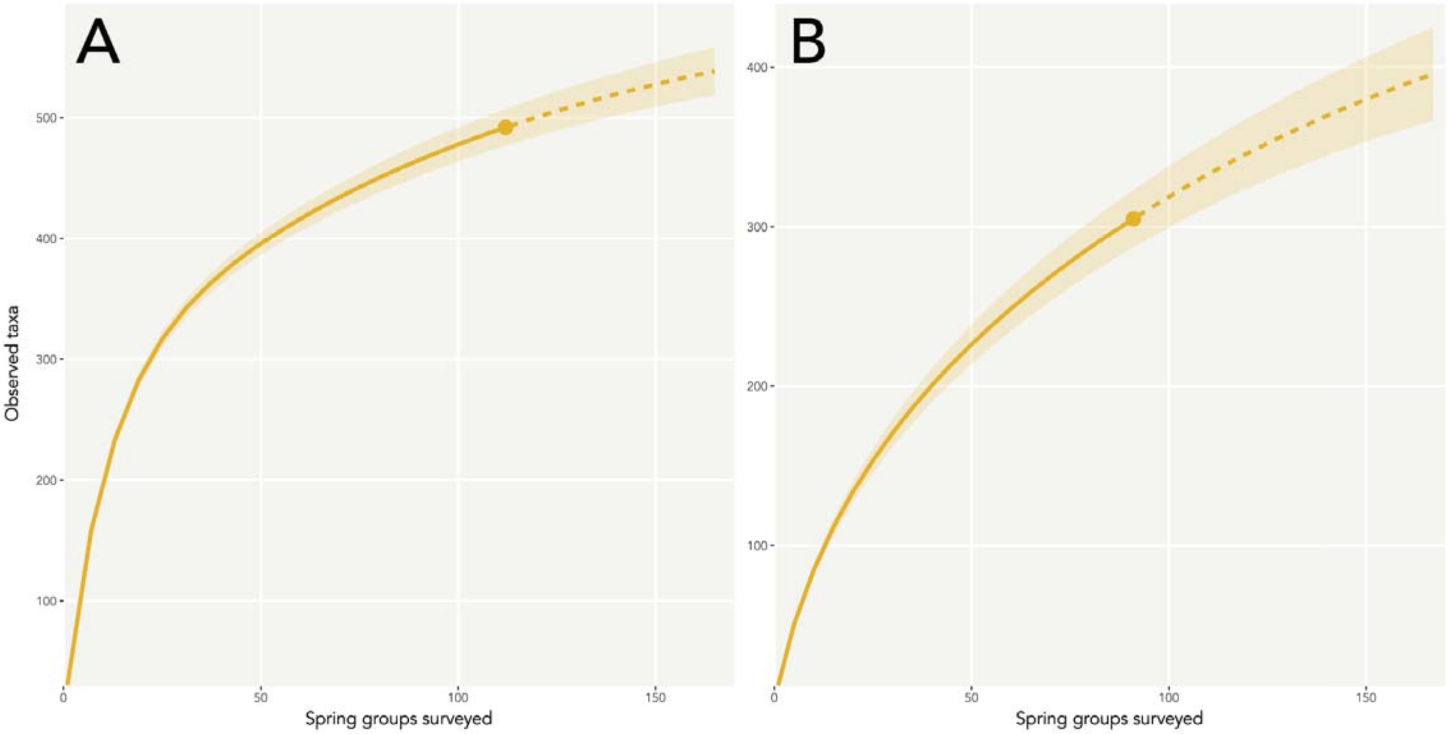

Fig. 3: Rarefaction curves predicting an increase in taxon richness if additional spring groups were surveyed, calculated from all occurrence records in the dataset (A) and a subset of the dataset containing only confident records (B). As the curve does not flatten at the maximum number of known spring groups in the state (170), an increase in sampling effort *within* springs (as opposed to the sole sampling of additional springs) may also capture a more comprehensive representation of these communities.

3.2 Biodiversity metrics and community composition

Taxon richness was more heavily impacted by the exclusion of coarse occurrence records as most data in this category are not spring endemics, whereas endemicity rankings were essentially unchanged between spring locations. In other words, complexes may be taxon-rich without containing a large number of endemics (e.g., groups within the Francis Swamp complex; Figure 4) and vice versa (e.g., Beresford Hill). Groups with high levels of richness values generally corresponded to the Coward, Dalhousie, Billa Kalina, and Hermit Hill complexes and those containing large numbers of isolated endemics included Dalhousie, Francis Swamp, Mount Denison, and Coward (Figure 4; Supplementary File S2, available publicly via FigShare: https://doi.org/10.25909/24457120).

While there is some degree of overlap regarding taxon composition of spring complexes, particularly in the Kati Thanda–Lake Eyre region (Figure 5), locations with similar biodiversity metrics do not necessarily support the same biotic communities. The Peake Creek, Lake Cadibarrawirracanna, Neales River, and Mount Dutton complexes of the Kati Thanda–Lake Eyre supergroup are generally non-overlapping and groups from within the Dalhousie complex/supergroup are easily differentiated from other complexes (Figure 5). In contrast, groups from the Munda / Lake Frome complex are nested within those from the Kati Thanda–Lake Eyre supergroup. Groups belonging to the same complex are also generally more similar to one another than those in different complexes. Thisapparent lack of connectivity is perhaps unsurprising given the aridity of the surrounding landscape. Overall, spring groups within the Dalhousie supergroup/complex are the most distinct in the dataset in that they support taxa not known to be associated with other spring complexes, including highly isolated endemics (Figures 4, 5).

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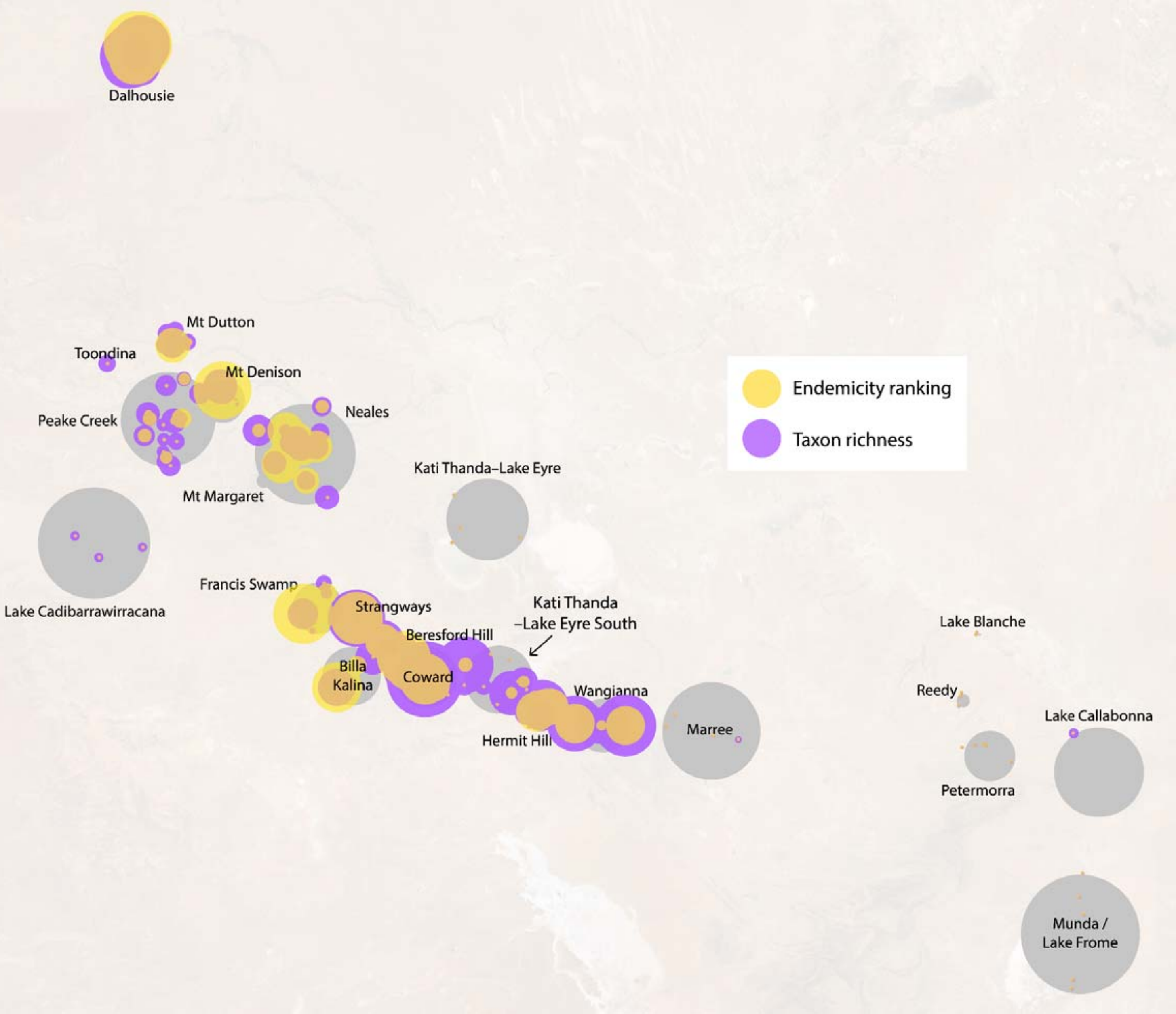

Fig. 4: Rankings of endemicity and biodiversity (i.e., considering non-endemic biota) in SA GAB spring groups calculated from occurrence records in the literature. Data shown here were calculated using all occurrence records in the dataset. Metrics calculated from only confident records are available in Supplementary File S2. We use the term “taxon richness” over “species richness” here as several taxa in the dataset are putative species based on morphological and/or molecular divergences per their respective taxonomic authorities (Greenslade, 1985; Murphy et al., 2009; Guzik et al., 2012, 2019; DeBoo et al., 2019; Stringer et al., 2019).

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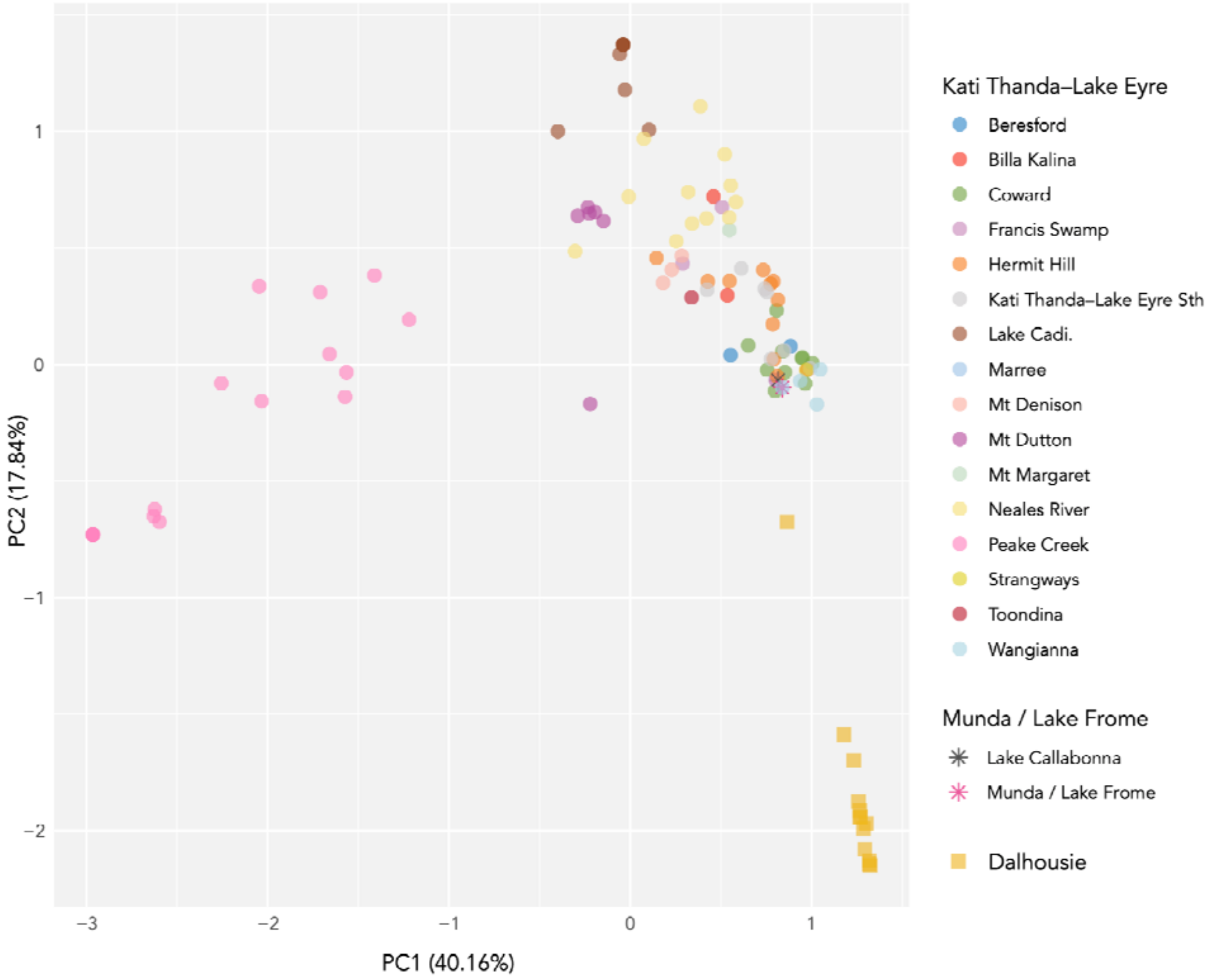

Fig. 5: Principal components analysis (PCA) showing composition of faunal, floral, and fungal communities reliant on South Australian GAB springs. Both coarse and confident occurrence records in the dataset were used to calculate Jaccard distances between spring groups. Spring groups lacking occurrence records are not shown here. Groups are coded by their respective spring complex (colour) and supergroup (shape). Axis labels refer to the amount of variability explained by each principal component (PC).

4 Discussion

Here, we present a robust literature review of the natural heritage value of the artesian wetlands of Australia, focusing on SA GAB wetlands as the state contains the majority of springs throughout the continent's arid zone. The data we have collated highlight several key trends: 1) invertebrates are a poorly-known component of GAB biodiversity; 2) the composition of GAB biota differs considerably by location; and 3) the true extent of GAB biodiversity is far greater than is currently appreciated in the literature. We discuss each of these findings below, as well as conservation implications for GAB springs more broadly and how a centralised biodiversity resource for the GAB could be implemented in future.

4.1 Biodiversity of South Australia's GAB springs

We recorded almost 500 taxa associated with GAB springs and their surrounding wetlands. Invertebrates (namely insects, crustaceans, and arachnids) represented the largest proportion of this biota and the largest group of endemics (Figure 2). Invertebrates are poorly documented from biodiversity, ecological, and conservation standpoints relative to the remainder of GAB biota, and are also overrepresented in extinction records (Table 1). These groups may therefore be the most at

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risk of decline due to difficulties in devising management strategies. In contrast, while vertebrates were the third-most speciose group associated with the system (N = 102), almost all were widespread species not of conservation concern (Fensham & Price, 2004) (Figure 2). We note here that vertebrates such as waterbirds are nonetheless dependent on the springs as breeding grounds (Badman, 1985), however, and may make more extensive use of these habitats in non-flood years and/or as "stepping stone" habitats to sustain migrations to nearby Kati Thanda–Lake Eyre. For example, the little grassbird (*Poodytes gramineus* (Gould, 1845)) and clamorous reed warbler (*Acrocephalus stentoreus* (Hemprich & Ehrenberg, 1833)) are not restricted to GAB springs but have an obligate relationship with stands of the common reed *Phragmites australis* (Cav.) Trin. ex Steud. in GAB wetlands in that region (Read, 1997).

Based on all available information on the occurrence extents of fauna, flora, and funga associated with GAB springs in SA, the composition of these biota is far from uniform. It has long been recognised that certain locations in the SA GAB springs are more speciose than others, but this has only been formally quantified with respect to endemic taxa and without consideration of the distinct spring groups within the Dalhousie complex (Rossini et al., 2018). Here we have showed that the bulk of endemic biodiversity at Dalhousie is contributed by the Irrwanjira / Main Pool group, and groups within the Francis Swamp, Mount Denison, and Coward complexes, which in fact house a more speciose and isolated endemic biota than initially recognised based on published records (Supplementary File S1). Further, taxon-rich locations are not necessarily rich in endemics (Figure 4). Overall, these data indicate the disturbance or extinction of any given spring group could represent an enormous loss of biodiversity when both endemic and non-endemic taxa are considered together. The biodiversity of the South Australian GAB has not been adequately surveyed (Figure 3) and over two-thirds of records we collated were coarse, meaning they lacked occurrence information at the spring group level. While records are helpful in distinguishing spring group locations and suggest considerable structure in taxa occupying different spring complexes and supergroups (Figure 5), they nonetheless highlight a lack of detailed past surveys and the sparseness of published information on GAB biodiversity.

The observed variability in the dataset may also be associated with sampling bias. Spring groups with the highest endemicity rankings, such as those within the Dalhousie and Coward complexes, are also those consistently associated with high sampling effort in previous surveys (Badman, 1985; Greenslade, 1985; Mitchell, 1985; Sokol, 1987; Zeidler & Ponder, 1989; Noack, 1994; Ponder et al., 1995; Kovac, 2003). The Kati Thanda–Lake Eyre and Dalhousie supergroups corresponded to over 2,000 occurrence records, whereas observations within the Munda / Lake Frome supergroup were restricted to a single, coarse occurrence record of the copepod *Microcyclops dengizicus* (Lepeschkin, 1900) (Zeidler & Ponder, 1989). Munda / Lake Frome has clearly not been adequately sampled, although this does not necessarily imply the location lacks endemic taxa yet to be characterised (McLaren et al., 1985; Rossini, 2020). Indeed, widespread taxonomic groups expected to be present in springs, such as the Hymenoptera and other cosmopolitan insect groups, were also poorly represented in the dataset due to a presumed bias in sampling methods and a lack of past taxonomic expertise (ADA, pers. obs.). As such, we caution against the derivation of conservation priorities from locations with high measures of metrics such as species richness alone, but trends are nonetheless evident in this review regarding spring locations and taxonomic groups that have been undersampled.

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4.2 Conservation implications for South Australia's artesian springs

Populations of at least 13 taxa are thought to have become locally extinct in the SA GAB springs (Table 1). The bulk of these extirpations have occurred in spring groups that have ceased to flow as a result of drawdown, namely Venable, Palura Pintjanha / Priscilla, Marrinha / Hergott, Margaret, and Manda-wardunha / Mundowdna (Fensham et al., 2010). The Venable and Palura Pintjanha / Priscilla spring groups became extinct around 1990 following predictions by industry that mining activities would lead to a partial, if not complete, reduction in artesian flow at certain GAB springs (Kinhill-Stearns, 1982, 1983). Marrinha / Hergott ceased to flow in the mid-1980s as water was withdrawn to supply the nearby town of Marree (McLaren et al., 1985: 198). Other extirpations have been attributed to human modification of springs, the presence of overabundant invasive and native species, and potentially insufficient sampling effort. The apparent local extinction of the fish species, Lake Eyre hardyhead (*Craterocephalus eyresii*) at Toondina and Old Nilpinna may have been caused by spring excavations and competition from the invasive mosquitofish *Gambusia holbrooki* Girard, 1859, respectively (Gotch et al., 2016). Extirpations of other fish species at Dalhousie have been attributed to the overgrowth of the native reed *Phragmites* as a result of decreased grazing pressure following the exclusion of livestock (Kodric-Brown et al., 2007).

It is important to establish conservation priorities given the potential for further local, if not species-wide, extinctions in the SA GAB springs. Here, we ranked spring groups by the number of endemic species supported by each spring group and their degree of isolation. High-ranking locations mirror those proposed as conservation priorities in past studies. For example, McLaren *et al.* (McLaren et al., 1985) produced an inventory of fauna, flora, and funga to set out conservation priorities based on species diversity, the presence of rare species, "naturalness" (i.e., extent of interference by humans/livestock) and perceived vulnerability to degradation. Spring groups were then ranked as being of low, medium, or high conservation priority. High-ranking spring groups in this assessment include those found at Dalhousie and in the Coward and Mt. Denison complexes of the Kati Thanda–Lake Eyre supergroup. Further, Rossini *et al.* (Rossini et al., 2018) used a ranking system developed by Fensham and Price (Fensham & Price, 2004) (modified here to produce the endemicity rankings in the dataset) to conclude that groups within the Dalhousie, Strangways, Francis Swamp, Billa Kalina, and Mt Denison complexes were of high conservation significance relative to other springs. The highest-ranking spring groups by endemicity in the current study presented here corresponded to all six of the above complexes, often down to the spring group level (Supplementary File S2). We stress that these trends do not suggest certain spring groups are more important than others or that insignificant springs exist, as has been implied in past environmental impact statements (Kinhill-Stearns, 1983; Keane, 1997). This is especially the case for locations that could be perceived as having low biological importance, such as the extinct Papu-ngaljuru / Primrose spring group, but have outstanding cultural significance to Aboriginal peoples due to associated mythologies and its use as a major occupation site (Hercus & Sutton, 1985). Instead, our findings suggest that certain spring groups harbour high numbers of endemics relative to other locations (but remembering that insufficient sampling effort has occurred) and require targeted conservation efforts to preserve these short-range taxa.

In contrast to GABSI, which sought to increase artesian pressure Basin-wide and address the threat of drawdown, several conservation programs are currently in place which aim to directly improve the condition of SA GAB spring wetlands (Harris, 1992). Preliminary evidence suggests several of these practices have had a positive impact on SA GAB spring endemics. Springs are threatened by the presence of large-bodied and hard-hooved livestock which can

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graze on or trample wetland vegetation, foul the water through their faeces, and potentially reduce invertebrate biodiversity if stocking levels are high (Hutchinson & King, 1980; Kovac & Mackay, 2009; Fensham et al., 2010; Gotch et al., 2016). Fencing has been successful in restoring endemic biodiversity of SA GAB springs in some cases, e.g., the endemic salt pipewort *Eriocaulon carsonii* subsp. *carsonii* F. Muell. in the Hermit Hill complex (Fatchen & Fatchen, 1993) and aquatic invertebrates at springs that were heavily damaged by stock (Kinhill-Stearns, 1984). It is worth noting that the Dalhousie supergroup and portions of the Hermit Hill complex are also within National Parks, further reducing stocking pressures without the use of fencing (Harris, 1992). However, the complete exclusion of stock can also lead to the overproliferation of the native reed *Phragmites*, which occurs as a natural component of SA GAB ecological communities but when present at unnaturally high densities can reduce endemic floristic diversity (Davies et al., 2010; Lewis & Packer, 2020) and increase transpiration rates, reducing available habitat for aquatic animals (Fensham et al., 2010). Best practices for controlling *Phragmites* and preserving GAB spring invertebrates may involve allowing stock only to graze at certain periods during the year, as burning does not seem to be an appropriate tool to control its growth (Lamb et al., 2002). Invasive species such as the date palm (*Phoenix dactylifera* L.) and mosquitofish (*Gambusia holbrooki*), among others, are also of concern for the conservation of GAB spring endemics as they can reduce invertebrate diversity (Holmquist et al., 2011) and threaten native fauna through competition and predation (Gotch et al., 2016). Complete removal of date palms has now occurred at Dalhousie, which used to house a large population of the species (Fensham et al., 2010).

As stated above, there is a large proportion of endemic taxa at several complexes within the SA GAB, namely those contained within the Dalhousie and Kati Thanda–Lake Eyre supergroups. The data presented here reiterates the need for targeted surveys in these locations to not only gather additional biodiversity data, but also to develop an understanding of population dynamics, habitat requirements, and accidental human-mediated translocations of fauna, flora, and funga per the national recovery plan (Fensham et al., 2010). The plan notably highlights the fact that the construction of a robust biodiversity inventory for GAB springs has been hindered by a lack of survey effort and taxonomic expertise. The utility of emerging environmental DNA techniques to capture a holistic picture of SA GAB spring biodiversity in a non-invasive manner would overcome several of these limitations (Vörös, 2017; West et al., 2020; Saccò et al., 2022; Beasley-Hall et al., 2023); in this regard, the database developed as part of this study would assist in the selection of fieldwork locations for a pilot study in this regard. Once taxa are established as occurring within the SA GAB, monitoring efforts should be undertaken on a regular basis to develop deeper understandings of ecological knowledge as opposed to presence/absence information.

Although taxa reliant on GAB-fed springs are protected as a single ecological community under the EPBC Act, species-level listings are also far overdue. This is particularly the case for invertebrates dependent on the GAB. The majority of GAB molluscs and crustaceans meet the criteria to be listed as Critically Endangered (Rossini, 2020), but almost 90% of SA GAB invertebrates recorded here lack conservation listing at a global, federal, or state level, the bulk of which are either new species awaiting formal description or those completely lacking species-level identifications. This large knowledge gap is only exacerbated by a lack of understanding of the relationship between spring characteristics and biodiversity metrics (Rossini et al., 2018; Fensham & Laffineur, 2022) and indeed, relationships among spring ecological and hydrogeological characteristics themselves (Mudd, 2000; Green & Berens, 2013; Love et al. (eds), 2013). We hope that resources like the database developed here will inform the prioritisation of certain spring

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locations and taxonomic groups, ultimately leading to the listing of invertebrates and other spring endemics under relevant legislation on a per-species basis.

4.3 Towards a FAIR and centralised database of GAB spring biodiversity

This GAB database is a significant first step towards tailored conservation of spring biota and represents an important addition to understandings of spring biodiversity. There are at least 64 endemic taxa across 170 SA spring groups and an additional 366 non-endemics that occur in association with springs. Our findings present the most comprehensive collation of biodiversity data for the artesian springs of SA to date, both geographically and from a taxonomic standpoint. Data related to GAB spring biodiversity is often diffuse, inaccessible, and ultimately maintained in a decentralised fashion. Early surveys conducted on the springs in the 1980s were largely taxon-specific and conducted by museum employees or those working in industry, leading to their results either being published locally without digitisation or in the form of internal reports (Badman, 1985; Greenslade, 1985; McLaren et al., 1985; Mitchell, 1985; Thompson, 1985; Ling et al., 1989; Mollemans, 1989; Skinner, 1989; Zeidler, 1989). Currently, the only digitised database available to the general public is the Queensland Government's Springs Database (Queensland Government, 2018), which is freely available and also includes a Creative Commons Attribution 4.0 licence, a useability rating, and version information. In contrast, the existing data for SA are neither publicly available or centralised (Kinhill-Stearns, 1982, 1984; Kinhill, 1997). Moreover, nomenclature used to describe SA GAB spring vents and groups has not been standardised, leading to inconsistencies in names and identifying codes among datasets that refer to identical locations. Similar issues are evident for hydrogeological information related to the GAB springs (PGBH pers. obs.). There is a clear need to progress beyond these "silos" and establish a database for the GAB springs nationwide that is not only publicly accessible, but also supports iterative refinement, updating of biodiversity information over time, and standardises nomenclature used to refer to springs, particularly spring groups. To this end, in the database published here we have standardised spring nomenclature across the Government of South Australia's WaterConnect database and identifiers in use by industry stakeholders.

5 Conclusion

Here, we have presented the most robust review of biota supported by the Great Artesian Basin in South Australia. This dataset is an important resource that we hope will facilitate future studies on SA GAB spring endemics, investigations into their population dynamics, basic biology, and taxonomy, and ultimately facilitate the listing of relevant taxa under state and federal environmental legislation. Such resources are essential given the multitude of threats currently facing springs and their biota, with potential extirpations of populations of at least 13 species in the SA GAB springs to date. We have also highlighted springs of particular conservation concern which may assist in determining future conservation priorities for this system. The dataset presented here stresses three major points about GAB spring biodiversity. Firstly, the majority of taxa reliant on these wetlands are invertebrates, and these animals are also the most poorly known and conserved. Secondly, ecological communities reliant on artesian springs in SA are largely non-overlapping, irrespective of whether only endemic taxa, or endemics as well as "incidental" species, are concerned. The extinction or considerable disturbance of any spring group is therefore likely to lead to a considerable loss of biodiversity and/or genetic diversity. Finally, the artesian springs of SA have not been adequately sampled by past survey efforts and a considerable proportion of taxa likely remain to be documented, particularly in understudied locations such as the Munda / Lake Frome

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supergroup. There also remains a dearth of occurrence records for certain taxa for which taxonomic expertise has been lacking in the past, such as the wasps and allies (Greenslade, 1985). We recommend that datasets such as these are made publicly available with the capacity to be modified and updated on an ongoing basis, embodying the gold standard of digital asset storage.

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8 Statements and Declarations

8.1 Author contributions

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8.2 Competing interests

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9 Tables

Table 1: Records of possible local extinctions of fauna in the SA GAB springs. To our knowledge there are no records of floral extinctions in the SA GAB. ^ Taxon represents multiple genetically distinct clades which we consider putative species, but which of these were present in the below location(s) prior to their apparent extirpation is unknown. KT–LE Sth = Kati Thanda–Lake Eyre South. * GAB spring endemic.

Taxon	Broad grouping	Spring group(s)	Spring complex(es)
Phreatomerus latipes^*	Isopod	Venable, Marrinha / Hergott	Hermit Hill, Marree
*Ngarawa dirga**	Ostracod	Venable, Manda-wardunha / Mundowdna	Hermit Hill, Marree
*Fonscochlea accepta**	Hydrobiid snail	Venable, Palura Pintjanha / Priscilla	Hermit Hill, KT–LE Sth
Fonscochlea aquatica^*	Hydrobiid snail	Margaret	Francis Swamp
*Fonscochlea billakalina**	Hydrobiid snail	Margaret	Francis Swamp
Fonscochlea variabilis^*	Hydrobiid snail	Venable, Palura Pintjanha / Priscilla	Hermit Hill, KT–LE Sth
Trochidrobia punicea^*	Hydrobiid snail	Venable, Palura Pintjanha / Priscilla	Hermit Hill, KT–LE Sth
Trochidrobia smithii^*	Hydrobiid snail	Margaret	Francis Swamp
Sinumelon pedasum	Camaenid snail	Irrwanjira / Errawanyera	Dalhousie
Chlamydogobius gloveri	Fish	Irrwanjira / Errawanyera, Frog Dreaming, Kirki / Dalhousie Proper, Cadni Dreaming	Dalhousie
Craterocephalus eyresii	Fish	Old Nilpinna, Thuntinha / Toondina	Peake Creek, Toondina
Leiopotherapon unicolor	Fish	Idnjundura / Kingfisher, Ilpikwa	Dalhousie
Mogurnda thermophila	Fish	Frog Dreaming	Dalhousie