

Diversity and Distribution of Amphibians and Freshwater Fishes on Australian Islands

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Data Availability

The Occurrences of Freshwater Fishes and Frogs of Australian Islands database is available in the Supporting Information.

Statements and Declaration

The authors have no relevant financial or non-financial interests to disclose. The authors declare no competing interests.

Author Contribution

Samuel C.L. Ho, Salit Kark, Simon P. Hart, Peter W.J. Baxter contributed to the study conception

and design. Material preparation, data collection was performed by Samuel Ho. Data analysis was performed by Samuel Ho and Simon P. Hart. Michael P. Hammer contributed to the verification of presence absence, and the life history traits of freshwater fishes. Samuel C.L. Ho, Peter J. Unmack and Simon P. Hart contributed to interpretation and discussion of results. The first draft of the manuscript was written by Samuel C.L. Ho and were edited and revised by all co-authors. All authors read, revised and approved of the final manuscript.

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Data Availability

All data generated for this manuscript is attached as supplementary material.

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Abstract

Aim

Freshwater ecosystems cover less than 3% of the earth's surface, yet support nearly 10% of all known animal species, majorly represented by freshwater fishes (69%) and amphibians (24%), both of which are highly threatened groups. Geographically isolated freshwater species, such as those inhabiting islands, are at high risk. Australia, with ~9300 islands, is home to diverse island freshwater fauna. However, the lack of published literature on their island occurrence, threats, and management impedes effective conservation across islands. We aim to describe the distributional patterns of amphibians and freshwater fishes on islands and analyze the island characteristics that influence these patterns.

Location

Australia's Islands

Methods

We compiled the first database of occurrences of amphibians and freshwater fishes of Australia's islands. Utilizing the database, we used regression analysis to examine the main drivers of distributional pattern, species richness, and species composition on Australia's islands.

Results

We found 102 amphibians and 95 freshwater fishes, 55 fishes were obligate freshwater species, 21 were euryhaline and 19 were diadromous. Both amphibians and freshwater fish richness were higher on islands with more precipitation. While freshwater fishes were less diverse on islands than amphibians, potentially due to lower survey efforts, fishes had a higher proportion of threatened and exotic species. Islands closer to the mainland hosted higher amphibian richness, which likely retained mainland amphibian assemblages, or were more easily colonized. In contrast, larger islands hosted more freshwater fishes, where diverse habitats were likely to sustain more species.

Main Conclusions

Using the new database we compiled; we found that amphibian and freshwater fishes occurrences on islands likely resulted from different drivers. This study provides a baseline for follow-up studies on phylogeny and biogeography. This research contributes to the conservation of amphibians and freshwater fishes on islands by revealing potential hotspots of extinction risk and lays the groundwork for future spatial prioritization work.

Keywords

Amphibians, Australia, biodiversity, conservation, fishes, freshwater ecosystem, islands, island biogeography

1 Introduction

Freshwater ecosystems are widely recognized as important to humans and biodiversity yet are scarce and susceptible to threats (Albert et al., 2021; Dudgeon et al., 2006). Approximately 70% of the earth's surface is covered in water, of which only 2.5% is freshwater (Mishra, 2023), providing habitat for at least 126,000 animal species (Balian et al., 2008). Freshwater habitats are much smaller than marine habitats but are disproportionately rich in biodiversity, with freshwater fish species alone accounting for around half of all described fish species (Carrete Vega & Wiens, 2012). Freshwater is also crucial to the survival of all amphibian species, the second most diverse freshwater animal group (Balian et al., 2008). Some 4117 of 5828 frog species have at least one life-stage that lives in water, and a further 177 species are water-dependent (Vences & Köhler, 2008). Although freshwater habitats are some of the most biodiverse habitats on earth (Balian et al., 2008; Collen et al., 2014; Dudgeon et al., 2006), they continue to be under-represented in the conservation literature (Strayer & Dudgeon, 2010).

Freshwater ecosystems are hotspots of endangerment due to the convergence between rich biodiversity and many forms of human freshwater exploitation (Reid et al., 2019). Humans exploit freshwater resources for socio-economic development in many ways (Israilova et al., 2023), including agriculture, consumption, recreation, transportation and electricity generation (Albert et al., 2021; Mishra, 2023). In 2022, the World Wide Fund Living Planet Report showed that human-induced threats have led to the greatest decline of freshwater species by 83% (WWF, 2022).

Island ecosystems are also a hotspot of endangerment due to the large number of threatened and endemic species they harbor (Kier et al., 2009). Levels of endemism also vary between islands and are influenced by geographical factors such as total area, level of isolation, and latitude (Gillespie et al., 2013). Islands are particularly vulnerable to a range of threats, including habitat degradation and the introduction of invasive species (Heatwole & Rowley, 2018; Hervías et al., 2014). Alarmingly, island endemic species now represent 81% of all globally threatened or extinct species (Doherty et al., 2016). Research has typically focused on impacts of

invasive mammalian predators on island fauna (Doherty et al., 2015; Rayner et al., 2007; Rees et al., 2023), which have collectively impacted at least 738 species and contributed to 58% of modern bird, mammal and reptile extinctions. In contrast, the status of amphibians and freshwater fishes on islands remains poorly documented in the literature and is often overlooked in studies (Doherty et al., 2016; Legge et al., 2018).

Collectively, Australia has nearly 9300 islands, highly varying in size, climate, and distance from the mainland (Baxter et al., 2021) which heavily influence the species richness, species composition and level of endemism on the islands (Gillespie et al., 2013; MacArthur & Wilson, 2001). Most of Australia's continental islands exist due to the rise in sea levels following each glacial cycle during the Pleistocene epoch (Allen & Kershaw, 1996). As the climate warmed and ice melted, rising sea levels flooded low-lying areas, isolating higher landmasses as islands (Allen & Kershaw, 1996). Among Australia's many islands, 317 host a total of 281 threatened animal and plant species, with notable examples including Norfolk Island and Kangaroo Island, which harbor 55 and 27 nationally threatened species respectively (Baxter et al., 2021). To address this gap, a database documenting the occurrences of threatened and invasive species on Australian islands was developed to inform conservation management strategies (Baxter et al., 2021). However, noticeable gaps remain in the database, particularly in less-surveyed taxonomic groups such as fishes, amphibians, and invertebrates, and the omission of records of non-threatened native species.

Endemism and species richness on islands are highly relevant to prioritization and conservation efforts (Kier et al., 2009). In Australia, despite the presence of extensive palustrine and lacustrine freshwater wetlands on its islands, huge knowledge gaps persist on their inhabitant's diversity, ecology, population, and distribution due to lack of surveying effort (Hines & Meyer, 2011; Miles, 2007; Miles et al., 2013). These knowledge gaps are even more pronounced on smaller islands, with minimal publicly available data on the amphibians and freshwater fishes residing there, albeit with some exceptions such as Magnetic Island (MINCA,

2020). The substantial gap in knowledge impedes conservation actions on threatened species on islands, especially when many threatened species on islands are non-migratory which makes them more vulnerable (Garnett et al., 2022). To reduce this knowledge gap, we have created a database on the occurrences of all amphibians and freshwater fishes on Australia's islands. We then used this database to explore the island characteristics that influence freshwater vertebrate fauna richness on these islands. Our key aim is to reveal the spatial patterns for freshwater vertebrates, including threatened and invasive species, and to investigate the island characteristics that influence species diversity. We further aimed to provide scientific guidance for biodiversity conservation in Australia, and to provide a baseline for future prioritization work.

2. Methods

2.1 Data collection

We address the existing knowledge gaps in understanding and conserving freshwater fish and frogs on Australian islands by collating the first specific database containing the occurrences of freshwater fish and frogs on Australia's islands. To create this database, we leveraged the Island Occurrences of Threatened Australian Species (IOTAS) dataset and Invasive Species on Australian Islands dataset (Baxter et al., 2021). These databases were further supplemented by occurrence data from the Atlas of Living Australia (ALA; <https://www.ala.org.au/>). To obtain a complete species list of freshwater fishes, we integrated the species list from the "Ecology of Australian Freshwater Fishes" book (Humphries & Walker, 2013), and the "Fishbase List of Freshwater Fishes reported from Australia" (Nicholls, 2016) in ALA. We updated nomenclature of the integrated list where relevant. We downloaded all occurrence records of species from the integrated list from Atlas of Living Australia, and obtained the records on islands using *pairwise intersect* on ArcGIS pro (ESRI, 2011). We subsequently further filtered out species that are not considered freshwater fish based on the species list from Humphries & Walker (2013) and expert opinion.

To address the gaps in these databases due to the scattered nature of occurrence data in the

literature, we conducted a manual search for any peer-reviewed articles and government reports, consultancy reports, and reports from non-profit organizations. We first filtered out islands that do not have freshwater sources using two remoting sensing databases from the Australian government (Geoscience Australia), National Surface Hydrology Database and Digital Earth Australia Waterbodies v3.0 (Crossman, 2015; Dunn, 2024). After obtaining the list of islands that have freshwater sources (n=567), we proceeded to a manual search through grey literature online. We used Google Incognito Mode as the platform of search to prevent previous searches from influencing the search results. We used the keywords “freshwater”, “fishes”, “fish”, “frogs”, “amphibian”, “island”, in addition to the names of the island as the keywords of search. We gathered comprehensive present-absence data for frogs and freshwater fishes on Australian islands, encompassing exotic, native, and threatened species. To address problems raised by sampling biases in subsequent statistical analyses, we also recorded whether the data collected from our literature search was derived from a survey targeted towards amphibians or freshwater fishes, or if it was an incidental record.

In addition to the presence-absence of each species, we included their pertinent life history and status information of each species, including IUCN status, origin (native or exotic to Australia), and for fishes their life history trait (obligate freshwater, diadromous or euryhaline). Life history trait information was obtained from (Allen et al., 2002) and following expert opinion. In this study, freshwater species broadly included obligate freshwater, diadromous, and euryhaline species. Furthermore, we incorporated physical characteristics of each island from the IOTAS database into the new database, such as latitude, area (in squares kilometers and hectares), and distance to the mainland (in meters and kilometers; (Commonwealth of Australia 2015; Baxter et al., 2021). The climate of each island was also incorporated using the ABCB Climate Zone Map from the Australian Government. Climate was categorized into eight climate zones defined by the National Construction Code (NCC) of Australia.

2.2 Data Analysis

To account for large variations in climate of the islands, we generated continuous climatic variables instead of using the categorical NCC climate zones. We achieved this by generating a center point for each island and subsequently extracted all 19 climate variables (BIOCLIM) from WorldClim (Hijmans et al., 2005) that intersects the center point. We reduced the dimensionality of the 19 climatic variables using a principal component analysis using the *prcomp* function in the *stats* package in R. We then visualized the results with respect to the first two principal components with a biplot using the *fviz_pca_biplot* function in the *factoextra* package in R (Kassambara & Mundt, 2017). We extracted the scores of these principal components for each island and included them as climatic predictors in the subsequent regression model.

To assess how island characteristics influence species' richness, we used multiple linear regression models for fishes and frogs. We modeled island factors including island area, isolation (distance from mainland), and climate (PC1 & PC2) with species richness using a negative binomial generalized linear model (GLM) (*glm.nb* function in R package *MASS*(67)). This analysis was conducted in two parts for each group: first, on islands where dedicated survey(s) were conducted; and second, on islands where no dedicated surveys were conducted. This addresses the bias that islands that had dedicated amphibian or freshwater fish surveys conducted would have more comprehensive records of species, thus artificially inflating species richness. We also excluded oceanic islands from our analysis despite these islands being legally part of Australia, as they have different evolutionary histories compared to continental islands. Island biogeographic patterns of fauna on oceanic islands should not be treated and compared in same way as the continental islands (Cáceres-Polgrossi et al., 2024).

We further assessed how island characteristics would affect the proportion of obligate freshwater species that occur on islands (number of obligate freshwater fish species/ total number of freshwater fish species). We modeled island factors including island area, isolation, and climate (PC1 & PC2) with the proportion of obligate freshwater species richness using a binomial logistic regression model (*glm* function in R package *stats*).

We checked for collinearity between predictor variables for all models by assessing their variance inflation factors (VIF) using the *car* package in R. Only predictor variables with VIF of less than 5 were included in the final analysis. To check for model assumptions, we used the function *simulateResiduals* from the package *DHARMA* to check for deviated residuals. We also used the function *testZeroInflation* to check for zero inflation. We conducted all data processing in the R environment (version: 0.98.1103 <https://www.r-project.org>).

3 Results

3.1 Overall distribution of amphibians and freshwater fishes

We found that 567 islands out of the 9285 islands had ephemeral or perennial freshwater sources. Among these islands, 197 islands (35%) had either amphibians, freshwater fishes, or both recorded on them. Amphibian richness on islands ranged from one to 25 species while freshwater fish richness ranged from one to 28 species. K’gari had the highest combined amphibian and freshwater fish richness (47 species), followed by Groote Eylandt (43 species) and Curtis Island (43 species). Among the amphibians and freshwater fishes recorded, 14 were threatened (Critically Endangered, Endangered, or Vulnerable) and 11 were exotic (Table 1). Freshwater fishes had a noticeably higher proportion of threatened species (13%; 12 species) than amphibians (2%; two species) despite having fewer total species richness. Similarly, freshwater fishes also had a noticeably higher proportion of exotic species (9%; nine species) than amphibians (2%; two species) despite having fewer total species richness. A larger proportion of amphibian occurrences came from non-targeted sampling methods compared to the occurrences of freshwater fishes. Amphibians were recorded on 176 islands, 67 of which had targeted amphibian surveys conducted. Freshwater fishes were recorded on 84 islands, 64 of these islands had targeted freshwater fish surveys conducted on them.

We found 102 frog species from six families that occurred on Australia’s islands (Figure 1). Nearly half were Australo-Papuan treefrogs (Pelodryadidae; 48 species), while the second most represented family were the Australian water frogs (Myobatrachidae; 30 species) (Figure 1).

Two amphibian species recorded were assessed as Vulnerable by the IUCN red-list, four species were Near Threatened, 94 species were Least Concern, one species was Data Deficient, and three species were not assessed. The cane toad (*Rhinella marina*) and Asian common toad (*Duttaphrynus melanostictus*) were the only exotic species that occurred on the islands, the cane toad being the second most widespread species on islands (on 65 islands), after the green tree frog (*Litoria caerulea*; on 69 islands), while the Asian common toad was recorded only on Christmas Island, an oceanic island >1,500km away from mainland Australia. Other oceanic islands with amphibian occurrences were Norfolk Island and Lord Howe Island, both islands had two amphibian species that occurred on them, including the green tree frog which was found on both islands. Despite their occurrence on oceanic islands, the majority of amphibian occurrences were clustered on continental islands in Southeast Queensland and North Queensland (Figure 2). Islands with the highest levels of richness were in these clusters, such as Curtis Island which had the most amphibian richness recorded (25 species), followed by North Stradbroke Island (23 species) and Groote Eylandt (22 species) (Table. 2).

We found 263 fishes that occur in the freshwater or estuarine habitats on Australia's island. After filtering for freshwater fishes, we found 95 species from 33 families (Figure 1). Fifty-five fishes were obligate freshwater species, 21 were euryhaline species, and 19 were diadromous species. Of all the native freshwater fishes recorded, one species was Critically Endangered, seven were Endangered, three were Vulnerable, three were Near Threatened, 76 were Least Concern, three were Data Deficient, and three were not assessed. Among the nine exotic species, five of them were live bearers (Poeciliidae). The oceanic Christmas Island had the highest number of exotic species, including four live bearers and a cichlid (*Oreochromis* sp.), which comprised all recorded freshwater fishes on the island. Other oceanic islands with freshwater fishes recorded include Norfolk Island, where two poecilids and a freshwater eel species (*Anguilla australis*) were recorded, and Lord Howe Island, where three native diadromous fishes were recorded (*A. australis*, *A. reinhardtii*, *Galaxias maculatas*). However, *G. maculatas*

was not recorded in the most recent survey in 2017 (Reader et al., 2018). Overall, freshwater fish occurrences were clustered on continental islands along the east coast of Queensland, north Queensland, Northern Territory, and the north of Western Australia (Figure 3). Islands with the highest levels of richness were in these clusters, such as K'gari with the most freshwater fishes recorded (28 species), followed by Groote Eylandt (23 species) and North Stradbroke (20 species) (Table. 3).

3.2 Drivers of amphibian and freshwater fishes richness

We reduced the dimensionality of the 19 climatic variables into two principal components. The first and second principal components explained 60.8 % and 19.4 % of the climatic variation respectively. Higher PC1 score corresponded to cooler temperatures, which tended to be associated with high annual mean temperature (bio1), high minimum temperature of coldest month (bio6), high mean temperature of warmest quarter (bio10), high mean temperature of coldest quarter (bio11), high precipitation seasonality (bio15), all of which had absolute loadings greater than 0.27 (Figure 3). Higher PC2 scores corresponded to a more humid climate with low temperature variability, including low mean diurnal range (mean of monthly (max temp - min temp); bio2), low temperature annual range (bio7), high annual precipitation (bio12) and high precipitation of warmest quarter (bio18), all of which had absolute loadings greater than 0.35 (Figure 4).

Using regression analysis, we found that on islands where targeted amphibian survey(s) were conducted (n=67), isolation was negatively correlated with amphibian richness (Estimate = -9.266e-03, $z = -2.263$, $p = 0.0236$) while humid climate and low temperature variability had positive correlation with amphibian richness on islands (PC2: Estimate = 1.409e-01, $z = 2.663$, $p = 0.0078$) (Figure 5) and the area of the island had no significant correlation with amphibian richness. On islands where targeted amphibian survey(s) were not conducted (n=105), isolation (Estimate = -7.272e-03, $z = -1.721$, $p = 0.0852$) and island area (Estimate = 1.727e-05, $z = 1.91$, $p = 0.0565$) were nearly significant in influencing amphibian richness, while climate had no

significant correlation with amphibian richness. Building upon the results from surveyed islands, we identified five of the closest islands to the mainland that have not been subjected to targeted surveys for amphibians (Table 4).

We found that on islands where targeted freshwater fish survey(s) were conducted (n=61), the island's area was positively correlated with freshwater fish richness (Estimate = $5.12e-06$, $z = 2.49$, $p = 0.0128$) (Figure 5), while isolation and climate had no significant correlation with freshwater fish richness. For the same model where we included only obligate freshwater fish, we obtained similar results where only area was positively correlated with richness of freshwater fishes (Estimate = $8.190e-06$, $z = 2.204$, $p = 0.0275$) on islands with targeted fish surveys. On islands without targeted fish surveys (n=15), none of the island characteristics were significantly correlated with freshwater fish species richness on islands. In addition, we found that both climate variables were nearly significantly correlated with the proportion of obligate freshwater fish on islands (PC1: Estimate = $-1.234e-01$, $z = -1.633$, $p = 0.09627$; PC2: Estimate = $3.051e-01$, $z = -1.959$, $p = 0.05015$). Building upon the results from surveyed islands, we identified five of the largest islands that have not been subjected to targeted surveys for freshwater fishes, including their respective PC scores (Table 5).

4 Discussion

This study helps to fill major knowledge gaps in our understanding of the distribution and drivers of richness of amphibians and freshwater fishes on islands by creating and studying the first specific database of occurrences of amphibians and freshwater fishes on all Australian islands. By combining extensive primary and grey literature sources with existing databases such as ALA, further integrated with multi-layer spatial information, we aimed to provide large-scale and comprehensive data important for informing conservation decisions and to providing a baseline for future studies on phylogeny and spatial prioritization.

Here we show both groups' diversity hotspots on islands were generally congruent to their known mainland hotspots (Knight & Tyler, 2020; Unmack, 2001). Factors that shaped species

richness on islands were partially in line with the classic island biogeography theory (MacArthur & Wilson, 1963, 2001). Islands closer to the mainland that have a more humid climate and lower temperature variability hosted higher amphibian richness, which matches the general environmental requirements of amphibians. Larger islands hosted higher freshwater fish richness potentially due to greater habitat diversity and resource availability.

The paucity of amphibian and freshwater fish records on islands with freshwater sources could be due to unsuitable habitats or limited sampling efforts on these islands. While the Digital Earth Australia Waterbodies included water bodies larger than 2,700 square meters that were present for more than 10% of the time, it could include ephemeral freshwater sources that were dry for almost 90% of the year. To survive in such ephemeral habitats, amphibians and freshwater fishes usually require special adaptations to avoid desiccation (Kerezszy et al., 2017; Walls et al., 2013). However, the lack of freshwater fauna records could also be due to the lack of sampling effort. For instance, only 67 of the 176 islands with amphibian occurrences had targeted amphibian surveys, highlighting the overall lack of dedicated surveys on islands where amphibians were already known to exist. For freshwater fishes, while most islands with freshwater fishes recorded also had targeted surveys conducted, this does not indicate that freshwater fishes were sampled comprehensively. Freshwater fishes may be less represented in citizen science than frogs (Feldman et al., 2021), potentially due to lower detectability as the latter produce vocalizations during mating seasons which could be recorded and uploaded to citizen science platforms (Rowley et al., 2019). In contrast, detecting fish traditionally requires dedicated methods such as snorkeling, electrofishing, or netting (Gundelund et al., 2021; Portt et al., 2006), which likely resulted in fewer citizen science records compared to frogs. This emphasizes the need for more systematic and targeted surveys to record the distribution of freshwater fishes, which may be underrepresented in current data.

4.1 Amphibian occurrences on islands

Amphibians were highly represented on islands, comprising nearly half of all species across Australia (~230 species). The hotspots of amphibians on continental islands corresponded closely

with hotspots in mainland Australia, including the north of Northern Territory, Cape York Peninsula of northern Queensland, the extreme southwest of Western Australia, and the south-east Australia. The overlap in hotspots could be due to similar ecological conditions of the island to the mainland, where the island was able to sustain the mainland amphibian's richness. The most dominant family on islands (Pelodyadidae) is ecologically and morphologically diverse, occupying different niches (Knight & Tyler, 2020). On islands the Australo-Papuan treefrogs were only represented by *Litoria* spp and *Cyclorana* spp, including both terrestrial and arboreal species. The second-most represented family is Myobatrachidae which is endemic to Australia. Of all Australian amphibian families, Myobatrachidae has the greatest diversity in life history traits, ranging from aquatic to direct development (Anstis, 2018). Their diverse life history traits, hypothesized to be evolving towards being direct developers (Anstis, 2018), potentially contributed to their success in colonizing or surviving on islands.

The two Vulnerable amphibian species we found—southern bell frog (*Litoria raniformes*) and wallum sedge frog (*Litoria olongburensis*)—both face threats including chytrid fungus, habitat degradation and invasive species (Geyle et al., 2021; Gillespie et al., 2020; Wassens, 2008). Both species can also be found on mainland Australia, however this does not diminish the conservation significance of their populations on islands. In fact, a considerable portion of their populations may reside exclusively on islands, where levels of threat could potentially be higher than the mainland (Russell & Kueffer, 2019; Tye et al., 2018), and or they act as important refuge populations (Mills et al., 2004). The island populations could also represent cryptic species yet to be formally described (Parkin et al., 2024). For example, scarlet-sided pobblebonk (*Limnodynastes terraereginae*) was initially believed to occur on K'gari, North Stradbroke Island (Minjerribah) and Whitsunday Islands. However, recent genetic analysis revealed that *Lim. terraereginae* is a cryptic species, and the individuals found on these islands belong to *Lim. grayi*, a newly described species (Parkin et al., 2024).

The high number of occurrences of cane toads on islands is concerning given their well-

documented impact on native wildlife (Shine, 2010). Cane toads (*Rhinella marina*) not only compete with native amphibians and fishes for food and breeding sites, but their toxicity throughout all life-stages poses significant threats to a range of native predators (Burnett, 1997; Doody et al., 2021). Some native freshwater fishes were known to die from eating eggs and tadpoles of toads in captivity (Greenlees & Shine, 2011), however the extent of this interaction in the wild is unknown. Moreover, the recorded number of exotic amphibian species on Australian islands likely underestimated the true extent of amphibian invasions. Amphibians that are native to specific regions of mainland Australia could act as invasive species when introduced to other parts of the continent, including islands (Plenderleith et al., 2015). For example, the green tree frog (*Litoria caerulea*) and bleating tree frog (*Litoria dentata*), although native to many parts of mainland Australia, has established populations on islands where it did not historically occur such as oceanic islands like Norfolk Island and Lord Howe Island via anthropogenic means (McCormack & Coughran, 2009; Plenderleith et al., 2015). Therefore, even “native” species that were found on these islands likely resulted by human-mediated introductions. Due to their regional nativeness, these species are often overlooked in assessments of invasiveness, making them “silent” invaders that are harder to detect and manage.

4.2 Freshwater fish occurrence on islands

Areas of highest freshwater fish richness were generally congruent with mainland hotspots (Unmack, 2001). Their presence on islands, like amphibians, could be due to the island retaining the mainland assemblage from the most recent period of connectivity during low sea-levels, or the fishes colonizing it after isolation (primarily diadromous or euryhaline species). The continental part of Cape York Peninsula had the highest recorded richness in freshwater fishes, however there were only moderate richness on its islands. This could be due to the generally small island size in Cape York Peninsula, where freshwater fish richness was limited by the availability and diversity of freshwater habitats on the island.

Several families of freshwater fishes were particularly prominent on islands, potentially

attributable to their life history traits, adaptability, and overall diversity in mainland Australia. Notably, the sleepers (Eleotridae), rainbowfishes (Melanotaeniidae), galaxids (Galaxiidae), and gobies (Gobiidae) were well-represented on the islands (Figure 1). Many species of sleepers, galaxids and gobies are not obligate freshwater species, tolerating a certain degree of salinity or being diadromous (McDowall, 2004). These traits facilitate their dispersal across marine barriers, allowing them to colonize islands more readily than obligate freshwater species. Rainbowfishes (Melanotaeniidae), although not diadromous, are diverse on the mainland and exhibit remarkable adaptability to different freshwater habitats. Therefore, a high diversity of rainbowfish still persist on islands after being separated from the mainland.

Several factors potentially contributed to the higher proportion of threatened freshwater fishes than amphibians found on islands, but most notably, geographical isolation is likely important (Angermeier, 1995; Lintermans et al., 2020). Non-migratory freshwater fishes, in particular, are highly vulnerable to localized threats due to their limited ability to respond to imminent danger (Garnett et al., 2022). For instance, the barrow cave gudgeon (*Milyeringa justitia*) is found exclusively in aquifers accessed via freshwater bore holes on Barrow Island, where its limited habitat is threatened by water abstraction, sedimentation and water pollution from mining, leading to its critically endangered status (IUCN, 2023; Larson et al., 2013). Other examples include the Oxleyan pygmy perch (*Nannoperca oxleyana*) and ornate rainbowfish (*Rhadinocentris ornatus*), both highly restricted to within southeastern Queensland, which were also classified as Endangered and Vulnerable by the IUCN red list (IUCN, 2023). Non-obligate freshwater species may have higher mobility in responding to localized threats, however they face different threats such as the blockage of ocean-freshwater linkages that could be detrimental to their reproductive cycles involving movement (Beger et al., 2010).

The introduction of invasive freshwater fish species poses a significant threat to native island ecosystems. Among the nine exotic species recorded, five were livebearers from the family Poeciliidae, known for their rapid reproduction and adaptability which contributes to them being

successful invaders worldwide (Deacon et al., 2011). The oceanic Christmas Island presents a stark example, where the majority of recorded freshwater fishes are exotic species, including four livebearers and a cichlid (*Oreochromis* sp.). The complete dominance of invasive species on Christmas Island suggests that native freshwater fishes were either absent or have been entirely displaced. In contrast, another oceanic island, Lord Howe Island, with only native diadromous species. Invasive freshwater fishes not only compete and predate on native freshwater fishes, but are known to suppress native amphibian growth (Falaschi et al., 2020). The high diversity of alien fishes found on islands raises conservation concerns for all freshwater fauna in the same habitat.

4.3 Influence of island characteristics on amphibian diversity

On islands where targeted amphibian surveys were conducted, islands close to the mainland hosted more species. This pattern aligns with the classic island biogeography theory which states that island species richness declines with increasing isolation due to reduced immigration rates (MacArthur & Wilson, 2001). Because amphibians typically have limited dispersal abilities across saltwater barriers (Duellman & Trueb, 1994), islands closer to the mainland were more accessible for colonization events (e.g. hitch-hiking on floating vegetation or debris; (Vences et al., 2003), leading to higher species richness. It is also possible that islands closer to the mainland were more likely to retain mainland amphibian richness and assemblages following geographical isolation. Islands with high precipitation and climatic stability (positive PC2 value) tended to support more amphibian species. Amphibians are highly water-dependent, relying on moist environments for physiological processes such as cutaneous respiration and for breeding (Duellman & Trueb, 1994). Therefore, these findings are consistent with the ecological requirements of amphibians, highlighting the importance of sufficient rainfall, high humidity, and stable temperatures for their persistence and reproductive success.

However, the lack of correlation between amphibian richness and temperature is somewhat counterintuitive, given the general trend that species richness is higher closer to the tropics where temperatures are typically warmer (Harvey et al., 2020; Willig et al., 2003). This

discrepancy could potentially be explained by a combination of ecological and biogeographical factors. Warmer climates in the context of Australia's islands could be associated with high evaporation rates and less reliable water sources, which increases the risks of desiccation. Moreover, some species may possess physiological and behavioural adaptations that enable them to thrive in cooler environments (Feder & Burggren, 1992). These adaptations may allow them to exploit niches that are less accessible to species in warmer regions, contributing to relatively high local richness in these environments.

Our finding that island area did not have a significant effect on amphibian richness in this subset of islands contrasts with the species-area relationship commonly observed in island biogeography, where larger islands tend to support more species due to greater habitat diversity and resource availability (MacArthur & Wilson, 2001). For amphibians, however, factors such as habitat quality, availability of freshwater, and microclimatic stability may be more critical than island size (Hortal et al., 2009). Smaller islands with suitable freshwater sources, especially the ones closer to the mainland, may still retain amphibian populations that originated from the mainland, while habitat quality and climatic suitability may outweigh the benefits of larger island area in determining amphibian diversity.

On islands where no targeted amphibian surveys were conducted, sampling biases likely contributed to the correlation between richness and island size and distance from the mainland. Records in this subset, as far as we know, were derived from incomprehensive sampling methods, such as incidental records or data from citizen science platforms such as iNaturalist (Roger et al., 2023). These data are often biased towards more accessible locations that are frequently visited by humans, leading to underrepresentation of more remote or less accessible areas (Geldmann et al., 2016). In the context of our study, islands that are larger and closer to the mainland are more likely to be visited by humans, hence were more subjected to opportunistic sampling, which could inflate the observed richness of those islands.

4.4 Influence of island characteristics on freshwater fishes richness

On islands where targeted freshwater fish surveys were conducted, larger islands supported significantly more freshwater fish species. This pattern aligns with the classic island biogeography theory which states that island species richness tends to increase with island size due to greater habitat diversity and resource availability (MacArthur & Wilson, 2001). Larger islands are more likely to have a variety and permanency of freshwater habitats, including streams, ponds, and wetlands, which can support a greater diversity of fish species. Islands that exhibited the highest freshwater fish richness were large islands such as K'gari, Groote Eylandt, and North Stradbroke Island (Table 3), all of which possess substantial freshwater habitats, including lakes, streams, and wetlands, which provide suitable environments for a variety of freshwater fishes (Hammer et al., 2021; Marshall et al., 2011; Yule, 2019).

Isolation may not play such a crucial role in determining freshwater fish richness on islands, as it did for amphibians. Geological events such as past land connections during lower sea levels and bathy river connections may have increased connectivity between island freshwater systems and the mainland, facilitating the dispersal of freshwater fishes (Unmack, 2001). The non-significant effect of isolation can also be potentially attributed to the presence of euryhaline and diadromous species, which can tolerate a range of salinities and migrate between marine and freshwater environments. The marine phase of diadromous fish life cycles facilitates dispersal via ocean currents, enhancing their likelihood of establishing populations in island freshwater habitats (McDowall, 2004). This is particularly evident in amphidromous fish species, such as gobies in the subfamily Sicydiinae and catadromous species like members of the genus *Kuhlia*, which are frequently encountered on islands (McDowall, 2004). These species are better suited to overcome the dispersal barriers imposed by high salinity, allowing them to colonize islands regardless of their distance from the mainland.

If dispersal abilities were solely responsible for the distributional patterns, we would expect isolation to be negatively correlated with richness on islands considering only obligate freshwater fishes, which we assume have limited capacity to disperse across saltwater.

Additionally, we might anticipate the proportion of obligate freshwater fishes relative to non-obligate fishes (euryhaline and diadromous species) would decrease further away from the mainland. Interestingly, our results were counterintuitive: island area remained the only significant predictor, while the proportion of obligate freshwater fishes was nearly significant in negatively correlating with climate variables (PC1 and PC2).

There are two potential explanations for this phenomenon. First, the current species present on islands may be remnants of mainland populations that persisted after the islands were isolated from the mainland. In this scenario, fishes did not disperse from the mainland to colonize the islands but were already present when the islands became isolated. Second, distance from the mainland may not play an important role in geographical isolation for all freshwater fishes, possibly due to the inherent higher salinity tolerance of many Australian freshwater fish species (although most cannot survive full salinity). Unsubstantiated beliefs claim most Australian fish families are secondarily freshwater (Myers 1938) and moved inland only in the last few million years (Myers, 1938; Unmack, 2001). Consequently, numerous fish species may still retain marine traits inherited from their ancestors, giving them an advantage in colonizing islands (Augsburger et al., 2017; Franklin & Gee, 2019). Historical geological events have reduced the barriers imposed by marine habitats on fish dispersal. In this context, parameters such as maximum sea depth, and the channel flow rate between the island and mainland could be a better parameter at representing isolation than distance from mainland. These two explanations are not mutually exclusive as new species from the mainland could still colonize islands with existing fish populations.

Unlike amphibians, the overall diversity of freshwater fishes on islands was not significantly influenced by the island's climate. However, when examining community composition, we found that the proportion of obligate freshwater fishes on islands was significantly correlated with high temperatures (negative PC1), low precipitation and high temperature variability (negative PC2), represented mainly by islands in Western Australia and

the Northern Territory. This pattern may be attributed to a relative decrease in diadromous or euryhaline fishes in such climates, however substantial knowledge gaps persist regarding the global distribution of diadromous and euryhaline fishes.

4.5 Conservation Implications

This study provides insights into the richness and distribution of freshwater fishes and amphibians on Australian islands, highlighting key factors influencing their occurrences. Our findings have important implications for the conservation of the two groups, particularly in the context of habitat conservation, protection of threatened species, management of invasive species, and created a baseline database for future work on conservation prioritization. Protecting islands close to the mainland could be effective in conserving amphibian richness on islands, while conserving diverse freshwater habitats on islands could be effective for conserving freshwater fish richness. Our study identifies key knowledge gaps in amphibian and freshwater fish surveys on Australian islands, highlighting islands with potential for high species richness that haven't had a targeted survey conducted (Table 4, 5; Supplementary Material). Assuming amphibian richness increases on islands closer to the mainland and freshwater fish richness increases on larger islands, prioritizing these sites for future surveys will address gaps in species occurrence data and inform more accurate conservation strategies and spatial prioritization.

Extraction of freshwater sources on islands should be carefully monitored to prevent over-exhaustion of the resources (Lehner & Döll, 2004), which could degrade the habitat of threatened species such as the barrow cave gudgeon (Larson et al., 2013). It is also important to maintain ocean-freshwater linkages for diadromous species (Pelicice et al., 2015; Su et al., 2021).

Amphibians and obligate freshwater fish are highly dependent on wet climate. As climate change alters precipitation patterns and increases temperature extremes, amphibian populations on these islands are likely to face heightened risks of habitat loss and population declines (Hof et al., 2011). Tims et al. (2023) reported that fishes in higher latitudes, particularly those that are already threatened, face increased risk of climate-driven habitat degradation and loss. Tims and Saupe

(2023) further predicted that climate change will drive a poleward shift in the distribution of Australian freshwater fishes, though their data primarily concern mainland populations rather than island occurrences. If these predictions hold true, obligate freshwater fishes on islands may be at even greater risk, as their isolation and geographic fixation limit opportunities for migration to more suitable habitats in response to changing climate conditions.

Invasive species pose a significant threat to global biodiversity, ranking as the second biggest threat, particularly to island ecosystems (Allendorf & Lundquist, 2003). In freshwater environments, invasive species are known to predate upon them, outcompete native species, and transmit diseases (Britton, 2023; Cucherousset & Olden, 2011; Kiruba-Sankar et al., 2018). Presently, Australia hosts 34 freshwater fish species that have established feral populations, a few of which are present on islands (Diggle et al., 2007). Notable examples include guppies (*Poecilia reticulata*), mosquito fish (*Gambusia affinis*), green swordtail (*Xiphophorus hellerii*) and Mozambique tilapia (*Oreochromis mossambicus*), all of which are notoriously invasive species with documented damages to local ecosystems (Esmaili et al., 2014; Russell et al., 2012; Shine, 2010). Research indicates that these invasive species prey upon native freshwater fauna, including amphibians and other fishes, thereby posing a significant threat to species with restricted distributions on islands (Heatwole & Rowley, 2018; Kiruba-Sankar et al., 2018; Sorensen, 2021). Of particular concern is the successful colonization of even small, remote islands such as Norfolk Island, where the number of invasive freshwater fauna surpasses that of native species (McCormack & Coughran, 2009). While most exotic freshwater fishes in Australia were introduced via aquarium trade (García-Díaz et al., 2018), it has been a growing concern that new species invade Australia via range expansion from Papua New Guinea, with Mozambique tilapia and climbing perch already recorded on northern islands of the Torres Strait (Waltham et al., 2023). To manage the impacts of invasive species, direct removal of invasive species from islands has been a successful management strategy (Saunders et al., 2010). However, this strategy has mostly been applied to every other animal except fish (Britton et al., 2011). Britton et al.

(2011) have discussed the possibility of removing invasive freshwater fauna from islands, however the lack of funding and available removal techniques remains a barrier to controlling invasive species impacts on islands (Britton et al., 2011; Leprieur et al., 2009).

4.6 Considerations and Future Directions

Several limitations must be considered when interpreting these results. (1) The heterogeneity and availability of freshwater habitats on many islands is poorly documented despite its known positive correlation with species richness in most cases (Agra et al., 2023). Although large islands with high amphibian and freshwater fish richness were documented as having stable and heterogenous freshwater habitat types, that may not represent all islands, especially islands located in drier climate. (2) We did not control adaptive radiation of freshwater fauna on islands, which could inflate the richness of species (Losos & Ricklefs, 2009). However, more than 90% of the species recorded in our database were not island endemic species, which likely limited the effect of inflation on our results. (3) Sampling biases may not be fully addressed by classifying islands into those with or without targeted surveys. We only recorded whether data was derived from a targeted survey for records collected from our online literature search. There are potentially islands where targeted surveys were conducted of which we obtained the data from ALA but were not found during the manual literature search. These islands would not be treated as islands with targeted surveys in our analysis. This is a concern considering the large numbers of islands that potentially were in this category, notably for amphibians. Furthermore, for islands where targeted surveys were conducted, the differences in sampling methods and sampling effort were not accounted for, which would affect the comparability of the data collected from the islands. (4) Some species on islands could represent cryptic species, while the lack of taxonomical or phylogenetic research on island populations could lead to the overlooking of island endemic species that are yet to be classified.

Despite the limitations, our research has created an important resource for future research and provided important insights into the patterns and distribution of amphibians and freshwater

fishes on Australia's islands. Future studies could build on our findings by conducting targeted field sampling for noted gaps, and phylogenetic analyses to compare island populations with their mainland counterparts. This can provide insights into evolutionary divergence and potential speciation events driven by geographic isolation. These studies could help identify unique evolutionary lineages on islands that could potentially be a concern of conservation. Additionally, conservation efforts should be directed towards islands with high species richness, particularly those supporting a high proportion of threatened species. Identifying conservation priorities will be crucial for mitigating the impacts of habitat loss, invasive species, and climate-driven changes on island biodiversity.

5 Conclusion

By conducting a manual literature search online in addition to collating existing databases, we created the first database documenting the Occurrences of Freshwater Fishes and Frogs on Australian Islands. The database encompasses records of 102 amphibian and 98 freshwater fish species: 55 fishes were obligate freshwater species, 21 were euryhaline and 19 were diadromous. Amphibians were recorded on more islands and exhibited greater richness, likely due to limited survey efforts for fishes. Despite this, fishes had a higher proportion of threatened and exotic species. Using regression analysis we explored how island area, isolation (distance from mainland in kilometers), and climate affect species richness. We found that both amphibians and freshwater fish richness were higher on islands with wet climates. Islands closer to the mainland hosted higher amphibian richness, likely from retaining mainland amphibian assemblages after isolation, or being more easily colonized. In contrast, larger islands hosted more freshwater fishes, where diverse habitats were likely to sustain more species. Isolation had no significant effect on freshwater fish richness on islands, potentially due to geological events that facilitated their colonization of islands, or most species were already present on the land masses prior to isolation. Our study lays important groundwork for conservation by summarizing the distributional patterns of island-dwelling amphibians and freshwater fishes in Australia. By further analyzing the

potential drivers of such patterns, we provide a reference for follow-up studies on their phylogeny. This research also reveals potential hotspots of extinction risk and provides a baseline for future spatial prioritization work.

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Data Availability

The occurrences of freshwater fishes and frogs of Australian islands database is available in the Supporting Information.

Statements and Declaration

The authors have no relevant financial or non-financial interests to disclose. The authors declare no competing interests.

Figure Legend

Figure 1 Total number of species (n) of amphibians and freshwater fishes recorded on Australian islands, including the number of species per family and its percentage (%) relative to all species.

Figure 2 Map showing the number of amphibian species found on each island.

Figure 3 Map showing the number of freshwater fishes found on each island.

Figure 4 A biplot from principal component analysis of 19 bioclimatic variables (bio1-bio19) from WorldClim on all Australian islands where amphibians or freshwater fishes were recorded (n=197). Islands were colored by the Australian state they were in.

Figure 5 The effect of island variables on amphibian and freshwater fishes richness on Australian islands. The black dots represent individual islands, and the grey shaded area represents the 95% confidence interval for the regression. **(a)** The effect of isolation (distance from mainland in square kilometers) on amphibian richness (n=67). **(b)** The effect of PC2 (humid climate with low temperature variability, associated with bio2, bio7, bio12 and bio18) on amphibian richness (n=67). **(c)** The effect of island area (hectares) on freshwater fish richness (n=61).

Figure 1

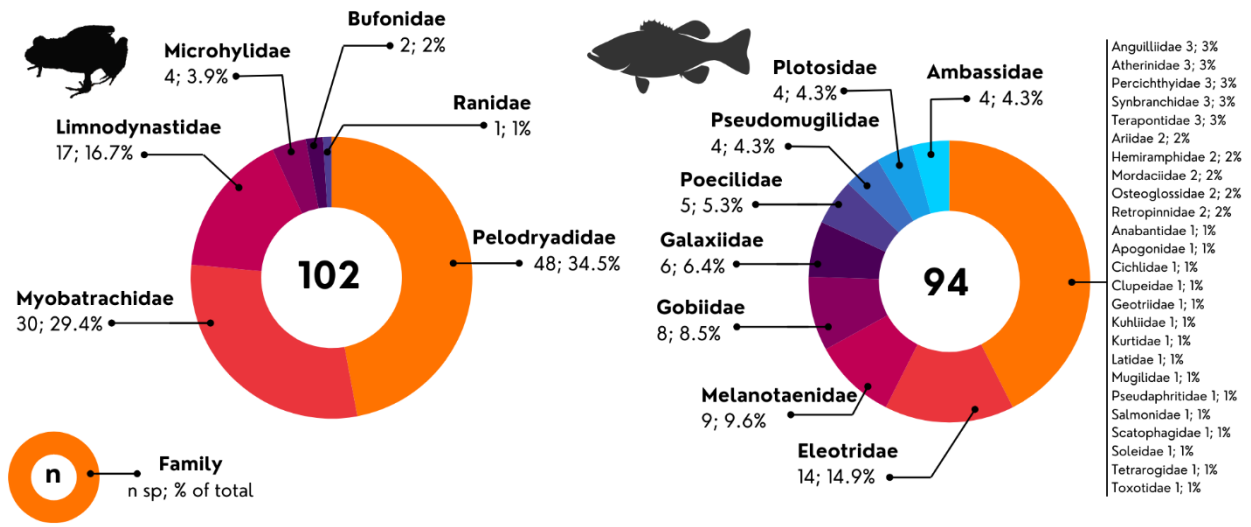


Figure 2

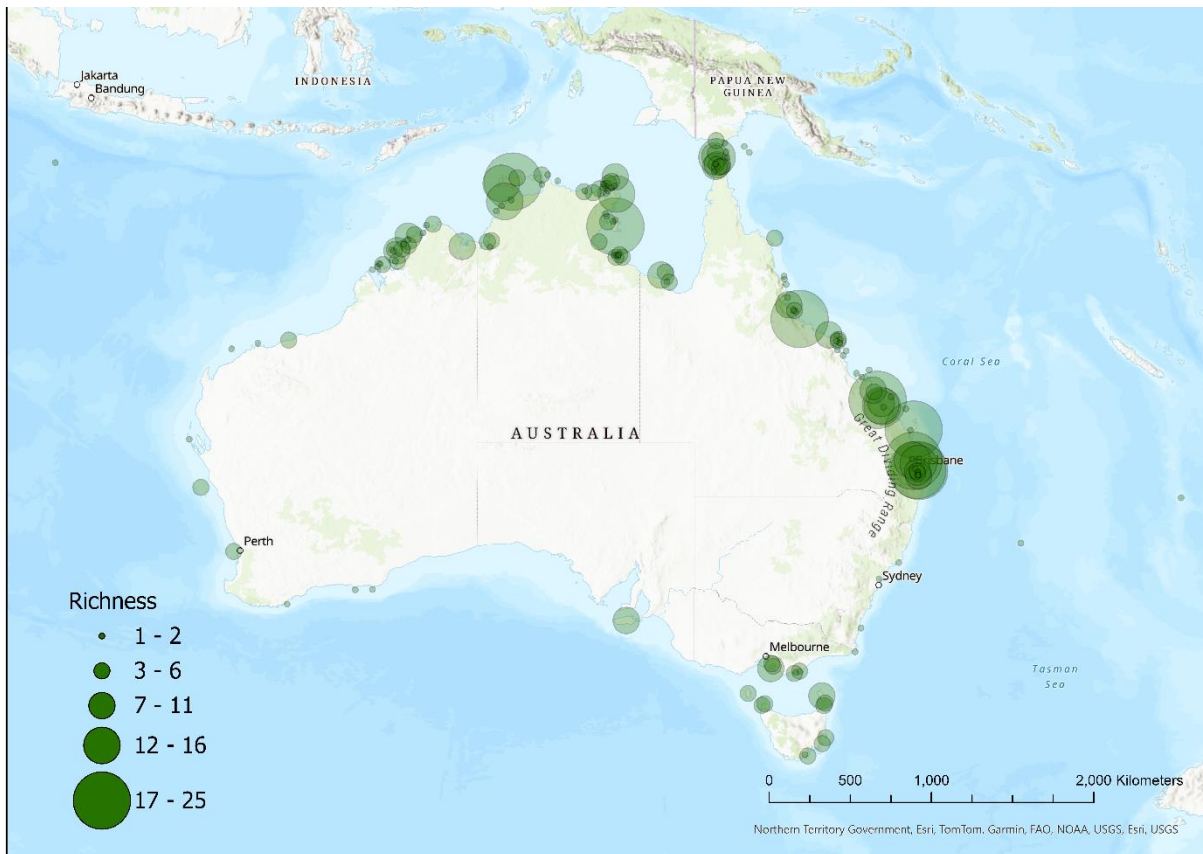


Figure 3

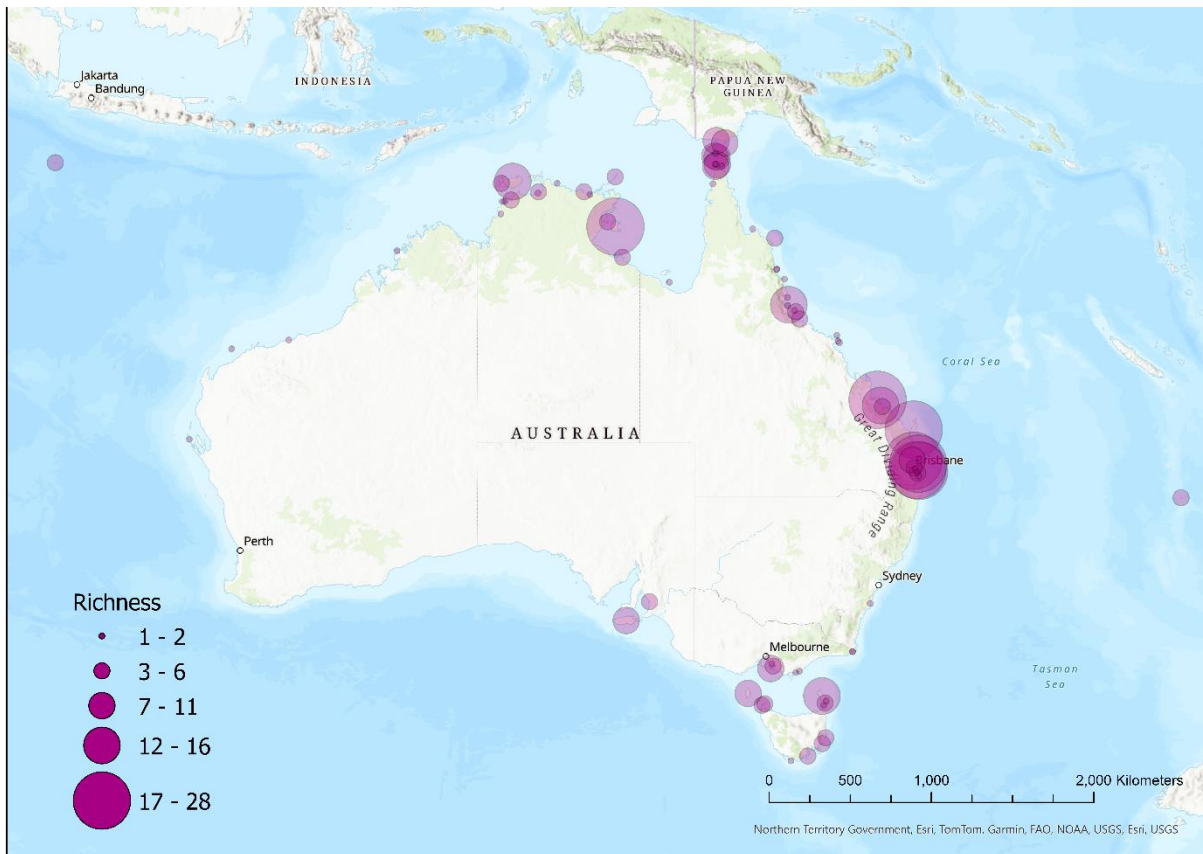


Figure 4

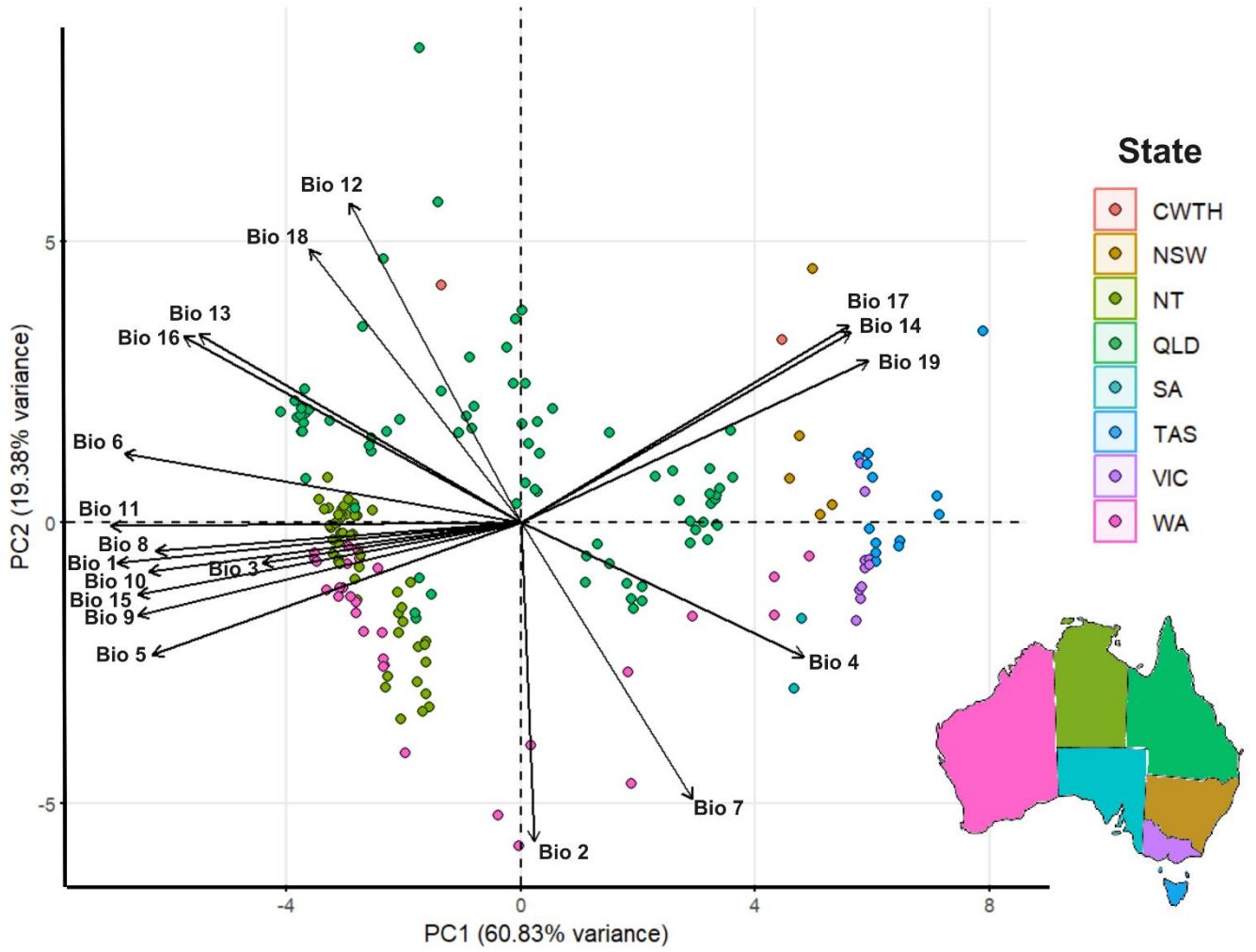


Figure 5

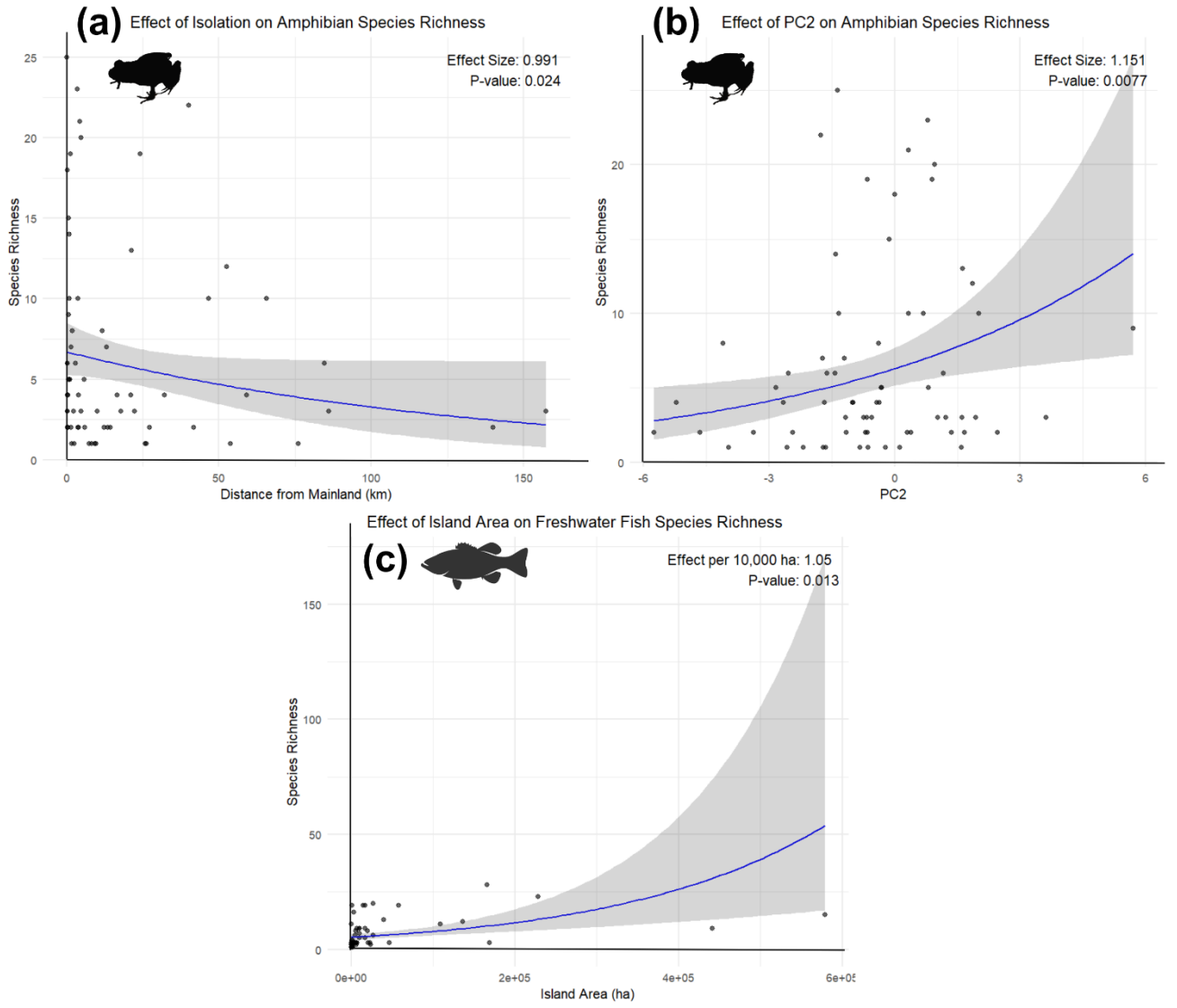


Table 1

Summary of the total number of amphibian and freshwater fish species occurring on islands (N total), including the number of exotic species (N exotic) and their conservation status based on the IUCN Red List. The categories include Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Assessed (NA).

	Amphibians	Freshwater Fishes
Total number of species	103	95
Total number of exotic species	2	9
IUCN Status		
CR	0	1
EN	0	7
VU	2	3
NT	4	2
LC	95	76
DD	1	3

NA

1

3

Table 2

Top 10 Australian islands with the highest amphibian richness, including exotic and threatened species counts, state, tenure, longitude, latitude, distance from mainland in kilometers (km), area in hectares (ha), and climate zone.

Island Name	Richness	Exotic	Threatened	State	Tenure	Longitude	Latitude	Distance(km)	Area(ha)	Climate Zone
Curtis Island	25	1	0	QLD	Mixed tenure	151.15	-23.61	0.13	57646	2
North Stradbroke Island	23	1	2	QLD	Mixed tenure	153.45	-27.54	3.56	26949	2
Groote Eylandt	22	1	1	NT	Aboriginal freehold - inalienable	136.64	-14.02	40.07	228518	1
Magnetic Island	21	1	0	QLD	Mixed tenure	146.83	-19.14	4.45	5066.9	1
Peel Island	20	1	2	QLD	Freehold	153.36	-27.50	4.79	520	2
Melville Island	19	0	0	NT	Aboriginal freehold - inalienable	130.96	-11.54	24.08	578577	1

K'gari	19	1	2	QLD	Conservation	153.14	-25.26	1.27	166170	2
					reserve					
Bribie Island	18	1	1	QLD	Mixed tenure	153.14	-26.99	0.26	14757	2
Bathurst Island	16	0	0	NT	Aboriginal freehold	130.32	-11.64	56.68	169318	1
					- inalienable					
Goat Island	15	1	2	QLD	Conservation	153.07	-26.96	0.68	96	2
					reserve					

Table 3

List of top 10 islands with the highest freshwater fish richness in Australia, including the island's latitude, longitude, area (hectares), distance from mainland (km), and climate zone.

Island Name	Richness	Exotic	Threatened	State	Tenure	Longitude	Latitude	Distance(km)	Area(ha)	Climate Zone
K'gari	28	1	5	QLD	Conservation reserve	153.14	-25.26	1.27	166170	2
Groote Eylandt	21	0	0	NT	Aboriginal freehold - inalienable	136.64	-14.02	40.07	228518	1
North Stradbroke Island	20	2	3	QLD	Mixed tenure	153.45	-27.55	3.56	26949	2
Bribie Island	19	3	4	QLD	Mixed tenure	153.14	-26.99	0.26	14757	2
Peel Island	19	4	2	QLD	Freehold	153.36	-27.50	4.79	520	2
Curtis Island	18	2	0	QLD	Mixed tenure	151.15	-23.61	0.13	57646	2

Moreton Island	19	1	3	QLD	Conservation	153.41	-27.15	21.23	17149	2
					reserve					
Boyne Island	16	2	0	QLD	Conservation	151.32	-23.93	0.14	3285	2
					reserve					
Melville Island	15	0	0	NT	Aboriginal	130.96	-11.54	24.08	578577	1
					freehold -					
					inalienable					
Hinchinbrook Island	13	0	1	QLD	Conservation	146.24	-18.36	0.72	39613	1
					reserve					

Table 4

List of top 5 islands closest to mainland Australia that have not been subjected to targeted amphibian surveys, including the island's amphibian richness, state, tenure, longitude, latitude, distance from mainland (kilometers), area (hectares), climate zone, and their PC values.

Island Name	Richness	State	Tenure	Longitude	Latitude	Distance (km)	Area (ha)	Climate zone	PC1	PC2
			Aboriginal Freehold -							
Howard Island	3	NT	Inalienable	135.40	-12.15	0.05	27324	1	-3.11106	-0.69487
NA	1	NT		130.33	-12.89	0.06	10	1	-3.09927	-0.74374
NT Island Number										
C033	4	NT		129.78	-14.81	0.06	1868	1	-2.2681	-2.73759
NA	1	QLD		153.08	-26.91	0.08	11	2	2.895586	0.012299
St Margaret Island	4	VIC	Conservation Reserve	146.83	-38.62	0.09	1889	6	5.805823	-1.3591

Table 5

List of top 5 largest islands in Australia that have not been subjected to targeted freshwater fish surveys, including the island's freshwater fish richness, state, tenure, longitude, latitude, distance from mainland (kilometers), area (hectares), climate zone, and their PC values.

Island Name	Richness	State	Tenure	Longitude	Latitude	Distance (km)	Area (ha)	Climate Zone	PC1	PC2
Dirk Hartog Island	2	WA	Crown leasehold	113.05	-25.79	1.51	62775	3	1.882565	-4.65187
Bruny Island	3	TAS	Mixed tenure	147.29	-43.33	1.35	35552	7	7.111917	0.460283
Augustus Island	1	WA	Aboriginal reserve	124.55	-15.36	1.588	19179	1	-3.32523	-1.19583
Clarke Island	1	TAS	Vacant crownland	148.17	-40.53	21.12	8176	7	6.068104	-0.37087
Magnetic Island	6	QLD	Mixed tenure	146.83	-19.14	4.45	5067	1	-0.07313	0.334549