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Distribution mapping of specialized amphibian species in rare, ephemeral habitats: Implications for the conservation of threatened “acid” frogs in south-east Queensland

Alannah Filer1 | Hawthorne L. Beyer2 | Ed Meyer1 | Berndt J. Van Rensburg1,3

1School of Biological Sciences, University of Queensland, St Lucia, Queensland, Australia
2Centre for Biodiversity and Conservation Sciences, School of Biological Sciences, University of Queensland, St Lucia, Queensland, Australia
3Department of Zoology, Centre for Invasion Biology, University of Johannesburg, Johannesburg, South Africa

Correspondence
Alannah Filer, Bldg 8, University of Queensland, St. Lucia, Brisbane, QLD 4072, Australia. Email: alannah.filer@uq.net.au

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Abstract
The acid frogs of eastern Australia are a highly specialized group of threatened species endemic to acidic coastal wetlands of southern Queensland and New South Wales. The distribution of these species overlaps with areas of increasing development where land-use intensification poses a significant threat. Successful conservation of these species requires that areas of high conservation value for acid frogs are properly identified and protected, particularly in south-east Queensland which supports important populations of all four acid frog species: *Litoria olongburensis*, *Litoria freycineti*, *Crinia tinnula*, and the Queensland-endemic *Litoria cooloolensis*. Species distribution modeling using rigorously vetted species occurrence data was used to identify areas of potential acid frog habitat with >89% predictive power for all species. Key predictor variables for acid frog species occurrence included: soil sandiness, vegetation, presence and/or type of wetland, and soil clay content. All species' predicted distributions occurred primarily in coastal regions, overlapping with densely human-populated areas. Our modeling and analysis of species’ distributions highlight local government areas where protection of wallum habitat is most important for the conservation of acid frogs, as well as areas of higher conservation value providing habitat for multiple acid frog species.

KEYWORDS
acid frog, amphibian, conservation, *Litoria olongburensis*, local government area, native Australian frogs, protected area, south-east Queensland, species distribution model, wallum sedgefrog

1 INTRODUCTION

Of Australia’s 240 frog species, over 90% are endemic (IUCN, 2018). A high proportion of these are considered threatened, with 47 species currently listed as vulnerable, endangered, or critically endangered by the International Union for Conservation of Nature (IUCN; Hero et al., 2006; IUCN, 2018). In Queensland, the state with the highest amphibian diversity in Australia, >25% of the 130 extant frog species are listed as vulnerable or endangered, and three have gone extinct (Department of Environment and Science, 2019; Queensland Government, 2020).
A recent analysis of global threats to species found that agriculture and aquaculture have contributed most to amphibian declines (affecting 78% of the 2,267 threatened or near threatened species), followed by biological resource use (69%), residential and commercial development (47%), invasive species and diseases (30%), and pollution (28%; Maxwell, Fuller, Brooks, & Watson, 2016). One of the major threats to frog species in this state (and other states along Australia’s eastern seaboard) is ongoing habitat loss and degradation due to human activity. Along the eastern coastline of Australia, lowland coastal wetlands providing habitat for frog species have been subject to widespread destruction and degradation as a result of urbanization, agroforestry and other development impacts (Gurran, Blakely, & Squires, 2007; Redclift, Navarrete, & Pelling, 2011). Human impacts on wetland habitat pose a particular threat in rapidly-developing coastal areas such as south-east Queensland (SEQ) where rapid population growth and urbanization continue to encroach on coastal “wallum” habitat (Hines & Meyer, 2011).

The “wallum” is an area of sand plains and dunes characterized by low nutrient acidic soils and groundwater-dependent wetlands that extends from southern Queensland into northern New South Wales (Hines & Meyer, 2011; Ingram & Corben, 1975; Meyer, Hero, Shoo, & Lewis, 2006). Wallum soils are described as being unusually oligotrophic and acidic (pH 3.4–5.5; Coaldrake, 1961; Griffith, Bale, & Adam, 2008) reflecting the geology of the region, allowing the formation of “perched” swamps and lakes containing ion-poor water with high levels of dissolved organic acids (Coaldrake, 1961; Griffith et al., 2008; Griffith, Bale, Adam, & Wilson, 2003; Simpkins, Shuker, Lollback, Castley, & Hero, 2013). While the frog fauna of these wetlands is depauperate compared with wetland habitat elsewhere, wallum wetlands do provide habitat for a unique assemblage of threatened frog species known as “acid” frogs. This includes the Wallum Sedgefrog _Litoria olongburensis_, Cooloola Sedgefrog _Litoria coolooolensis_, Wallum Rocketfrog _Litoria freycinetii_, and Wallum Froglet _Crinia tinnula_ (Meyer et al., 2006). These species are considered susceptible to a range of threatening processes, including altered water quality (in particular, increased pH or nutrient loading), exotic fish, changes in local hydrology, and colonization of disturbed wallum wetlands with elevated pH levels by closely related competitor species such as _Litoria fallax_, _Litoria nasuta_, and _Crinia parinsignifera_ (Ingram & Corben, 1975; Kikkawa, Ingram, & Dwyer, 1979; Lewis & Goldingay, 2005; Meyer et al., 2006).

Wallum wetland habitat known, or likely, to support acid frog species in SEQ has been subject to significant disturbance in the past, and is under continued pressure from development, especially near rapidly growing urban centers like the Sunshine Coast (Australian Bureau of Statistics, 2010; Maganov et al., 2003; Meyer et al., 2006; Shuker & Hero, 2012). Consequently, all acid frog species are listed as vulnerable or endangered by the IUCN (2018) and, with the exception of _L. coolooolensis_, as vulnerable under state legislation (Department of Environment and Science, 2019; Queensland Government, 1992). The wallum sedgefrog (_L. olongburensis_) is also listed as vulnerable under federal legislation (Australian Government, 1999; Department of Environment and Science, 2019; Meyer et al., 2006; Shuker & Hero, 2012).

The protection of acid frog habitat is important for the conservation of these species, particularly in areas of core habitat along the SEQ coastline (Bryan, 1973; Hines & Meyer, 2011; Meyer et al., 2006). However, existing published data on the distribution of acid frogs and habitat mapping (e.g., Meyer et al., 2006) provide limited guidance in regards to the management and effective conservation of species-specific acid frog habitat. This is important, as planning decisions made by state and local government have a significant bearing on the future conservation and management of acid frog species and their habitat, particularly in areas of high human population growth such as in SEQ. To better inform local and state government planning, and assist with efforts to conserve these species in Queensland, we undertook a review of distributional data for all four acid frog species, and developed separate models of predicted occurrence/potential habitat for each.

Here, we collate multiple sources of acid frog occurrence data, and use these data to estimate the contemporary distributions of all four acid frog species within the biologically important SEQ region, where rapid population growth and development pose a significant ongoing threat (Meyer et al., 2006; Shuker & Hero, 2012). By creating species-specific distribution models we identify key areas at a local government level for the conservation of individual acid frog species, as well as highlight areas of importance for the conservation of the acid frog species as a group. We compare these new species-specific models to the original recovery plan generic habitat association model (Figure 1; Meyer et al., 2006) in order to better understand the potential implications of pooling data among species, thereby potentially masking species differences in association with environmental variables. Finally, we examine the estimated distribution of each acid frog species in relation to land tenure to assess the potential extent of acid frog habitat occurring outside the current protected area network; drawing attention to areas vulnerable to habitat destruction and disturbance that require immediate attention from decision makers.
within relevant local government areas (hereafter referred to as LGAs).

Focusing on the appropriate scale at which conservation is likely to be implemented when relating the distribution of threatened species to relevant decision makers, as well as identifying areas in need of more effective protection, is critical for reducing the rate at which species continue to be lost. To do this, it is crucial to use contemporary data at the finest resolution available for the region (Chown, van Rensburg, Gaston, Rodrigues, & van Jaarsveld, 2003; van Jaarsveld et al., 1998). Our modeling approach, representing relevant LGAs and the most up to date and finest resolution data available, is therefore important for, and applicable to, the conservation of sensitive frog species across Australia and other areas of the world, where planning decisions by local government have a significant bearing on conservation outcomes for threatened species.

**FIGURE 1** Mapped core habitat of the wallum frog species in Queensland as of 2002. Source: Reprinted from Meyer et al., 2006. Copyright 2006 by The State of Queensland, Environmental Protection Agency. Reprinted with permission

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**2 | MATERIALS AND METHODS**

**2.1 | Species occurrence data and vetting procedure**

Queensland-wide occurrence data for all four acid frog species (\(L.\) olongburensis, \(L.\) cooloolensis, \(L.\) freycineti, and \(C.\) tinnula) were sourced from online, public access databases including the Atlas of Living Australia, New South Wales Office of Environment and Heritage (NSW OEH), and Queensland WildNet, as well as unpublished records from surveys conducted by E.M. between 1996 and 2017.

The data were rigorously vetted to remove duplicate records, records for which locality data appeared to be erroneous or grossly inaccurate, and records that did not contain enough information to adequately assess their validity (date of record and location data), in order to avoid the potential for large inaccuracies in the analysis.
As part of the vetting procedure, the identity of voucher specimens held by the Australian Museum was subject to expert verification (by A.F. and E.M.). Additional vetting of occurrence records was implemented to ensure that only contemporary records (post-1990) were used, as older records may not accurately reflect the current distribution of acid frog species. This cut-off date was selected to ensure an adequate number of data points were retained for modeling the potential distribution of each species (with between 85 and 360 records retained for each species). Records with an estimated spatial accuracy greater than 500 m were also removed as these could limit our ability to define environmental predictors of occurrence. These vetting procedures corrected numerous errors in the occurrence databases, and resulted in the removal of 150 erroneous records (~18%) from the 853 non-duplicate data records from the SEQ bioregion. A total of 703 occurrence records across the four frog species were retained for use in distribution mapping and modeling (see Supporting Information S1 and Table S1 for further details on vetting procedures).

2.2 Study area

Due to issues with the availability and compatibility of spatial environmental data from New South Wales, as well as unresolved issues regarding the taxonomy of *C. tinnula* in this state (see Read, Keogh, Scott, Roberts, & Doughty, 2001), analyses were limited to the SEQ bioregion (as based on the Interim Biogeographic Regionalisation for Australia version 7; Department of the Environment and Energy, 2012). This bioregion encompasses all known Queensland records of acid frog species, and includes the entire known distribution of *L. cooloolensis*, more than half of the known distribution of *L. olongburensis*, and a significant proportion (at least 20%) of the current known distributions of *L. freycineti* and *C. tinnula*.

2.3 Distribution modeling

We developed species occurrence models using 13 predictor variables including environmental, climatic, and anthropogenic factors (see Table S2) that were selected a priori on the basis of an assessment of which of these were biologically most meaningful in the contexts of our investigation (Shuker & Hero, 2012; Shuker, Simpkins, & Hero, 2016). Environmental layers included dominant vegetation types (Department of the Environment and Energy, 2016), soil properties (amount of clay, sand, and soil pH CaCl_2; Viscarra Rossel et al., 2014a, 2014b, 2014c), land zone (from regional ecosystem classification scheme; Department of Environment and Science, 2018), wetlands (presence and type; Department of Science, Information Technology and Innovation, 2015), and elevation and slope (Department of Natural Resources and Mines, 2013). Land use (see Table S3 for alterations made to the original layer; Australian Bureau of Agricultural and Resource Economics and Sciences, 2016) and the distance to major roads (Department of Transport and Main Roads, 2016) were used to account for the level of human disturbance/occupancy. Climatic layers included mean annual temperature, rainfall, and rainfall-modified solar radiation for Australia sourced from CSIRO (Williams et al., 2015). Data for all environmental, climatic and anthropogenic layers were aligned to a 100 m × 100 m cell resolution (using a maximum combined area approach when converting polygon data, and nearest neighbor and bilinear resampling methods when resampling categorical and continuous data, respectively), and were clipped to the extent of the Interim Biogeographic Regionalisation for Australia’s SEQ bioregion, with a southern limit defined by the Queensland–New South Wales border (Department of the Environment and Energy, 2012).

2.4 Modeling procedure

Species distribution modeling typically involves the development of a model that discriminates between a binary sample of observed occurrence records (1) and a random sample of “background” locations (0) using a suite of predictor variables. A random forest model was chosen for the analysis of the species occurrence data due to its proven predictive accuracy concerning modeling species distributions using environmental data (Duan, Kong, Huang, Fan, & Wang, 2014; Lawler, White, Neilson, & Blaustein, 2006; Mi, Huettmann, Guo, Han, & Wen, 2017; Peters et al., 2007), as well as its ability to deal with both continuous and categorical data (Cutler et al., 2007; Peters et al., 2007; Strobl, Malley, & Tutz, 2009; Williams et al., 2009). There are several other modeling frameworks that could be used to develop species distribution predictions such as Maxent (Phillips, Anderson, & Schapire, 2006) or GLMs (Manly) boosted regression trees (McCullagh & Nelder, 1989). We do not evaluate these alternative frameworks here because comparisons have demonstrated that random forest models are among the top-performing frameworks (Duan et al., 2014; Lawler et al., 2006; Williams et al., 2009), and the k-fold cross-validated prediction accuracies (kappa scores) associated with our models were high, ranging between 0.84 and 0.92 (see Section 3). Hence, there was little scope for any
other modeling approach to perform better. In applications where predictive accuracies are poor (e.g., less than 50%), such evaluations would be well advised.

Background locations were sampled using 50,000 random points generated within the study area (SEQ bioregion). Random forest models are sensitive to large imbalances in sample sizes among classes, therefore the model was implemented using a stratification procedure that resampled 66% of occurrence records, and an equivalent number of background locations, at each step. This resampling ensured that classification accuracies were balanced among each of the classes. The SEQ random forest models were run using 1,500 trees with three variables tried at each split. Random forest is a bootstrapping procedure that inherently calculates an out-of-bag error estimate using samples that were not used to train the model (a form of model validation from which the model accuracy is calculated). However, we also performed k-fold cross validation to provide another estimate of classification accuracy, quantified using the mean kappa statistic among each fold. The 13 environmental, anthropogenic and climatic layers were used to generate mapped probabilities of occurrence for each of the four acid frog species examined. Processing of spatial data occurred in ArcGIS 10.3 (ESRI, 2011) and R 3.5.1 (R Development Core Team, 2014) using the raster, sp, rgdal, and rgeos packages.

The binary predicted distribution of each species (using a 0.5 probability threshold to categorize the continuous probability prediction, which resulted in balanced error rates in the presence and absence samples) was overlayed with a map of current local government boundaries (Department of Natural Resources and Mines, 2017), and the boundaries of current protected areas (i.e., national parks, conservation parks, state forests, resource reserves, scientific national parks, timber reserves, and forest reserves; Queensland Government, 1992). This resampling ensured that classification accuracies were balanced among each of the classes. The SEQ random forest models were run using 1,500 trees with three variables tried at each split. Random forest is a bootstrapping procedure that inherently calculates an out-of-bag error estimate using samples that were not used to train the model (a form of model validation from which the model accuracy is calculated). However, we also performed k-fold cross validation to provide another estimate of classification accuracy, quantified using the mean kappa statistic among each fold. The 13 environmental, anthropogenic and climatic layers were used to generate mapped probabilities of occurrence for each of the four acid frog species examined. Processing of spatial data occurred in ArcGIS 10.3 (ESRI, 2011) and R 3.5.1 (R Development Core Team, 2014) using the raster, sp, rgdal, and rgeos packages.

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3 | RESULTS

Model validation indicated that the species distribution models had high predictive power, with all four models having classification accuracies greater than or equal to 89% (L. olongburensis [accuracy = 93%, kappa = 0.92], L. cooloolensis [accuracy = 95%, kappa = 0.89], L. freycineti [accuracy = 93%, kappa = 0.89], and C. tinnula [accuracy = 89%, kappa = 0.84]).

Predictor variables contributing the most to random forest distribution models included soil sandiness, vegetation type, soil clay content, distance to nearest road, presence/type of wetland, and landscape slope (see Table 1 for details). Soil sandiness was a key predictor in distribution models for all four acid frog species, and contributed the most in determining the distribution of L. olongburensis, L. cooloolensis, and L. freycineti. Dominant vegetation was also an important predictor variable for L. olongburensis, L. freycineti, and C. tinnula (in which vegetation type, not soil sandiness, was the most important predictor variable). For L. cooloolensis, vegetation type was not an important predictor variable, while the distance to the nearest road and the presence/type of wetland were. Distance to the nearest road and the presence/type of wetland were also important predictor variables in distribution models for other acid frog species,

| Species                  | Predictor Variables                                      | Accuracy       | Kappa        |
|--------------------------|---------------------------------------------------------|----------------|--------------|
| L. olongburensis         | Quantity of sand in the soil, Dominant vegetation       | 93%            | 0.92         |
| L. cooloolensis          | Quantity of sand in the soil, Land zone                 | 95%            | 0.89         |
| L. freycineti            | Quantity of sand in the soil, Distance to nearest major road | 93%            | 0.89         |
| C. tinnula               | Quantity of sand in the soil, Landscape slope           | 89%            | 0.84         |

Table 1: The five predictor variables contributing most to each of the random forest species distribution models. Variable contribution was determined using the mean decrease in accuracy for each random forest model.
along with soil clay content (which contributed significantly to the distribution models of *L. olongburensis*, *L. freycineti*, and *L. cooloolensis*; see Table 1).

Similarities and differences in the distribution models for acid frog species are clearly evident in Figure 2, which shows the modeled distribution and known occurrences...
TABLE 2  Predicted area of occurrence for each acid frog species within local government areas (LGAs) in the south-east Queensland (SEQ) bioregion. Percentage values represent the proportion of a species’ total predicted distribution for SEQ occurring within a particular LGA, as well as the proportion of this predicted distribution within each LGA not included within a protected area (rounded to the nearest whole integer). LGAs in SEQ with no predicted occurrence of acid frog species are not included in this table. LGAs are listed by total percentage of acid frog distribution predicted to occur within them.

| LGA                      | Number of acid frog species present | Litoria olongburensis | Litoria cooloensis | Litoria freycineti | Crinia tinnula |
|--------------------------|------------------------------------|-----------------------|--------------------|--------------------|---------------|
|                          | % of predicted distribution in LGA | % of predicted distribution in LGA not protected | % of predicted distribution in LGA | % of predicted distribution in LGA not protected | % of predicted distribution in LGA | % of predicted distribution in LGA not protected |
| Fraser Coast Regionala   | 4                                  | 34                    | 4                  | 49                 | 3             | 27            | 3               | 31             | 28            |
| Sunshine Coast Regiona   | 4                                  | 18                    | 72                 | 10                 | 69            | 23            | 71              | 14             | 76            |
| Gympie Regionalb         | 4                                  | 11                    | 12                 | 10                 | 9             | 12            | 10              | 10             | 22            |
| Noosa Shireb             | 4                                  | 10                    | 52                 | 9                  | 46            | 11            | 55              | 7              | 59            |
| Moreton Bay Regionala    | 4                                  | 9                     | 62                 | 5                  | 49            | 8             | 53              | 10             | 74            |
| Gold Coast cityb         | 4                                  | 8                     | 94                 | 4                  | 81            | 9             | 93              | 7              | 95            |
| Redland cityb            | 4                                  | 7                     | 59                 | 8                  | 53            | 7             | 58              | 5              | 69            |
| Brisbane cityb           | 4                                  | 3                     | 3                  | 5                  | 2             | 3             | 2               | 4              | 57            |
| Bundaberg Regional       | 1                                  | 0                     | —                  | 0                  | —             | 0             | —               | 5              | 45            |
| Gladstone Regional       | 1                                  | 0                     | —                  | 0                  | —             | 0             | —               | 4              | 53            |
| Logan city               | 1                                  | 0                     | —                  | 0                  | —             | 0             | —               | 0              | 95            |

aLGAs that cover >3% of each acid frogs’ total predicted distribution.
of each acid frog species in SEQ. As this figure shows, the predicted SEQ distributions of *L. olongburensis* (*N* = 168 presence sites; area = 4,312 km$^2$), *L. cooloolensis* (*N* = 90 presence sites; area = 3,054 km$^2$), *L. freycineti* (*N* = 85 presence sites; area = 4,447 km$^2$), and *C. tinnula* (*N* = 360 presence sites; area = 7,774 km$^2$) were largely concentrated within a narrow coastal strip. None of the four acid frog species were predicted to frequently occur in or around the Brisbane City Region, where human disturbance is known to be high.

The SEQ bioregion covers portions of 22 LGAs administered by separate councils (Figure 2). Acid frogs were not predicted to occur in half (11) of these LGAs (see Table 2 for list). Of these, all species were predominantly predicted to occur in eight LGAs along the coast (where each LGA covered greater than 3% of all acid frog species’ total predicted distribution; Figure 2 and Table 2). There was considerable overlap in the predicted distribution of the four species (see Figure S1 for a depiction of overlap), with Fraser Coast Regional Council and Sunshine Coast Regional Council encompassing significant portions (>27% and >10%, respectively) of each species’ predicted distribution within Queensland (Table 2 and Figure 2). All four acid frog species were predicted to occur on the four sand islands; Fraser Island (Fraser Coast Regional), Bribie Island (Moreton Bay Regional and Sunshine Coast Regional), Moreton Island (Brisbane City), and North Stradbroke Island (Redland City).

The location of acid frog records included in the analyses is shown in Figure 2. *Crinia tinnula* had the highest number of discrete occurrence records used in the analyses (360), just over double *L. olongburensis*’ records (168). The number of *L. cooloolensis* (90) and *L. freycineti* (85) records were lower again, and roughly half the number of *L. olongburensis* occurrence records. As shown in Figure 2, the majority of these records are from the Sunshine Coast Regional Council, Redland City, and Fraser Coast Regional Council LGAs (see Table S4 for details on the number of occurrence records in each LGA). These LGAs encompass significant portions of each species’ predicted distribution within Queensland.

A large proportion (>47%) of each species’ predicted distribution occurred within the boundaries of high protection protected areas within the SEQ bioregion (Table 3 and Figure 3). The predicted distribution of *L. cooloolensis* overlapped with high protection protected areas the most (77%), followed by *L. olongburensis* (62%), *L. freycineti* (59%), and finally by *C. tinnula* (47%; Table 3). This coverage by protected areas is exemplified in key LGAs such as Fraser Coast Regional Council (Table 2 and Figure 3). Conversely, protected area coverage of potential acid frog habitat under the jurisdiction of Gold Coast City, Sunshine Coast Regional Council, Redland City, Moreton Bay Regional Council, and Noosa Shire have significant opportunity for improvement (Table 2). All five of these LGAs are located along the southern Queensland coast encompassing portions of wallum wetland habitat (east Australia’s coastal sandy lowlands) and are all regions where all four acid frog species are predicted to occur (Table 2 and Figure S1). Of the eight most important LGAs (Table 2), Gold Coast City, Sunshine Coast Regional Council, and Redland City were the three regions with the poorest protected area coverage of potential acid frog habitat (>53% predicted acid frog distribution occurring outside of protected areas for each species). Brisbane City (or in the case of *C. tinnula*, Gympie Regional Council) and Fraser Coast Regional Council are examples of LGAs with the best proportional protected area coverage of acid frog distributions (Table 2).

### 4 | DISCUSSION

Species distribution models provided over 89% accuracy in predicting the occurrence of acid frog species in SEQ, indicating the strong fit our models had to the occurrence...
FIGURE 3  Overlap of all acid frog species’ occurrence records (red) with protected areas within the south-east Queensland bioregion: (a) *Litoria olongburensis* (b) *Litoria cooloolensis* (c) *Litoria freycineti* and (d) *Crinia tinnula*. Each map is overlayed with current protected areas in two categories; High protection protected areas (national parks, scientific national parks, and conservation parks; green) and Low protection protected areas (state forests, resource reserves, timber reserves, and forest reserves; orange). Each map is overlayed with the 2017 local government area (LGA) borders. Only the names of the LGAs that contain a portion of predicted acid frog distribution have been included.
data. Our models showed that all four species were predicted to occur almost exclusively within ~30 km of the coastline of SEQ (Figure 2), with the amount of sand present in the soil serving as the only key explanatory variable for all four acid frog species (Table 1). This reflects a strong association with coastal wallum, an area of sandplains and dunes situated between the shoreline and foothills of the coastal ranges of southern Queensland (Bryan, 1973; Coaldrake, 1961). Additionally, the presence/type of wetland habitat and dominant vegetation were regularly selected as important variables for a number of the acid frogs (Table 1), most likely reflecting the strong association of these species with sedgeland, wet heath and Melaleuca-dominated communities common in wallum environments (Griffith et al., 2003; Meyer et al., 2006).

While the predicted distribution of acid frog species was broadly similar, differences were apparent in the extent of potential habitat for each species in SEQ; such as the unexpected restricted range of _L. freycineti_. Additionally, _C. tinnula’s_ predicted distribution extends further north and inland than other acid frog species, while _L. cooloolensis’_ habitat is much more limited in mainland areas, occurring predominantly on the large sand islands. This dissimilarity is particularly evident in the known occurrences of each species (Figure 2). As hypothesized, these important differences between the acid frogs are not apparent in the broad-scale mapping of potential acid frog habitat provided in the national recovery plan for acid frog species (Figure 1; Meyer et al., 2006). These maps therefore misrepresent the extent of habitat suitable for individual acid frog species, and may not be useful when attempting to target conservation toward a single species, such as for _L. olongburensis_. Currently the only acid frog listed nationally under the Environment Protection and Biodiversity Conservation Act 1999 (Australian Government, 1999; Department of Environment and Science, 2019).

Differences in the modeled distribution of acid frog species may, in part, reflect differences in habitat preferences, with _L. olongburensis_ showing a preference for ephemeral perched swamps, _L. freycineti_ and _C. tinnula_ for ephemeral swamps and soaks, and _L. cooloolensis_ for coastal lakes (Meyer et al., 2006). The particular preference of _L. cooloolensis_ for lacustrine wetlands is likely highlighted by the relative importance of wetland type in determining the distribution of this species (Table 1). Therefore, the relative paucity of _L. cooloolensis_ records is not unexpected given the relative scarcity of lake systems in wallum areas (with the majority of _L. cooloolensis_ records associated with lakes on taller dunes and dune islands including Fraser Island and North Stradbrook Island; Meyer et al., 2006). In contrast, the paucity of _L. freycineti_ records was unanticipated, and is more difficult to explain given the extent of potentially suitable habitat for this species in SEQ (as identified in this study). The limited number of _L. freycineti_ records in SEQ is not obviously related to detectability or lack of survey effort, and further research is needed to determine factors limiting the distribution and abundance of this species in wallum areas. Indeed, the scarcity of _L. freycineti_ records suggests the conservation of this species should be viewed as a priority in Queensland, where areas of suitable habitat are under threat from ongoing development. Of particular concern in this regard, is the loss of _L. freycineti_ habitat from development areas on the Sunshine Coast, which supports the largest known populations of this species in Queensland (E. Meyer, unpublished data). The protection and management of remaining _L. freycineti_ habitat/populations should therefore be considered a priority by LGAs in Queensland.

Our analysis identified eight key LGAs that cumulatively span 89–100% of the predicted distributions of _L. olongburensis, L. cooloolensis, L. freycineti_, and _C. tinnula_ in Queensland (Table 2). Five of these LGAs (Fraser Coast Regional Council, Sunshine Coast Regional Council, Gympie Regional Council, Noosa Shire, and Moreton Bay Regional Council) encompass over 73% of the predicted distributions of these species (Table 2 and Figure 2). All of the aforementioned LGAs are coastal and, as such, support large and continuously growing human populations (Hobday & McDonald, 2014). Threats to native species in such populated and rapidly developing areas are many and varied (Luck, Ricketts, Daily, & Imhoff, 2003; Sodhi et al., 2008), and include deforestation, invasive species, and habitat degradation and fragmentation. These impacts pose a particular threat to specialist species with highly restricted ranges, like the acid frogs (Hugo & van Rensburg, 2008; Sodhi et al., 2008). Managing human impacts on acid frog habitat in the aforementioned LGAs is therefore important for the long-term conservation of acid frog species.

According to a recent global assessment by Dinerstein et al. (2017), the ecoregions of coastal SEQ fall within the most extreme “nature imperiled” classification due to the limited amount of natural habitat remaining, and the limited extent (<20%) of protected habitat within this bioregion. Our results support this notion with limited/poor protection of potential acid frog habitat in five of the eight key LGAs identified as important for acid frog conservation (Table 2 and Figure 3), with a total of 23–52% of each species potential distribution falling outside of any protected areas in the SEQ bioregion (Table 3). In all five of these key LGAs, more than 46% of the acid frog distributions predicted to occur within their boundaries are on unprotected land. This percentage goes up to over 69% and 81% in the case of Sunshine Coast Regional Council and Gold Coast City LGAs (Table 2). Importantly, Sunshine Coast Regional Council contains the largest proportion of occurrence records for all acid frog species (Figure 2 and Table S4). Along with Moreton Bay Regional Council and...
Noosa Shire, this LGA also forms the core of the mainland distribution for all of the acid frog species except *L. cooloolensis* (Figure 2). This is concerning given the known developmental pressure and rapid growth in urban centers like the Sunshine Coast (Australian Bureau of Statistics, 2010). Beneficially, however, the majority of the protected area coverage of the potential acid frog distribution falls within national, national scientific, and conservation parks which have the highest levels of protection (Table 3), preventing the use of the land for commercial practices and/or resource use/extraction which may affect the quality of the sensitive wallum habitat (Forestry Act, pp. 21–28, Queensland Government, 1959; Nature Conservation Act, pp. 27–40, Queensland Government, 1992). It should be noted, however, that the majority of this protection occurs on the large sand islands (such as Fraser Island), and protection on the mainland where there is significant developmental pressure is more limited.

The modeling approach used in our study was unable to take into account site-specific factors affecting the occurrence of acid frog species such as water pH, wetland hydroperiod, water quality, the presence and abundance of competitor species and predators (Shuker et al., 2016; Shuker & Hero, 2012; Simpkins et al., 2013), or broader biogeographic factors affecting the distribution of acid frog species (e.g., historical barriers to dispersal). Therefore, the modeled distributions presented here are likely to overestimate the actual distribution of acid frog species, particularly in more heavily populated areas, where historical occurrence records may not reflect recent habitat degradation, as a result of the high level and intensity of human disturbance. Notwithstanding this, our distribution models represent a substantial improvement on existing mapping within the national recovery plan (Meyer et al., 2006), and can better inform conservation planning for threatened acid frog species in southern Queensland, at both the state and local government level. The outputs of our modeling and analyses can also be used by local government, developers and other stakeholders (including local environmental and indigenous interest groups) to identify and assess potential impacts of coastal development on acid frog habitat and, in doing so, better ensure human impacts on threatened acid frog species in SEQ are properly managed.

Our model was able to relate the target species’ distribution to relevant decision makers’ jurisdictions, highlighting areas of acid frog distribution occurring outside of protected areas that need significant consideration in future conservation planning efforts. Considering the broader conservation implications of our main findings, our predicted distribution maps can therefore be used to trigger impact assessments and more intensive biological surveys in areas where the threatened acid frogs (and in particular the nationally listed *L. olongburensis*) are predicted to occur. Such triggers are likely to result in the implementation of biodiversity offset policies, of which Australia is a world leader in the development thereof (Maron, Gordon, Mackey, Possingham, & Watson, 2015). As offsetting aims to counterbalance ecological impacts of development activities through habitat restoration and/or protection (Maron et al., 2015), our maps can be used to identify areas of habitat that may trigger offsetting activities, as well as candidate areas for habitat protection and restoration.

Additionally, our maps identify crucial areas of potential co-occurrence of multiple acid frog species that occur outside of protected areas (that are consequently under threat from human land uses). Private organizations, philanthropic entities and non-government conservation partners such as the Australian Wildlife Conservancy (AWC) aim to aid in conservation efforts by purchasing and protecting areas of ecological significance. Our study can help guide such organizations in purchasing conservation efficient areas for protection under these schemes in order to benefit the acid frogs in critically threatened areas.

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**CONFLICT OF INTEREST**
The authors have no conflict of interest in the publication of this paper.

**AUTHOR CONTRIBUTIONS**
All authors contributed to developing the concept of the paper. A.F. and H.L.B. developed and performed the spatial analyses. A.F. led the writing of the manuscript with contribution from H.L.B., E.M. and B.J.V.R.

**ETHICS STATEMENT**
The authors are not aware of any ethical issues regarding this work.

**DATA AVAILABILITY STATEMENT**
The occurrence record database used in this research is available at the University of Queensland UQ eSpace data
repository at "https://doi.org/10.14264/uql.2019.784," and will be available on request from lead author at alannah.filer@uq.net.au

ORCID
Alannah Filer ○ https://orcid.org/0000-0002-8988-4409

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