

Battling habitat loss: suitability of anthropogenic waterbodies for amphibians associated with naturally acidic, oligotrophic environments

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Abstract. Habitat destruction is a key threatening process for amphibians. Modified or anthropogenic waterbodies can be used to compensate for habitat loss, with several amphibian species utilising created or modified waterbodies. We measured usage of anthropogenic/modified waterbodies by adult and tadpole frog species, including threatened species, in coastal wallum habitat in eastern Australia. Nine road trenches/ditches, 8 artificial ‘lakes’, 6 golf course waterbodies and 13 natural waterbodies were surveyed for frog adults and tadpoles during the summer/spring period 2011–2012. Additionally, we examined the relationship between frog assemblages and environmental factors (water chemistry, aquatic predators, vegetation types), focusing on *Litoria olongburensis* and *Litoria fallax*. Frog species richness differed between waterbody types, with two of three threatened frog species present in both natural and anthropogenic/modified waterbodies. The frog assemblage was influenced by pH, turbidity, salinity and percentage cover of certain vegetation types. Measured abundance of *L. olongburensis* adults and tadpoles were highest in natural waterbodies with high sedge density and low pH. The measured abundance of adult *L. fallax* was highest within artificial lakes. We conclude that differences in water chemistry and vegetation density can affect the amphibian assemblage within these environments. Therefore, effective conservation of all frog species would be enhanced by conserving a variety of waterbody types. However, natural waterbodies are more likely to be used by threatened species and the conservation of these waterbodies provides the best conservation outcomes. Where habitat offsets may be required, environmental managers should critically assess the quality of constructed habitat for specialist frog species including those associated with acidic, oligotrophic environments.

Keywords: anuran, frog, habitat modification, *Litoria fallax*, *Litoria olongburensis*, vegetation, water chemistry.

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Introduction

Amphibian species are declining globally (Stuart *et al.* 2004), with habitat loss/modification being one of the main threatening factors (Collins and Storfer 2003; Beebee and Griffiths 2005; Nowakowski *et al.* 2017; Pyron 2018). This habitat loss could be compensated for by modified or anthropogenic waterbodies (e.g. Mazerolle *et al.* 2006; Ruhí *et al.* 2012), with several amphibian species within Australia (Hazell *et al.* 2004; Sievers *et al.* 2018), North America (Monello and Wright 1999; Brand and Snodgrass 2010; Brown *et al.* 2012) and Europe (Rannap *et al.* 2009; Brown *et al.* 2012; Ruhí *et al.* 2012; Magnus and Rannap 2019) utilising anthropogenic or modified waterbodies that were either specifically designed to compensate for habitat loss or were opportunistically used by amphibians. However,

species assemblages and richness can differ between anthropogenic/modified and natural waterbodies (Hazell *et al.* 2004; Magnus and Rannap 2019), potentially due to differences in environmental factors that influence amphibian species distributions within waterbodies. Additionally, waterbodies that are used may be considered as ecological traps, and may not be suitable for long term amphibian populations. For the purpose of this study, an ecological trap is referred to as a habitat/waterbody that an individual frog occupies where it could perform poorly (e.g. survivability, successful reproduction) when compared with natural habitats (Robertson and Hutto 2006).

Several ecological interactions can influence the distribution of amphibians within waterbodies, including aquatic predators (Kats *et al.* 1988; Hero *et al.* 2001; Vonesh *et al.* 2009;

Barry 2015), and/or competitors (Morin 1986; Wilbur 1987; Mokany and Shine 2003; Twomey *et al.* 2008). Water chemistry variables, including pH (reviewed in Pierce 1985; Sparling 2010) and salinity (Strahan 1957; Christy and Dickman 2002; Chinathamby *et al.* 2006; Rios-López 2008) may potentially lead to the exclusion of amphibian species from a waterbody due to tadpole water chemistry intolerances. Furthermore, turbidity may have an influence on structuring amphibian assemblages (Hecnar and M'Closkey 1996) while the abundance of particular vegetation species (Shuker and Hero 2013) or the proportion of the water margin with emergent vegetation (Hazell *et al.* 2004) can also have the ability to influence amphibian species richness or abundances within waterbodies.

Reductions in the availability of coastal waterbodies have occurred globally (e.g. Turner 1990; Levin *et al.* 2009), due to human population growth and expansion. Within Australia, the majority of freshwater, coastal waterbodies situated along the eastern seaboard between Fraser Island, Queensland, and Jervis Bay, New South Wales, are unique as they are both naturally oligotrophic (Hines *et al.* 1999) and acidic (Griffith *et al.* 2008; Hines and Meyer 2011; Simpkins *et al.* 2014; Shuker *et al.* 2016). The vegetation community within this area is known as 'wallum', and is defined as the vegetation communities that include *Banksia* woodland, sedgeland, heathland and *Melaleuca* swamps (Hines *et al.* 1999; Griffith *et al.* 2003). Populations of threatened 'acid' frog species (Ingram and Corben 1975) occur within wallum waterbodies (Hines *et al.* 1999; Lewis and Goldingay 2005) and areas where multiple acid frogs species may occur outside of protected areas have been identified (Filer *et al.* 2019). Furthermore, more than 30% of original heathland and *Melaleuca* cover in south-east Queensland was cleared between 1974 and 1989 (Catterall and Kingston 1993, cited in Hines *et al.* 1999) and areas within the acid frog species ranges have one of the highest human growth rates within Australia (Hines *et al.* 1999; Garden *et al.* 2010). Wallum habitats also contain modified and anthropogenic waterbodies (Simpkins 2012), which may be utilised by 'acid' frog species and constructed 'compensatory' waterbodies have been created to offset the loss of wallum ponds used by acid frogs. Therefore, these waterbodies could aid in reducing the impacts of habitat loss. Despite compensatory habitats being used to offset habitat and the presence of anthropogenic/modified waterbodies in wallum habitat, no peer-reviewed studies have examined whether frogs normally associated with naturally acidic, oligotrophic waterbodies use and successfully reproduce within these anthropogenic/modified waterbodies.

Consequently, we aimed to compare usage of natural and anthropogenic waterbodies by the adults and tadpoles of frog species within the coastal wallum of eastern Australia. This study allows us to (1) identify which environmental variables influence the frog assemblages within the various waterbodies of this unique habitat; and (2) determine the environmental variables that influence the relative abundance of the threatened wallum sedge frog, *Litoria olongburensis*, and a potential competitor, *Litoria fallax* (Meyer *et al.* 2006), across the natural/modified landscape. The outcomes of this study can help environmental managers creating habitat offsets to critically assess the quality of constructed habitat for frog species, including threatened, specialist species, which are associated with naturally acidic,

oligotrophic waterbodies, and their respective competitors. The results will also help determine whether human intervention through anthropogenic waterbody construction can compensate for habitat loss of specialist frogs that are unique to environments with low pH and nutrients.

Materials and methods

Study site selection and sampling design

Waterbodies were located within and around Tyagarah Nature Reserve (NR) (28.6067°S, 153.5693°E) and the southern section of Bribie Island National Park (NP) (27.0732°S, 153.1774°E). Waterbodies were selected using Google Earth satellite imagery to cover the style of waterbodies available at each site. All waterbodies were surveyed twice, first between 18 October 2011 and 5 December 2011, and again between 7 and 21 February 2012. Surveys for adult frogs, aquatic predators and tadpoles were conducted at 13 natural ($n = 5$ Tyagarah, $n = 8$ Bribie Island) and 25 anthropogenic waterbodies (total $n = 38$). Anthropogenic waterbodies consisted of roadside trenches/ditches ($n = 4$ Tyagarah; $n = 5$ Bribie Island), artificial 'lakes' ($n = 1$ Tyagarah; $n = 8$ Bribie Island) and golf course waterbodies ($n = 6$ Tyagarah). With the exception of golf course waterbodies, all waterbodies contained natural vegetation around the majority (>80%) of the waterbody perimeter.

Roadside trenches were classified as waterbodies that had been constructed next to roads or firebreaks where earth material had been removed to aid construction of the road or firebreak. Artificial lakes were classified as constructed waterbodies with the majority of the waterbody (>80%) as open water with vegetation fringing the perimeter. Golf course waterbodies were constructed waterbodies within the golf course boundaries and contained little vegetation around the perimeter (<10%). Waterbodies within wallum heathland can be composed of heterogeneous vegetation types. Therefore, one large natural waterbody had multiple transects established a minimum of 300 m apart to ensure transect independence. Survey transects were established 5 m from the waterbody perimeter and ran parallel to the waterbody perimeter. Transect length varied between 50 and 100 m, depending on waterbody size, with frogs being recorded 2 m on either side of the transect.

Litoria olongburensis appears to delay breeding to longer hydroperiods and can also respond quickly to wetland filling/inundation (Lowe *et al.* 2015). Hence, surveying was undertaken when waterbodies were within these ideal scenarios. Rainfall data was collected from the Australian Bureau of Meteorology Weather Station #058 216 for Tyagarah NR and #040 998 for Bribie Island NP. Sampling was conducted in 2011, with 246.9 mm rainfall recorded at Bribie Island and 373.4 mm recorded for Tyagarah NR during the 3 months prior to the date of the first survey. The 2012 surveys recorded 936.7 mm at Bribie Island and 405.2 mm for Tyagarah NR during the 3 months prior to the second survey date. All waterbodies surveyed had water present during both the 2011 and 2012 surveys.

Diurnal aquatic predator traps were placed at the beginning, middle and end of each transect. Traps were baited with Orca Floating Fish Food Pellets and were left for approximately 30 min before being collected. Diurnal dip-netting for predatory

fauna and tadpoles was conducted using a circular net, with an opening of approximately 30 cm in diameter and mesh size <0.5 mm. Five 'sweeps' of the dip-net and measurements of pH and salinity were undertaken at 10 m sampling intervals along each transect. Each 'sweep' encompassed three water column levels (bottom, middle, and top) to capture any variation in tadpole species richness or abundance that may occur along the water depth gradient (Heyer 1973). Water columns were deep enough to be reached at all parts of the transect.

Water pH and salinity were measured using a TPS Aqua-CPA Conductivity-TDS-pH-Temperature Meter (ver. 1.2) approximately 15 cm below the surface of the water at every 10 m sampling point along the transect. Two 25 mL surface water samples were collected at the beginning and the end of each transect. Turbidity was measured from the 25 mL water samples using a HACH DREL 2000 Direct Reading Spectrophotometer within 24 h of sample collection. Water chemistry measurements and samples were taken before dip-netting and trapping were conducted. Waterbody area was calculated using Google Earth satellite imagery.

Vegetation on the transect was categorised into five vegetation types; sedge, grass, lily, *Gahnia* spp. and *Melaleuca* spp. Percent density of each vegetation type was visually estimated using a 1×1 m quadrat centered at each 10 m sampling interval.

Nocturnal frog surveys were conducted by walking and visually searching the transect using a Princeton Apec Headtorch. The species and the number of individuals seen for each species were recorded for each transect. For *Crinia tinnula*, numbers of individuals were determined using acoustic calls due to visual observations being absent or low at the survey transects. The vegetation type an individual frog was first encountered on was also recorded. Substrate records were only conducted on the first survey.

Data analysis

The number of *L. olongburensis* visually recorded during the first survey was tallied for each transect and divided by the transect length to obtain a relative abundance of *L. olongburensis* per metre. All other species recorded visually in sufficient numbers were counted and divided by the transect length.

Visual incidental and transect observations and frogs heard calling <1 m outside the waterbody perimeter or calling within the waterbody during the first or second survey were recorded as occupying the waterbody. Tadpole species were considered present within a waterbody if they were recorded from any of the sampling points.

Predatory fish caught in aquatic traps were used in data analysis due to low counts of predatory fish caught during dip-netting. The number of fish recorded for a given transect was divided by the number of aquatic traps used within the waterbody to obtain a relative fish abundance for each transect.

Salinity, turbidity and pH were averaged for each transect. Mean density of each vegetation type for each transect was calculated by dividing the total percentage density of each vegetation type from each sampling point by the number of sampling points along the transect.

A Spearman Rank Correlation Test was performed in IBM SPSS Statistics ver. 19 (SPSS Inc., Chicago, IL, USA) to

determine correlated variables. Highly correlated variables were considered to be variables that had a correlation coefficient value ≥ 0.7 (*sensu* Garden *et al.* 2007; Simpkins *et al.* 2014). No variables were highly correlated and all variables were used in analyses.

A one-way ANOVA with Tukey's *post-hoc* analysis was used to determine significant differences in environmental variables between waterbody types. One-way ANOVAs were also used to compare the relative abundance of *L. olongburensis* and *L. fallax* in the four different waterbody types.

The frog community assemblage was analysed (using visual counts for *L. olongburensis*, *L. fallax*, *L. peronii*, *R. marina* and *L. tyleri*, and acoustic counts for *C. tinnula*) using non-metric multidimensional scaling (nMDS). These species were chosen as they were encountered in at least two waterbodies and were highest in relative abundance when compared with other species. Only waterbodies which contained one or more of these six species were used in nMDS analysis ($n = 27$). Bray-Curtis distance measures were used to determine waterbody similarities for the relative abundance of individual species. Random permutations ($n = 999$) were used to determine which environmental variables were significantly influencing the amphibian assemblage (Oksanen 2011). Analyses were performed using the statistical program R (R Core Development Team 2011) using the *vegan* (ver. 2.04) package (Oksanen *et al.* 2012).

Twenty-eight models focusing on the influence of variables on the relative abundance of *L. olongburensis* and *L. fallax* were constructed *a priori*. To obtain the maximum number of predictor variables to use in each model, a generalised 'rule of thumb' of $n/3$ (where n = number of waterbodies sampled) (Crawley 2007) was applied. Predictor variables in *L. olongburensis* models were average pH, average salinity, average turbidity, waterbody size, fish relative abundance, *L. fallax* relative abundance, % sedge density, % *Gahnia* density, % grass density, % lily density, and % *Melaleuca* density. Predictor variables in *L. fallax* models were the same as the *L. olongburensis* models, except *L. fallax* relative abundance was replaced with *L. olongburensis* relative abundance. Generalised additive mixed effects models, using a Quasi-Poisson link function to account for overdispersion and location as a covariate, were used to determine the importance of the predictor variables on *L. olongburensis* and *L. fallax* relative abundance.

Small sample Akaike's information criterion (AIC_c) was used for model selection, with the 'best' model having the lowest AIC_c value (Burnham and Anderson 2002). To determine the ranking of the models, ΔAIC_c values were calculated, where higher ΔAIC_c values indicated less accurate models for the given data (Burnham and Anderson 2002; Johnson and Omland 2004). If a model had a $\Delta_i \leq 2$, then there was considerable evidence that the model could be the 'best' model, given the data (Johnson and Omland 2004). If a model had a $\Delta_i \leq 2-4$, then there was moderate evidence that the model could be the 'best' model, given the data. Each model was assigned a model weight (w_i) which was used to determine the 'probability that model i is the best model for the observed data, given the candidate set of models' (Johnson and Omland 2004). The closer the w_i was to 1, the closer the model was considered the best model for the given data (Burnham and Anderson 2002). To determine the relative importance of variables within models

where $\Delta_i < 4$, the w_i values were summed from all models where $\Delta_i < 4$ and where the variable of interest occurred. The closer the relative importance value was to 1, the higher the relative importance of the variable (Grueber *et al.* 2011). All models were run in the freeware statistical package R (R Core Development Team 2011) using the *MuMIn* (ver. 1.7.2) (Barton 2012) and *vegan* (ver. 2.04) (Oksanen *et al.* 2012) packages.

Results

Waterbody characteristics and predatory fish

Waterbody characteristics varied among waterbody types (Table 1). Variables that were significantly different between waterbody types were pH ($df = 36$, $F_{2/34} = 5.36$, $P = 0.004$), turbidity ($df = 36$, $F_{2/34} = 3.925$, $P = 0.017$) and waterbody size ($df = 36$, $F_{2/34} = 6.001$, $P = 0.002$). Tukey's *post-hoc* analysis revealed pH was significantly higher in artificial lakes than in natural waterbodies ($P = 0.005$) and roadside ditches ($P = 0.011$). Tukey's *post-hoc* analysis also revealed turbidity

was significantly higher in natural waterbodies than in golf course waterbodies ($P = 0.011$) and natural waterbodies were significantly larger than roadside ditches ($P = 0.003$) and golf course waterbodies ($P = 0.024$). The number of predatory fish in each waterbody included individuals from the species *Gambusia holbrooki* (Eastern mosquito fish), *Rhadinocentrus ornatus* (Ornate rainbow fish), *Hypseleotris galii* (Firetail gudgeon), *Hypseleotris compressa* (Empire gudgeon), and *Hypseleotris* sp. (Midgleys carp gudgeon).

Frog assemblage/occupancy

A total of 10 adult frog species were encountered; six recorded in natural waterbodies, six in artificial lakes, five in roadside ditches and six in golf course waterbodies (Fig. 1). Relative abundances of *L. olongburensis* and *L. fallax* adults were higher during the 2011 survey. *Litoria olongburensis* and *C. tinnula* occupancy was highest within natural waterbodies while *L. fallax*, *L. tyleri* and *R. marina* occupancy was highest within

Table 1. Measured variable averages and ranges between the four waterbody types surveyed and for waterbodies with *L. olongburensis* and *L. fallax* FTU, Formazin Turbidity Unit

Variable	Natural waterbodies	Roadside trenches	Golf course waterbodies	Artificial lakes	<i>L. olongburensis</i> waterbodies	<i>L. fallax</i> waterbodies
pH (average)	3.96	3.96	4.73	5.41	4.07	4.81
pH (range)	3.7–4.85	3.64–4.57	4.32–5.91	3.79–7.97	3.43–5.83	3.79–6.84
Salinity (ppm)	119.75	100.57	4684	153.89	90.8	109
Salinity (ppm) (range)	50.22–108.67	73.56–206.67	40.6–27 700	96.1–317.5	47.78–209.7	64.64–198.17
Turbidity (FTU)	395	229	54	261.1	323	230
Turbidity (FTU) (range)	150.5–889.33	21–217.33	30–100.33	16.7–724	21–889.33	16.6–724
Area (m ²)	22 968	1196	337	11 056	15 574	8185
Area (m ²) (range)	1726–51 787	66–2666	750–5564	415–43 351	376–51 787	791–41 129
% Sedge	55	19	5	22	52	28
% Sedge (range)	0–100	0–61	0–16	0–88	2–100	0–88
Fish abundance	2.13	2.09	3.06	2.9	3.07	3.42
Fish (range)	0–13	0–8.3	0.33–9	0–9.33	0–13	0–9.33

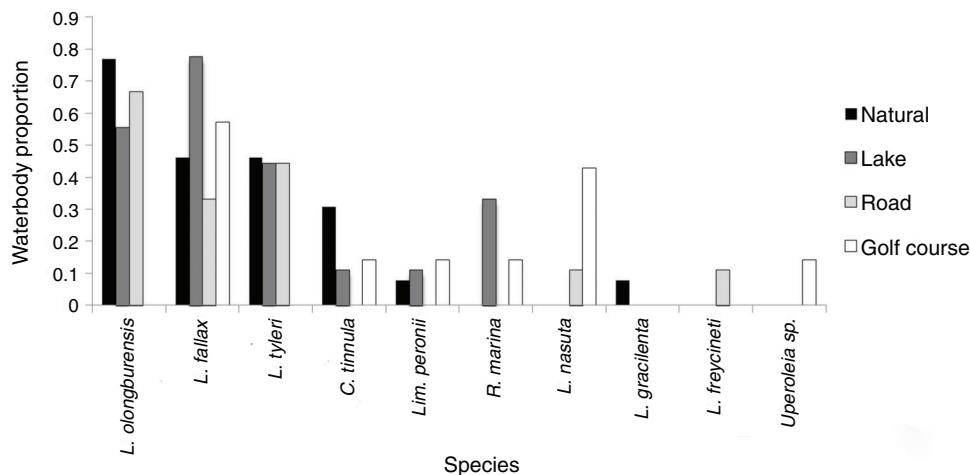


Fig. 1. Proportion of natural and anthropogenic waterbodies occupied for each recorded anuran species. Records are combined for both visual and acoustic records.

artificial lakes. *Litoria freycineti* was only recorded from roadside ditches while *L. gracilentia* was only recorded from natural waterbodies. Additionally, one *Uperolia* sp. was recorded from one golf course waterbody. *Litoria fallax* was the only species to occupy all four waterbody types (Fig. 1).

Water pH, salinity, % lily cover and % sedge cover were correlated with change in amphibian assemblage (Table 2). All species were separated on the nMDS plot, with *L. longburnensis*, *C. tinnula* and *L. tyleri* falling within close proximity of each other (Fig. 2).

Table 2. Correlations (R^2 values) between nMDS axis 1 and 2 and environmental variables influencing assemblage structure, with significant correlations ($\text{Pr}(> r)$) highlighted in bold

Variable	NMDS1	NMDS2	R^2	$\text{Pr}(> r)$
pH	0.724	0.69	0.293	0.018
Salinity	0.046	0.999	0.258	0.033
Turbidity	-0.988	-0.152	0.151	0.135
Area	-0.998	0.057	0.091	0.316
Fish	0.706	0.708	0.002	0.975
Sedge	-0.8	-0.599	0.251	0.039
Melaleuca	-0.925	0.38	0.079	0.369
Fern	-0.05	-0.999	0.105	0.241
Lily	0.941	0.339	0.311	0.016
<i>Gahnia</i>	-0.022	-0.999	0.211	0.061
Grass	-0.126	0.992	0.077	0.414

Litoria longburnensis and *L. fallax* relative abundance

Water chemistry variables differed between waterbodies containing *L. longburnensis* and *L. fallax*, with pH being higher and sedge cover being lower in waterbodies with *L. fallax* (Table 1). Waterbody type showed a significant relationship with *L. longburnensis* relative abundance ($\text{df} = 36$, $F = 3.558$, $P = 0.025$) but not for *L. fallax* relative abundance ($\text{df} = 36$, $F = 1.682$, $P = 0.19$). However, *L. fallax* was only recorded from two natural waterbodies while the highest abundance of *L. longburnensis* was recorded from natural waterbodies (Fig. 3). Additionally, no *L. longburnensis* were recorded from golf courses while the highest relative abundance of *L. fallax* was recorded from artificial lakes (Fig. 3).

Litoria longburnensis were recorded perched on sedge ($n = 153$), *Gahnia* sp. ($n = 14$), *Melaleuca* sp. ($n = 3$), fern ($n = 4$) and grass ($n = 2$). *Litoria fallax* were recorded perched on sedges ($n = 28$), *Gahnia* sp. ($n = 15$), lilies ($n = 14$), *Melaleuca* sp. ($n = 2$) and ferns ($n = 1$).

Tadpoles of *L. longburnensis* were recorded in 11 natural waterbodies and two roadside ditches, which were adjacent to natural waterbodies. Tadpoles of *L. fallax* were recorded from one natural waterbody adjacent to a roadside ditch. Tadpoles were only recorded during the summer survey in 2012 despite tadpole surveys being conducted during the 2011 and 2012 surveys.

One model for *L. longburnensis* relative abundance had a $\Delta_i \leq 2$ while no models had a $\Delta_i \leq 2-4$. The weighting of the

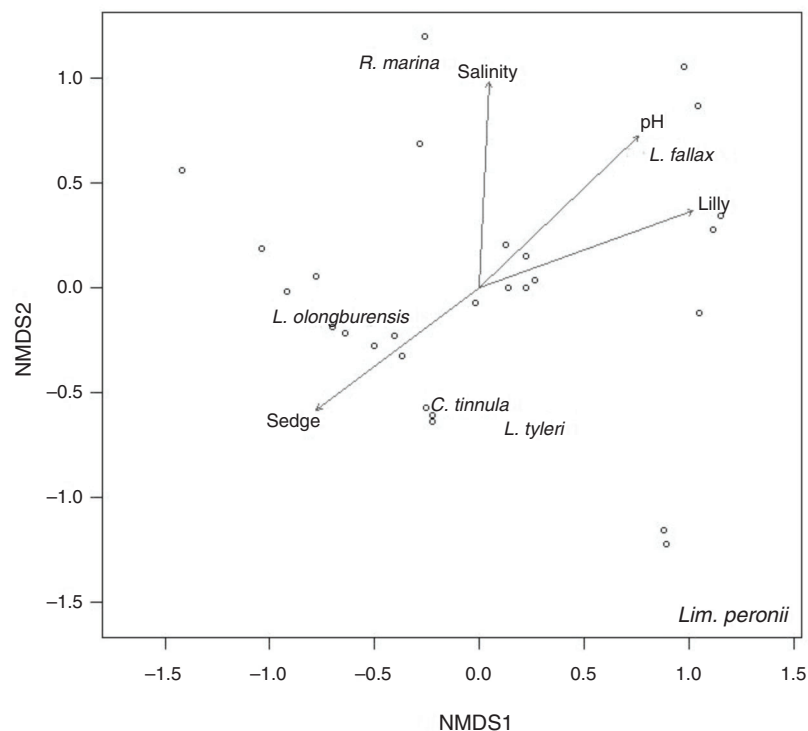


Fig. 2. nMDS ordination of waterbodies for anuran species where a relative abundance measurement was calculated. Stress associated with dimensions used in MDS ordination was 0.0268. Species ordinations are overlaid. Environmental variables significantly influencing the community structure are displayed. Circles represent waterbodies.

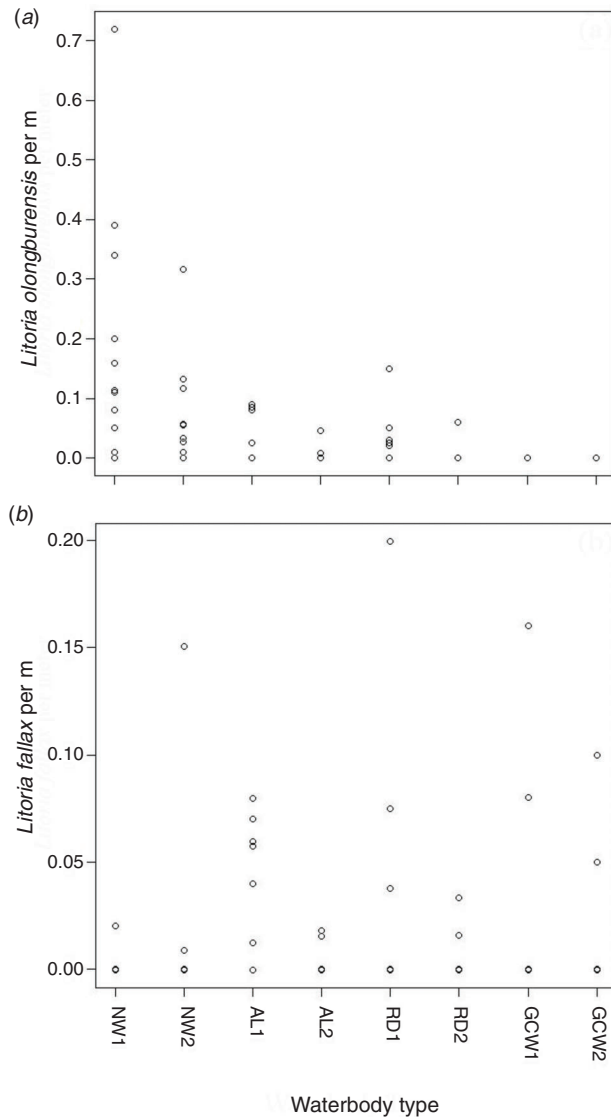


Fig. 3. 'Jitter' plot for relative abundance counts of (a) *L. olongburensis* and (b) *L. fallax* in natural and anthropogenic waterbodies. Abbreviations on the x-axis represent the first surveys at natural (NW1), artificial lakes (AL1), road side ditches (RD1) and golf course waterbodies (GCW1) and the second surveys at natural (NW2), artificial lakes (AL2), road side ditches (RD2) and golf course waterbodies (GCW2).

best model was 78.7%, indicating that the other models compared poorly (Table 3). This model contained % sedge density and pH. *Litoria olongburensis* abundance had a positive relationship with increasing % sedge density and a negative relationship with increasing pH. Both % sedge density and pH had high relative variable importance. However, pH had a confidence interval that intersected zero, reducing the evidence that this variable had a strong influence on *L. olongburensis* relative abundance (Table 4).

Five models for *L. fallax* relative abundance had a $\Delta_i < 2$ and five models had a $\Delta_i \leq 2-4$. The combined weighting for models with $\Delta_i \leq 2$ was 61.8%. The combined weighting for models with $\Delta_i \leq 2-4$ was 28.6%. This gave a total weighting of 90.4%

Table 3. Models with a Δ_i value < 4 for *L. olongburensis* and *L. fallax* adult relative abundance per metre for 2011 surveys

(+) indicates a positive relationship while (–) indicates a negative relationship between relative abundance and the model variable

Model	AIC _c	Δ_i	w_i
<i>Litoria olongburensis</i>			
(+) % Sedge – pH	150.8	0.00	0.787
<i>Litoria fallax</i>			
(–) % Sedge	159.5	0.00	0.219
(–) <i>L. olongburensis</i> abundance	160.6	1.08	0.127
(–) Waterbody size	160.9	1.46	0.105
(–) % Fern	161.4	1.88	0.085
(+) % Grass	161.4	1.96	0.082
(–) % <i>Melaleuca</i>	161.8	2.32	0.069
(–) Turbidity	161.8	2.34	0.068
(+) % <i>Gahnia</i>	162.1	2.64	0.058
(–) % Sedge + % <i>Gahnia</i>	162.3	2.85	0.053
(+) Predatory fish abundance	163.0	3.52	0.038

Table 4. Estimates for model averaged coefficients, standard error, confidence interval and relative variable importance for each parameter in models where $\Delta_i < 4$ for *L. olongburensis* and *L. fallax* tadpole relative abundance

(+) indicates a positive relationship while (–) indicates a negative relationship between relative abundance and the model variable

Parameter	Estimate	s.e.	CI	Relative variable importance
<i>Litoria olongburensis</i>				
(+) % Sedge	3.66	0.615	2.44, 4.86	0.94
(–) pH	–0.6	1.16	–2.88, 1.67	0.85
<i>Litoria fallax</i>				
(–) % Sedge	–0.81	1	–2.78, 1.16	0.33
(–) <i>L. olongburensis</i> abundance	–3.95	4.38	–12.53, 4.62	0.13
(–) Waterbody size	–0.00004	–0.00003	–0.0001, 0.00002	0.11
(–) % Fern	–7.01	7.76	–22.22, 8.19	0.09
(+) % Grass	0.39	3.22	–5.92, 6.7	0.11
(–) % <i>Melaleuca</i>	–0.84	4.61	–9.87, 8.19	0.07
(–) Turbidity	–0.0014	–0.0017	–0.004, 0.002	0.08
(+) % <i>Gahnia</i>	1.64	2.65	–3.55, 6.83	0.14
(+) Predatory fish abundance	–0.023	–0.09	–0.15, 0.2	0.05

for all models with $\Delta_i \leq 4$, indicating that the other models compared poorly (Table 3). Models with a $\Delta_i < 2$ contained % sedge density, *L. olongburensis* relative abundance, waterbody size, % fern density and % grass density. All these variables, with the exception of % grass density, were negatively associated with *L. fallax* relative abundance. Models with a $\Delta_i \leq 2-4$ contained % *Melaleuca* density, % *Gahnia* density, % sedge density, turbidity and predatory fish. Predatory fish and % *Gahnia* density were the only variables within models where $\Delta_i \leq 2-4$ that were positively associated with *L. fallax* relative abundance. Percent sedge density had the highest relative

variable importance compared with the other variables within models where $\Delta_i \leq 4$. However, all variables had a confidence interval that included zero, indicating reduced evidence that these variables had a strong influence on *L. fallax* relative abundance (Table 4).

Discussion

Frog assemblages

Our results are similar to the majority of surveys conducted within the northern hemisphere (predominantly North America and Europe) that found frog species richness to be higher or equal in artificial, restored waterbodies (reviewed by Brown *et al.* 2012). Frog assemblage patterns in waterbodies are not consistent, however, and previous Australian studies have reported variable patterns in species richness within and among both natural and constructed waterbodies (Hazell *et al.* 2004; Lemckert and Mahony 2010; Smallbone *et al.* 2011; Hamer *et al.* 2012; Sievers *et al.* 2018).

The differences and similarities of our findings to previous studies are likely explained by the ability of individual species to respond to differences in the environmental variables that significantly influenced the frog assemblage (i.e. pH, % sedge density, % lily density). Vegetation variables significantly influencing the frog assemblage are likely a result of particular species 'favouring' certain varieties of vegetation. This was observed for *L. olongburensis*, which was found predominantly on sedge species and supports previous studies that found *L. olongburensis* prefers perching on certain sedge species (Shuker and Hero 2013). Intolerance to water chemistry levels by different frog species tadpoles explains the influence of water chemistry variables on the frog assemblage, as adults have been shown to avoid depositing eggs in waters where water chemistry variables are unfavourable for successful reproduction (Takahashi 2007). For example, post-Gosner stage 25 tadpoles of *L. fallax* failed to metamorphose when exposed to acidic waters (i.e. pH 3.5), whereas acid-water adapted tadpoles species (i.e. *C. tinnula*) successfully metamorphosed in pH waters of 3.5, 4.5, and 5.0 (Meyer 2004).

Intolerance to water chemistry variables only explains why some species may be influenced by water chemistry. Species that can tolerate a wide range of water chemistry variable levels may be excluded from or be less common in waterbodies due to competition or predation. It has been hypothesised that competition may explain the distributions of *L. fallax* and *L. olongburensis* within waterbodies across the studied landscape (Meyer *et al.* 2006), as shown by previous studies revealing competitive interactions between other amphibian species (Wiltshire and Bull 1977; Twomey *et al.* 2008).

Surprisingly, the acid frog species *L. freycineti* was only recorded from roadside ditches. This species is infrequently encountered in natural waterbodies within coastal wallum systems; however, it is occasionally recorded from disturbed sites (i.e. drainage lines (Meyer *et al.* 2006), on roads away from wetlands (J.-M. Hero, pers. obs.) and fire trails near water (C. A. Simpkins, pers. obs.). These disturbed areas often have lower vegetation density, which would likely increase detectability of this species when compared with natural waterbodies, where vegetation density is often dense. Therefore, the absence

of this species from natural waterbodies may be false and the interpretation of natural habitat usage for this species is difficult. However, our results do indicate that usage of artificial lakes and golf course waterbodies by this species is low, possibly due to higher pH levels and, within golf course waterbodies, competition from the non-acid frog species *L. nasuta*, which has been proposed as a potential competitor of *L. freycineti* (Meyer *et al.* 2006).

Variables influencing *L. olongburensis* and *L. fallax* relative abundance

The variables most strongly associated with *L. olongburensis* relative abundance were high sedge density and low pH. Sedge density positively influenced *L. olongburensis* abundance with individuals predominantly found perching on sedge species. Amphibians may have coloration that assists with camouflage in their natural environment (Toledo and Haddad 2009). This has been suggested to occur with *L. olongburensis*, with sedge and dorsal coloration or patterning possibly aiding with camouflage (Lowe and Hero 2012). Our results are consistent with a past survey that showed *L. olongburensis* were located predominantly within coastal wallum waterbodies containing sedges (Lewis and Goldingay 2005). Our findings are also consistent with Lewis and Goldingay (2005) whose data indicated *L. olongburensis* are a specialist species predominantly utilising ecological niches with high sedge density and waters where pH < 5.

It is difficult to determine the variables that were influencing *L. fallax* relative abundance as variables that were within the top models had low relative variable importance and had confidence intervals that included zero. This result suggests that a variable that is strongly influencing *L. fallax* relative abundance was not measured or that *L. fallax* is a generalist species, with the variables measured having the same relative influence on *L. fallax* relative abundance across the natural and modified landscape. Despite this, *L. fallax* numbers and occupancy within natural waterbodies (where pH was low and sedge density high) were low and were highest within artificial lakes (where pH was high and sedge was intermediate). As mentioned previously, this is likely a result of *L. fallax* tadpole intolerance to low pH waters (Meyer 2004). Additionally, our results indicate that *L. fallax* do not require waterbodies where sedge density is high.

Implications for conservation

Differing frog species occurring within different types of waterbodies indicate that a range of waterbody types, both natural and anthropogenic/modified, are required to effectively conserve the full range of assemblages and species currently present within the studied environment. Within wallum heathlands we recommend conservation should be primarily focused on natural waterbodies, where occupancy and presence of tadpoles for threatened, specialist species was highest. Hence, conserving natural waterbodies will be the conservation approach most likely to result in the persistence of the threatened species considered in this study.

The presence of *L. olongburensis* in artificial lakes and roadside ditches and the presence of *C. tinnula* in artificial lakes and golf course waterbodies indicate that these waterbodies can provide a form of habitat for adults of wallum associated

threatened frog species. These results provide evidence that recommendations to combat the effects of climate change in amphibian populations by establishing artificial waterbodies with longer hydroperiods (Shoo *et al.* 2011) can be implemented for *L. longgburensis* and *C. tinnula*. However, the low number of anthropogenic waterbodies with *L. longgburensis* tadpoles indicates that the majority of anthropogenic waterbodies are unfavourable for tadpole presence of this species. These waterbodies are likely unsuitable because they have environments with traits that are unfavourable for successful reproduction such as higher pH or incorrect water depths, as outlined by Simpkins *et al.* (2014). Conversely, while providing potential refuge habitat, these waterbodies may be ecological traps and would not be able to maintain continuing *L. longgburensis* and, potentially, *C. tinnula* populations. Furthermore, the road ditches with *L. longgburensis* tadpoles were adjacent to natural waterbodies. Under these circumstances, road side ditches may be able to permit recruitment as well as connectivity between waterbodies and further study is warranted on this subject.

With the exception of golf course waterbodies, the vast majority of waterbodies surveyed were surrounded by wallum heathland habitat. Therefore, results from this study may only be applicable to waterbodies where wallum heathland habitat is present. One ‘acid’ frog species (*L. cooloolensis*) has been located up to 1.3 km away from natural waterbodies within undisturbed environments (Simpkins *et al.* 2011). This suggests dispersal of *Litoria* ‘acid’ frog species (i.e. *L. longgburensis*) could occur over equal distances and, provided that natural habitat is still intact, modified/disturbed waterbodies that are established away from natural waterbodies may act as island habitats for adults of this species. Further study, where wallum heathland is not present around modified/disturbed waterbodies, is required to determine if ‘acid’ frogs can utilise waterbodies across disturbed landscapes.

Natural waterbodies where pH and sedge density are within the apparent preferred ranges for *L. longgburensis* should be given top priority for conservation as these would appear most likely to provide suitable habitat for this species. If construction or conservation of artificial waterbodies is undertaken for habitat loss compensation or in an attempt to reduce the risks of climate change, then the variables found here to be highly correlated with the presence and abundance of *L. longgburensis* (high sedge density, low pH) should be the target conditions for the waterbody. In addition to this, variables that are ideal for *L. longgburensis* tadpole presence (Simpkins *et al.* 2014) and recruitment (Lowe *et al.* 2015) need to also be attained.

Conflicts of interest

The authors declare no conflicts of interest.

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