



## Original Articles

## The effect of inundation on frog communities and chorusing behaviour

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## ABSTRACT

Globally, river regulation has degraded wetlands, including parts of the Murray-Darling Basin (MDB), an ecologically significant basin in Australia. Frogs in a floodplain environment largely depend on habitats created by river flows, but little is known about how frogs in the northern MDB are impacted by river regulation. We tested how wetland inundation affected frogs in a catchment of the northern MDB. We surveyed frogs between 2015 and 2019 to determine long-term changes in the community composition associated with wetland inundation from river flows. Additionally, we recorded nightly soundscapes for four days before and after the arrival of river flows between 2019 and 2020. The abundance and richness of frog species increased during larger inundation events leading to altered community composition (beta diversity). Warmer temperatures increased frog species richness, and frog community dominance decreased with decreasing vegetation cover (i.e., the relative abundance became more even across species). The abundance of five frog species (*Limnodynastes tasmaniensis*, *Limnodynastes fletcheri*, *Crinia parinsignifera*, *Litoria peronii*, and *Litoria latopalmata*) was higher in response to increased inundation extent. The total species richness of chorusing frogs increased after the arrival of river flows; six species chorused over the four nights preceding flow, whereas eight species chorused following the flow arrival, but the responses varied among species and sites. Frog species richness increased at three sites after flows, but not at others. After inundation, the choruses of *Limnodynastes tasmaniensis* increased whereas *Limnodynastes fletcheri* decreased. Our findings indicate that wetland inundation is beneficial for frog communities and suggest that chorusing behaviour varied in response to river flows inundating floodplain wetlands.

## 1. Introduction

River flows drive the community composition of floodplain biota by connecting river channels and floodplain wetlands (Kuiper et al., 2014), while river regulation impedes wetland connectivity and reduces biodiversity (Frazier and Page, 2006; Kingsford, 2000). Environmental watering is one useful strategy to restore connectivity and inundation in floodplain wetlands (Arthington et al., 2018). In this strategy, water is allocated to the environment and released from upstream storages (through water sharing rules and water licences; Arthington et al., 2018). Understanding responses of aquatic taxa, such as frogs, to inundation is crucial for understanding the ecological outcomes of water

management decisions (Holgerson et al., 2019; Rogers et al., 2012; Mathwin et al., 2021), and measuring long-term success of environmental watering is important for optimizing its delivery.

In floodplain wetlands, various biotic and abiotic factors influence how frogs respond to inundation. For example, rainfall, temperature, and seasonality in combination with wetland inundation can influence frog populations (Ocock et al., 2014, 2016; Wassens and Maher, 2011). Such relationships vary among species. For example, some species only call in warmer temperatures, whereas others can call in inundated habitat year-round, regardless of temperature (Amos, 2017; Wassens, 2011). Additionally, some species only respond to watering events that coincide with their breeding season (McGinness et al., 2014; Wassens

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et al., 2009). Due to favourable habitat conditions in periodically inundated sites, frog richness and abundance is often higher in temporary wetlands compared to permanent sites (Hoffmann, 2018), which can influence the beta diversity (comparisons of community composition between communities; Davis et al., 2017; Henning and Schirato, 2006).

The Murray-Darling Basin (MDB) is a large area of interconnected rivers and floodplain wetlands across south-eastern Australia, including wetlands recognised as internationally significant Ramsar sites, such as the Gwydir Wetlands in the northern MDB (Rogers and Ralph, 2010; RIS, 1999). Despite the regions' conservation significance and the heavy impact of river regulation and land modification across the catchment, little is known about frog diversity, community composition, and chorusing activities in relation to river flows and wetland inundation in the northern MDB (Kingsford, 2000). Most studies have been limited to examining short-term (i.e., seasonal and annual) trends (Moreira et al., 2017; Ocock et al., 2016), with longer-term trends still poorly understood. Though frog chorusing is a measure of potential breeding behaviour, most calling surveys are limited to call counts and presence or absence of calling males (Brodie et al., 2020; McGinness et al., 2014) rather than patterns in chorusing behaviour over time specifically in response to multi-year wetting and drying cycles.

The aims of our study were to 1) examine the variation in frog abundance, richness, dominance (the inverse of species evenness), and beta diversity over a five-year period and examine associations with wetland inundation, temperature, rainfall, and vegetation covers, and 2) use passive acoustic monitoring to compare variation in frog chorusing activity, before and after river flows inundated sites. We expected that in

the Gwydir River catchment, inundation from river flows would be beneficial for frog species.

## 2. Methods

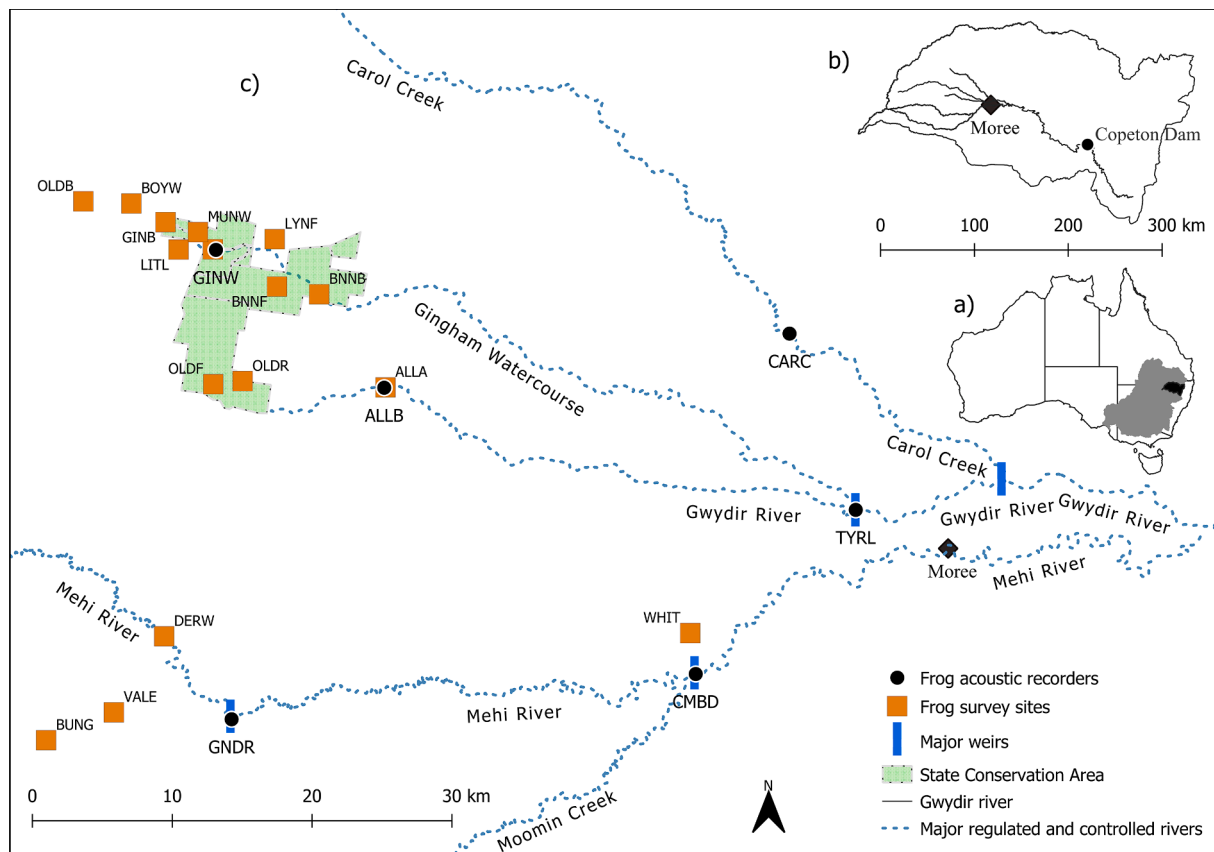
### 2.1. Study site

Sixteen sites (Fig. 1c) were monitored over a five-year period across the Gwydir Wetland system of the northern MDB, downstream and west of Moree, New South Wales, Australia (Fig. 1a). Habitats surveyed were permanent and temporary waterbodies including shallow open waterholes, in-stream channels, and lagoons with aquatic vegetation and surrounding woodland. We also deployed acoustic recorders at six sites including instream channels, pools, and wetlands across the system (Fig. 1c). Due to the region experiencing severe drought conditions in spring 2019, the sites had limited inundated floodplain habitat available unless filled with river flows, an ideal scenario to test how frogs respond to inundation from river flows.

### 2.2. Data collection

#### 2.2.1. River flows

River flows included water from managed environmental water delivery from Copeton Dam (Fig. 1b) along with natural run-off water (local rainfall and tributaries) that inundated sites during the monitoring period. Measurement of river flow (megalitres/day) from the nearest gauging station (Water NSW 2020) and dates of environmental watering events (Table 1) were used to determine peaks in flow that



**Fig. 1.** Locations of a) the Gwydir River catchment (shaded black) in the Murray-Darling Basin (shaded grey), b) Gwydir River Catchment and location of Moree city and Copeton Dam in the upstream of the frog survey sites, and c) 16 frog survey sites and six acoustic data collection sites. Abbreviation used for 16 frog survey sites: Bunnor Bird Hide (BNNB), Bunnor Floodplain (BNNF), Gingham Waterhole (GINW), Little Lagoon (LITL), Lynworth Floodplain (LYNF), and Munwonga Wetland (MUNW), Ardblair Waterhole (previously known as Boyanga Waterhole, BOYW), Gingham Bridge (GINB), Old Boyanga Wetland (OLDB), Allambie Bridge (ALLA), Old Dromana Floodplain (OLDF), Old Dromana Ramsar (OLDR), Bungunya Wetland (BUNG), Valetta Wetland (VALE), Derra Waterhole (DERW), and Whittaker's Lagoon (WHIT). See Table 2 for abbreviation used for six acoustic survey sites.

**Table 1**

Environmental water delivery events aligned with the frog surveys from 2015 to 2020.

Frog surveys		Environmental water delivery dates and duration
Year	Months	
2015	Sept, Nov	28 Aug – 6 Sept 2015, 1 Nov – 1 Dec 2015, 7–11 Nov 2015
2016	Sept, Nov	24 Jun – 7 Aug 2016, 17–21 Sept 2016, 25 Dec 2016 – 28 Feb 2017
2017	Feb, Sept, Nov	25 Dec 2016 – 28 Feb 2017, 13 Jan – 3 Apr 2017, 26 Aug – 4 Sept 2017, 1–31 Sept 2017, 19 Dec 2017 – 18 Jan 2018, 14–29 Nov 2017
2018	Sept, Nov	6 Sept 2018 – 14 Feb 2019, 1–30 Sept 2018, 17 Jul – 7 Feb 2019
2019	Mar, Sept, Oct, Nov	6 Sept 2018 – 14 Feb 2019, 17 Jul 2018 – 7 Feb 2019, 15–25 Oct 2019*
2020	Feb, Mar	5–28 January 2020*

\* two watering events aligned with the deployment of the acoustic recorders.

aligned with the frog surveys.

### 2.2.2. Five-year frog surveys

From 2015 to 2019, acoustic and visual encounter surveys (VES) were completed in September and November of each year with additional surveys completed in February 2017 and March 2019. Five-minute listening surveys were conducted prior to timed VES which were completed by two experienced surveyors for a total of one person-hour. Visual encounter surveys commenced at least 30 min after sunset and were completed by 2:00 am using head torches (maximum 1000 lm). Each individual frog was counted and identified to species including individuals that were heard (but not seen) in close proximity to the surveyor (within a radius of approximately one metre). There was just one group of burrowing frogs that were not confirmed to species level: *Cyclorana verrucosa*, which is physically indistinguishable from *Cyclorana cultripes*, and we were only able to confirm the presence of *Cyclorana cultripes* based on audio records of its call. For each species of frog calling during the timed-audio surveys, the number of individuals heard was estimated using the following categories: no calling, rare (1–5 individuals), common (6–10 individuals), abundant (11–20 individuals), or very abundant ( $\geq 20$  individuals). Visual encounter surveys and listening surveys data were combined for analyses. Because the listening data were recorded in categories, the midpoints of each audio category were used for abundance, evenness, and beta diversity calculations. For example, if 12 individuals were seen and the audio survey abundance category of “rare” was recorded (for between 1 and 5 individuals heard calling), the total number was entered as 15 in the analyses.

Ambient air temperature was recorded at the beginning of the survey using a Kestrel pocket weather meter (Model: 3500 Delta T). The percent of water inundated at a site at the time of each survey (hereafter “inundated area”) was estimated in the daytime by visually assessing each site and comparing the observed inundated area with wetland delineation maps of the sites. Rainfall data were derived from the Australian Bureau of Meteorology (BoM) rainfall gauge data (BoM, 2020) using the nearest weather station within a 12–70 km radius of each survey site. Using these data, cumulative rainfall was calculated over four periods prior to each survey (rain in past 24, 48, 72, and 96 h). Several vegetation categories were measured at each site on each survey occasion: emergent vegetation (tall and short), aquatic vegetation (low growing, floating, and submerged), total vegetation (sum of emergent and aquatic vegetation), dry bare ground, terrestrial vegetation cover, and open water (i.e., no vegetation). To determine the percent area covered by each vegetation category, three random 5 × 5 m quadrats were placed at the site. For each quadrat, vegetation category estimates could total >100 % when combined because layers of different vegetation types could grow above and among one another.

### 2.2.3. Acoustic recordings

We recorded soundscapes for four nights immediately before and after the arrival of river flows following two environmental water releases (Table 1). We deployed a Bioacoustic Audio Recorder (BAR) (Firmware: V2.99, FRONTIER LABS) at each site to record choruses continuously from 1700 h to 0700 h with a sample rate of 44.1 kHz in stereo WAV file format, resulting in 14 h of recordings per night. We compared frogs’ calling in sites before and after river flow, which we considered one flow event per site. At all sites, flow events happened in November, except for Gingham Waterhole where flow occurred in Feb–Mar (Table 2). One night of recording was missed at the Gingham Waterhole (fourth night after flow arrival) due to equipment failure (Table 2).

We recorded river flow as a binary category (before arrival of water = false or after = true). Nights when water arrived at sites were determined by using river flow measurements (megalitres/day) from the nearest gauging station (Water NSW 2020) and examining sentinel hub images for site inundation (Sentinel, 2020) following the environmental watering events. We obtained daily rainfall and minimum temperature from BoM (2021) using the nearest weather station for each site (9–43 km).

To analyse our acoustic recordings, we used long-duration ‘false-colour’ spectrograms (FCS) to visually detect different frog choruses (Brodie et al., 2020, 2022; Fig. 2). False-colour spectrograms are graphical display tools calculated from acoustic indices (Indraswari et al., 2020) to visualise long duration audio recordings (up to 24 h), compressed into a single spectrogram and viewable as a single image (Towsey et al., 2014). Acoustic indices are numeric summaries of the energy distribution in a recording based on amplitude or spectral content (Sueur et al., 2014). We used QUT Ecoacoustics Audio Analysis Software v20.11.2.0 (Towsey et al., 2017) to generate the FCSs following methods in Towsey et al., (2014, Towsey et al. 2015). Each frog chorus was identified by the colour, call frequency, and signal shape (Table 3) in the FCS and confirmed by listening to the corresponding sections of the recordings.

Chorus duration reflects the number of calling males (Friedl and Klump, 2002; Calsbeek et al., 2022). Our aim was to detect frog species and calculate the chorus duration (in minutes) of each species per night recorded to determine how breeding behaviour (chorusing) was affected by the arrival of flow. Choruses were sometimes interrupted by brief pauses that made it difficult to precisely delineate choruses using the FCS. Therefore, to standardise the chorus calculation methods, we considered five minutes or more of continuous calling by a single species as a chorus and we ignored pauses < 20 min if continuous choruses for 5 min or more occurred on either side of the pause. Most pauses were substantially shorter than 20 min, and most choruses were longer than 5 min, so this approach should have had minimal impact on the results.

We used Raven Pro 1.6 (<https://ravensoundsoftware.com/>) to visually identify and measure the frequency range of the typical call of each species detected in spectrograms (Table 3). We used call frequency range to assist in identifying different frog species in the FCS (Fig. 2), and used the ‘imager’ package (Barthelme, 2020) and interactive functions in R (Brodie, 2020) to explore the FCS and confirm the identity of the frog species calling in the audio segments (Brodie et al., 2020, 2022). We then used Audacity (version 2.4.2, <https://www.audacityteam.org/>), which allows viewing and scrolling through long recordings in a continuous spectrogram, to identify the start and end of species’ choruses to calculate chorus duration (in minutes).

### 2.3. Statistical analyses

Statistical analyses were carried out using R- 4.0.1 (R Core Team, 2020) for the five-year frog monitoring data and R- 4.1.0. (R Core Team, 2021) for the acoustic recorder data.

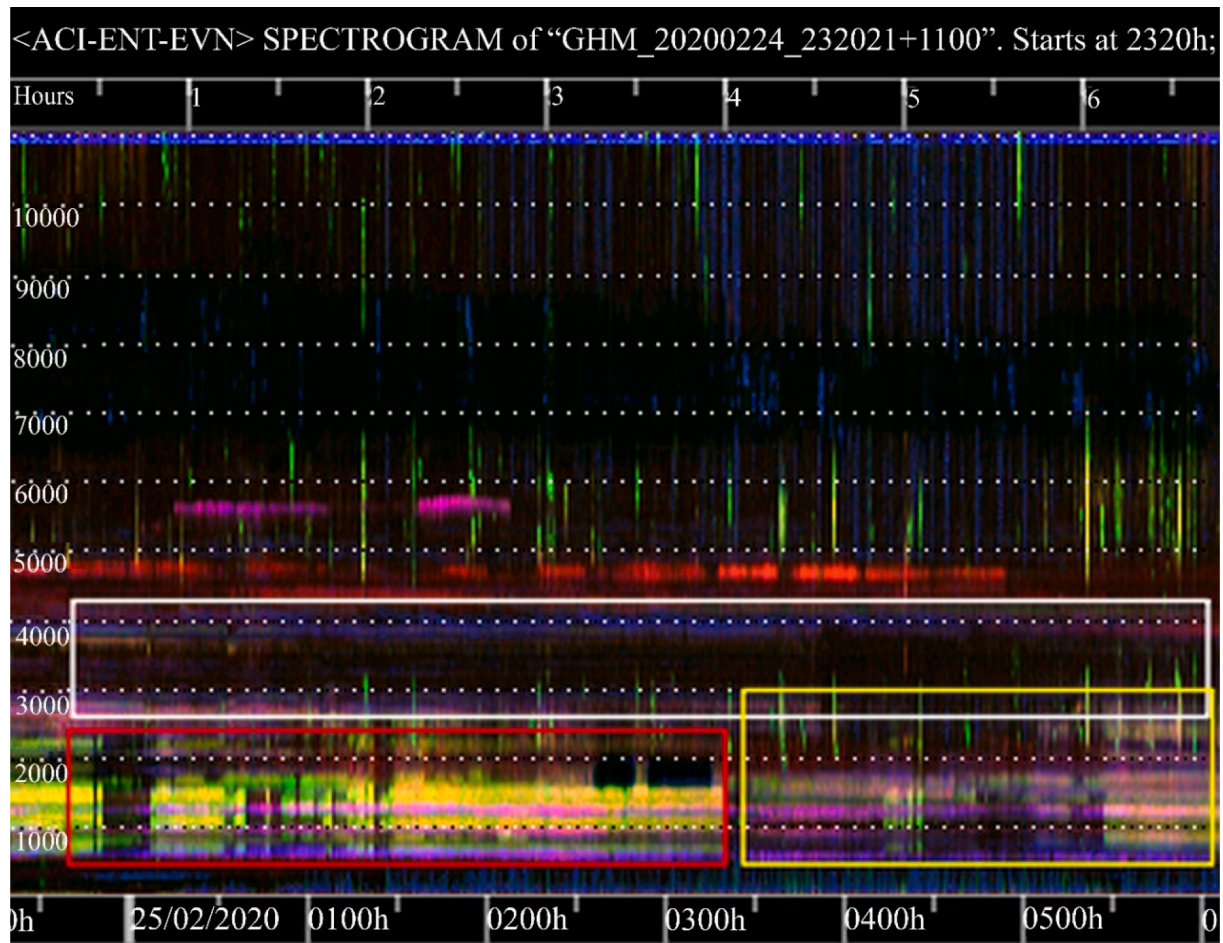


**Table 2**

Key characteristics of sites with acoustic recorders including acoustic recording dates, and rainfall recorded 24 h before flow arrival, minimum daily temperature, and general site hydrology (Temporary-T, Permanent-P).

Sites	Type	Total rainfall within 24 h (in mm)		Mean minimum temperature (°C)		Soundscape recording dates	
		Before flow	After flow	Before flow	After flow	Before flow	After flow
Allambie Bridge (ALLB)	River channel (T)	0	0	11.4	13.0	7–10 Nov 2019	11–14 Nov 2019
Carol Creek (CARC)	Creek (P)	0	4.6	18.8	14.4	30 Oct to 2 Nov 2019	3–6 Nov 2019
Combanello (CMBD)	In-stream weir (P)	0	4.6	18.8	14.4	30 Oct to 2 Nov 2019	3–6 Nov 2019
Gingham Waterhole (GINW)	Floodplain wetlands (T)	35.5	0	19.4	17.6	24–27 Feb 2020	28 Feb – 1 Mar 2020*
Gundare (GNDR)	In-stream weir (P)	0	0	13.3	15.1	13–16 Nov 2019	17–20 Nov 2019
Tyreel (TYRL)	In-stream weir (P)	0	4.6	18.8	14.4	30–31 Oct, 1–2 Nov 2019	3–6 Nov 2019

\*sites with 7 nights of data (one night missed due to equipment failure).



**Fig. 2.** An example of part of a false-colour spectrogram at Gingham Waterhole (abridged for clarity). Time is shown on the x-axis (2320 h–0605 h) and sound frequency on the y-axis (0–11,000 Hz). One pixel represents 1 min and approximately 43 Hz frequency range. Horizontal dotted lines delineate 1000 Hz frequency intervals. Frog chorus identified are: *Crinia parinsignifera* by purple shade marks in the frequency range 2200–4200 Hz (white square) from 0000 h to 0647 h, *Cyclorana alboguttata* by light green marks in the frequency range 500–2400 Hz (red square) from 0000 h to 0700 h, and *Limnodynastes fletcheri* by purple marks in the frequency range 400–3000 Hz (yellow square) from 2320 h to 0700 h. Other sounds identified are: insects - red 4000–5000 Hz and bright pink 5000–6000 Hz. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 2.3.1. Five-year frog surveys

We used mixed effect models to examine the influence of environmental variables on total frog abundance, species richness, and species dominance (the inverse of Shannon's evenness). We assessed species richness and dominance separately because combined alpha diversity measures (e.g., Shannon's diversity index) confound richness and evenness (e.g., a high Shannon's diversity can result from either high richness and low evenness or low richness and high evenness). Different types of models were used for each response variable based on the data distributions after checking the data for normality using QQ plots and

residual plots. Abundance data were analysed with zero-inflated negative binomial models via *glmmTMB* package (Brooks et al., 2017; Appendix Table A1), and richness and dominance were analysed with general linear mixed effects models via the *lmer* function in the *lme4* package (Bates et al., 2015; Appendix Table A2–A3). Only surveys where at least two species of frog were documented were included in the dominance models (dominance is not informative with only one species), whereas all surveys were included in the richness models, even if no frogs were documented. Dominance was calculated by subtracting Shannon's evenness from one, and a square root transformation was

**Table 3**

Frog species detected during acoustic monitoring and the frequency range of typical calls. Mean and standard deviation (SD) of call duration of each species are shown before (BF) and after flow (AF) as well as the number of sites where each species was detected.

Species	Abbr.	Call frequency range (Hz)	Mean and SD of call duration in minutes		No. of sites frogs detected	
			BF	AF	BF	AF
<i>Crinia parinsignifera</i>	CP	2200–4200	303.3 (SD ± 325.4)	571.4 (SD ± 151.1)	1	2
<i>Cyclorana alboguttata</i>	CA	500–2400	381.8 (SD ± 223.4)	0	1	0
<i>Cyclorana cultripes</i>	CC	600–800	0	202.3 (SD ± 350.5)	0	1
<i>Cyclorana verrucosa</i>	CV	200–1900	0	96.8(SD ± 193.5)	0	1
<i>Limnodynastes fletcheri</i>	LF	400–3000	224.2 (SD ± 255.4)	95.5(SD ± 187.8)	3	2
<i>Limnodynastes salmini</i>	LS	300–4000	0	283.0 (SD ± 335.9)	0	1
<i>Limnodynastes tasmaniensis</i>	LT	650–3600	132.3 (SD ± 192.5)	283.4 (SD ± 225.4)	3	5
<i>Litoria latopalmata</i>	LL	1300–3700	121.8 (SD ± 186.8)	44.3(SD ± 118.9)	4	4
<i>Litoria peronii</i>	LP	800–2600	261.6 (SD ± 239.0)	345.4 (SD ± 258.5)	4	4

applied to achieve an acceptable model fit.

For all models, inundated area, temperature, rain, and vegetation were included as the fixed effects, and study site and survey date (nested in season) were included as random intercepts (survey date was defined as each month \* year combination, and seasons were: autumn, spring, and summer). For the rain category, several cumulative measurements were calculated (rain in the preceding 24, 48, 72, or 96 h). Therefore, for each analysis, we determined which measurement of rainfall was most appropriate by constructing a model for each measurement and selecting the model with the lowest AIC as the final model for analysis (REML was set to false for model selection and true for the final analysis). Similarly, vegetation variables (emergent aquatic, aquatic, total vegetation [emergent and aquatic], dry bare ground, terrestrial vegetation cover, and open water) were correlated because they were estimates of percent cover. To select the most appropriate vegetation predictor variable for each model, we again constructed models using each variable and selected the model with the lowest AIC for the final analysis.

Finally, we tested the effects of the environmental variables on frog community composition (beta diversity measured with Bray-Curtis dissimilarities) using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) via the *adonis2* function in the *vegan* package (Oksanen et al., 2020; Appendix Table A9). We used survey month as strata and included study site as the first term in the model. Inundated area, air temperature, rainfall, and vegetation variables were also included. The order of these terms was based on the order of significance (most to least) in the abundance models, while the rainfall and vegetation variables were the same as those selected for the abundance models. To account for differences in total abundance, all numeric data were transformed to proportions prior to calculating Bray-Curtis dissimilarities, i.e., for each survey the total number of individuals per species was divided by the total number of individuals in the survey (McKnight et al., 2019). Additionally, when sample sizes allowed, a separate abundance model was constructed for each frog species

(Appendix Table A4–A8).

### 2.3.2. Acoustic recordings

We used mixed effects models to test the effect of arrival of river flows on frog chorusing. First, we ran a model using data from all frog species (Appendix Table B1). From this model, we calculated the mean chorus duration for all nights before and after arrival of water at each site (average four nights before and four nights after water arrived) and included chorus duration as the response variable. We included river flow, frog species, rainfall in the previous 24 h (summed across all nights before and after river flow arrived), and minimum air temperature (averaged across all nights before and after river flow arrived) as fixed effects (with an interaction between river flow and species), and study site as a random effect. Following this model, we ran species specific models for the four species that called in at least three sites: *Limnodynastes fletcheri*, *Limnodynastes tasmaniensis*, *Litoria latopalmata*, and *Litoria peronii* (Fig. 5A, Appendix Table B2–B5). These models were structured in the same way as the previous model with the exclusion of the species term and interaction. Additionally, rainfall was not included for the *Limnodynastes fletcheri* model because it only rained twice.

We used a similar model to test the arrival of river flow on frog species richness (Appendix Table B6). We calculated frog species richness across all nights before and all nights after arrival of river flow for each site. We again included river flow, rain, and temperature as fixed effects (calculated as before) with site as a random effect.

We constructed the models in the *lme4* package (Bates et al., 2015) and assessed significance with the ‘Anova’ function in the *car* package (Fox and Weisberg, 2019) using a type II sum of squares. For all models, we checked model assumptions using QQ plots and residual plots. For the chorus duration model using all species data, we had to square root transform the chorus duration data to achieve acceptable model fit. All other models used the raw data. For all models, we used a combination of all four nights (before flow and after flow) rather than treating each night as a replicate because treating each night as a replicate resulted in models that were too complex to be fit reliably with the small samples sizes.

## 3. Results

### 3.1. Five-year frog surveys

A total of 12 species and 6 651 individual frogs were recorded. *Limnodynastes tasmaniensis* was the species with highest recorded abundance ( $n = 2\ 810$ ) and *Cyclorana verrucosa* had the lowest abundance ( $n = 1$ , further taxonomic verification required). The most widespread species were *Limnodynastes fletcheri*, *Limnodynastes tasmaniensis*, and *Crinia parinsignifera* which were detected at all the sites, followed by *Litoria peronii* which was detected in 14 of the sites surveyed. Among years (all surveyed sites combined), observed species richness was highest in 2018 ( $n = 10$ ) and lowest in 2016 and 2019 ( $n = 8$  for both). The highest frog abundance was recorded in 2017 ( $n = 2\ 159$ ), followed by 2016 ( $n = 1\ 651$ , 23.53 % lower detection from 2017) and 2018 ( $n = 1\ 386$ , 35.80 % lower detection from 2017), and lowest was in 2019 ( $n = 262$ , 87.86 % lower detection from 2017).

Abundance and richness of frog species were significantly higher at sites with larger inundated areas (both  $P < 0.0001$ ; Table 4, Fig. 3A and 3B), and with every 25 % increase in inundation at a site, the abundance and richness of frogs increased by 0.56 individuals ( $r^2 = 0.1175$ ) and by 0.63 species ( $r^2 = 0.1175$ ). Rainfall did not significantly affect frog abundance and richness (both  $P > 0.05$ ; Table 4). Species richness was significantly higher with warmer air temperatures ( $P = 0.045$ ; Table 4, Fig. 3D), with a maximum of seven species present when air temperature was over 16 °C. Dominance of frogs was significantly lower in sites with a higher proportion of open water (thus less vegetation cover) ( $P = 0.004$ ; i.e., evenness was higher where there was more vegetation; Fig. 3C), and with every 25 % decrease in vegetation cover the

**Table 4**

Fixed terms in the final models and associated p-values for abundance, richness, dominance, beta diversity (PERMANOVA), and single-species abundance. (See more details in [Appendix Table A1–A9](#)).

	Inundated area	Air temperature	Rainfall	Vegetation cover
Abundance	<0.001	0.510	0.122	0.500
Richness	<0.001	0.045	0.432	0.872
Dominance	0.097	0.072	0.855	0.004*
Beta diversity	0.003	0.024	0.150	0.019
<i>Limnodynastes tasmaniensis</i>	<0.001	0.365	0.311	0.992
<i>Limnodynastes fletcheri</i>	0.0004	0.304	0.298	0.103
<i>Crinia parinsignifera</i>	<0.001	0.669	0.996	0.771
<i>Litoria peronii</i>	0.0003	0.099	0.175	0.103
<i>Litoria latopalmata</i>	0.041	0.053	0.104	0.652

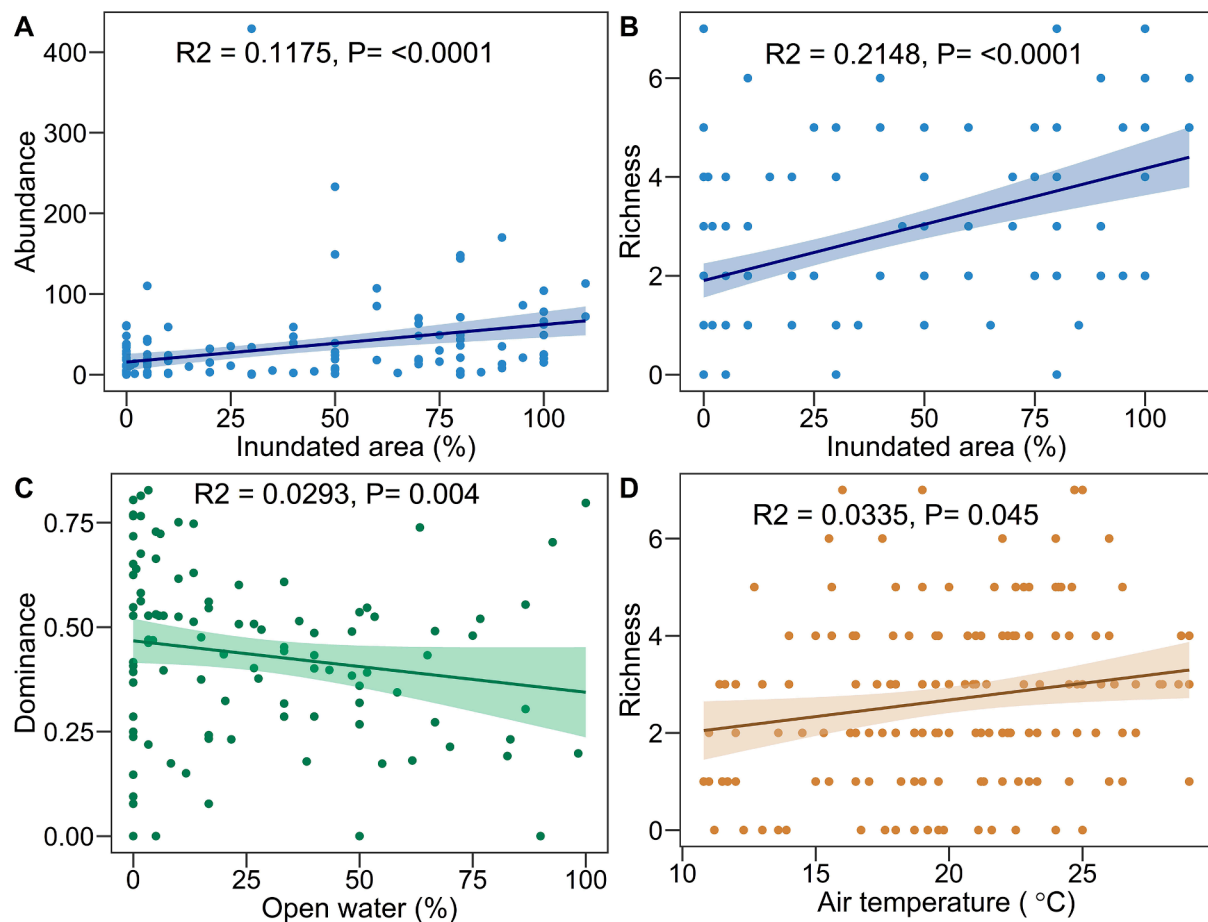
\*For this model, “open water” (i.e., areas of water with no vegetation) had negative association and was selected by lowest AIC indicating the best fit. Thus, this negative influence suggests a positive association with vegetation.

dominance decrease by 0.06 individuals ( $r^2 = 0.0293$ ). Species dominance was not affected by the area inundated, air temperature, or rainfall (all  $P > 0.05$ ; [Table 4](#)). The frog community composition (beta diversity) differed significantly among sites ( $P = 0.0002$ ) and inundation, temperature, and vegetation significantly affected frog community composition (all  $P < 0.05$ ), but rainfall did not significantly affect community composition ( $P = 0.15$ ) ([Table 4](#)). Abundance of *Limnodynastes tasmaniensis*, *Limnodynastes fletcheri*, *Crinia parinsignifera*, *Litoria*

*peronii*, and *Litoria latopalmata* were significantly higher at sites with greater inundated areas (all  $P < 0.05$ ; [Table 4](#), [Fig. 4](#)). The abundance of frogs increased by 1.17 frogs for every 25 % increase of inundation in *Crinia parinsignifera* ( $r^2 = 0.1563$ ), by 0.50 in *Litoria peronii* ( $r^2 = 0.0849$ ) and *Limnodynastes tasmaniensis* ( $r^2 = 0.0708$ ), and by 0.30 in *Limnodynastes fletcheri* ( $r^2 = 0.0138$ ) and *Litoria latopalmata* ( $r^2 = 0.0272$ ).

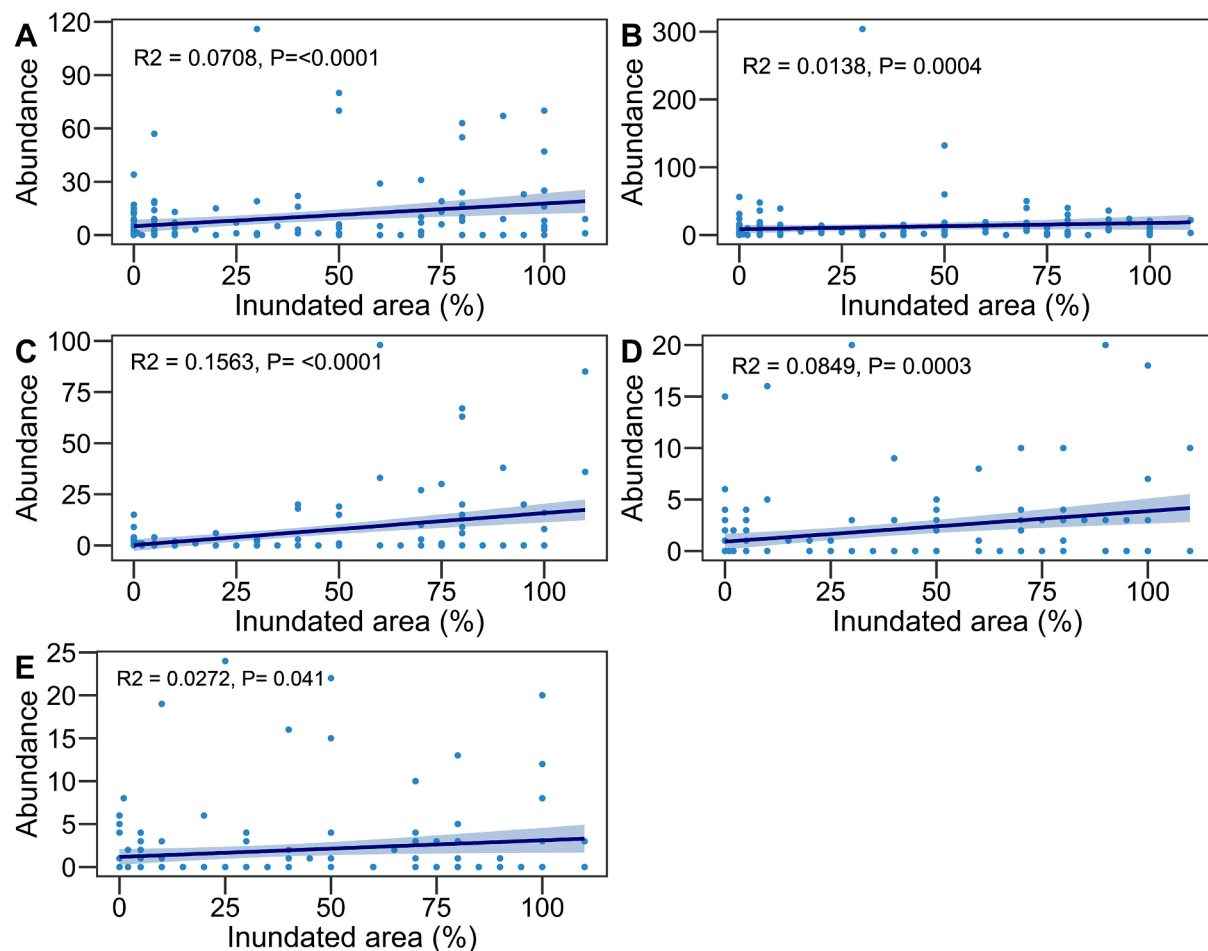
### 3.2. Acoustic recordings

During the acoustic monitoring, a total of nine frog species were detected ([Table 3](#)). In the call duration model with all nine species, there was a significant main effect of species ( $\chi^2 = 16.9$ ,  $P = 0.031$ ), but the main effects of arrival of water ( $\chi^2 = 2.6$ ,  $P = 0.107$ ), temperature ( $\chi^2 = 1.1$ ,  $P = 0.298$ ), and rain ( $\chi^2 = 0.005$ ,  $P = 0.945$ ) were not significant. However, the interaction between river flow and species was significant ( $\chi^2 = 18.8$ ,  $P = 0.016$ ), indicating that the arrival of water had different effects on different species ([Fig. 5A](#), [Table 3](#)). Subsequent species-specific models showed that chorus duration increased by 117.55 min with flow for *Limnodynastes tasmaniensis* ( $\chi^2 = 41.9$ ,  $P < 0.001$ ), decreased by 154.01 min for *Limnodynastes fletcheri* ( $\chi^2 = 25.0$ ,  $P < 0.001$ ), and was not significantly affected for *Litoria latopalmata* ( $\chi^2 = 0.1$ ,  $P = 0.770$ ) and *Litoria peronii* ( $\chi^2 = 0.3$ ,  $P = 0.583$ ). Chorus duration decreased by 11.28 min and 32.12 min with increasing temperature for *Limnodynastes fletcheri* ( $\chi^2 = 9.47$ ,  $P = 0.002$ ) and *Limnodynastes tasmaniensis* ( $\chi^2 = 5.5$ ,  $P = 0.021$ ), but chorus duration increased by 42.10 min with increasing temperature for *Litoria latopalmata* ( $\chi^2 = 5.6$ ,  $P = 0.018$ ). Rainfall was not significant in any model (all  $P > 0.143$ ), but few nights of rain occurred during the study, resulting in limited power.



**Fig. 3.** Effect of inundated areas on frog (A) abundance (all species combined), (B) richness, (C) effect of open water (or vegetation cover) on frog dominance (for this model, the “open water” variable was the habitat variable with the best fit; higher proportions of open water indicated a lack of vegetation within the waterbody), and (D) effect of air temperature on frog richness. Each point represents an individual survey and regression line with 95% confidence interval (shaded area).





**Fig. 4.** Effect of inundated areas on abundance of (A) *Limnodynastes tasmaniensis*, (B) *Limnodynastes fletcheri*, (C) *Crinia parinsignifera*, (D) *Litoria peronii*, and (E) *Litoria latopalmata*. Each point represents an individual survey and regression line with 95% confidence interval (shaded area).

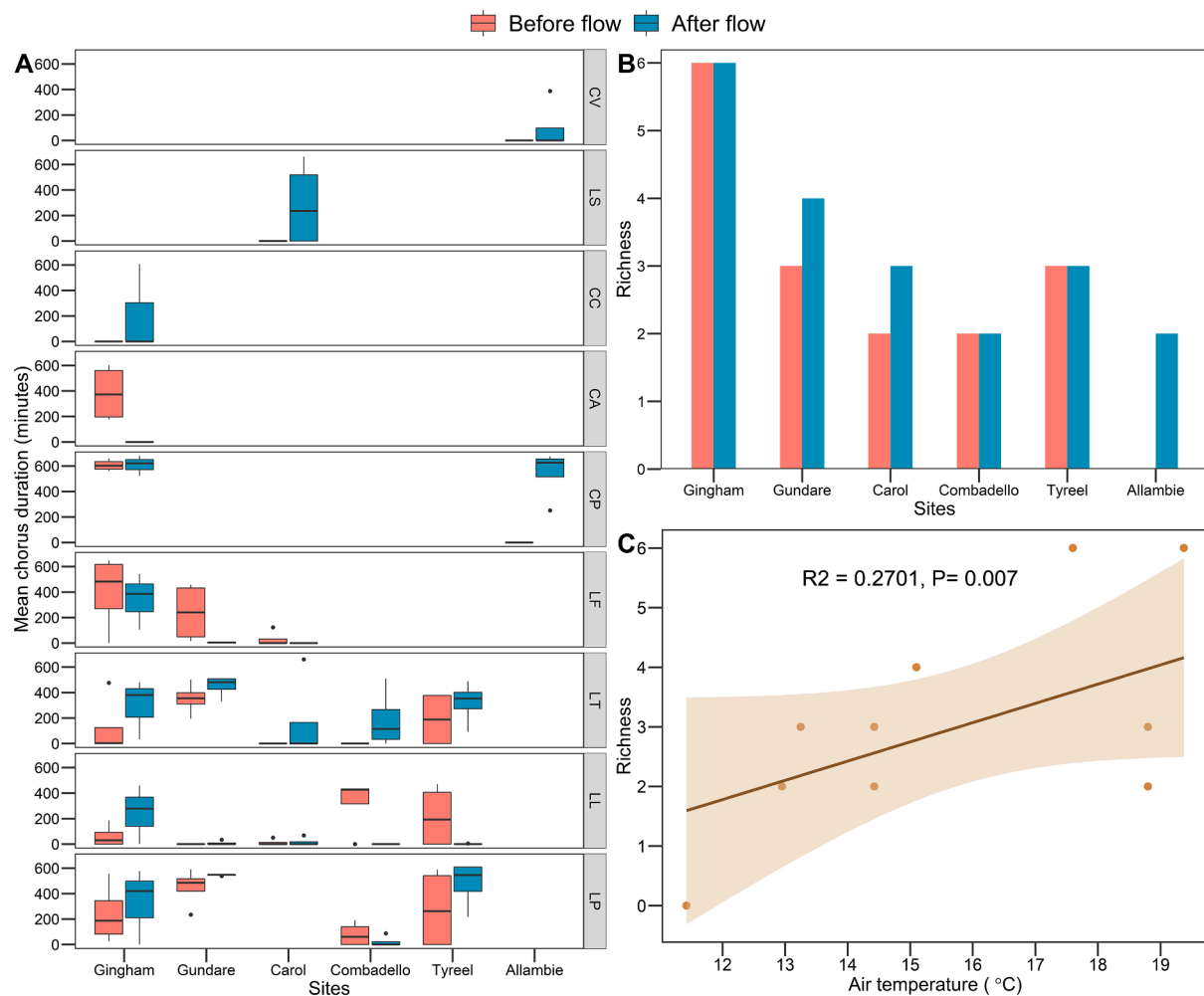
The highest frog richness ( $n = 7$ ) was detected at the Gingham Waterhole and lowest ( $n = 2$ ) at Allambie Bridge (Fig. 5). Frog species richness increased at three sites after flows, but not at others (Fig. 5B). There was a small but statistically significant increase in richness following river flows ( $\chi^2 = 14.3$ ,  $P < 0.001$ ), with an average increase in richness of 0.67 species per site. Across all sites, six species chorused over the four nights preceding and eight species chorused following the flow arrival (Fig. 5A). Richness also increased with increasing temperature ( $\chi^2 = 7.2$ ,  $P = 0.007$ ), with a maximum of six species was detected when air temperature was over 17 °C (Fig. 5C). But richness was not affected by rainfall ( $\chi^2 = 2.7$ ,  $P = 0.103$ ).

#### 4. Discussion

Wetland inundation had multiple effects on the frog populations in the floodplain environment of Gwydir River. At the community level, beta diversity (comparisons of community composition between communities) was affected by the increase of inundated areas along with vegetation cover and air temperature over the course of the five-year survey. These results support the concept that higher inundation after river flows provides important breeding habitats and ultimately plays a key role in structuring frog communities in floodplain habitats (Eskeew et al., 2012; Henning and Schirato, 2006; Ocock et al., 2016). However, community dominance (the inverse of species evenness) decreased with an increasing proportion of open water (no vegetation). This decrease of community dominance with decreasing vegetation covers highlights the importance of vegetation requirements for wetland dependent frog species (Jansen and Healey, 2003; Spencer and Wassens, 2010).

Both higher inundation over the five-year period and inundation immediately after arrival of river flows increased frog richness, which is consistent with previous studies (Hoffmann, 2018; Mac Nally et al., 2014; McGinness et al., 2014). The effect sizes were small, with richness increased by two species from 0 % inundation compared to 100 % inundation (Fig. 3B), and richness per site increasing by an average of 0.67 species following the arrival of flow (Fig. 5B). For three sites, no change followed by the arrival of flow yet richness increased in other three sites (Fig. 5B). Taken together, these results suggest that inundation is important for some of these frog species, and higher inundation after river flows provide a mosaic of habitats for frogs. Indeed, while an increase of two species sounds small in absolute terms, the highest richness detected at any site was only seven species, making an increase of even one species important.

Inundation is also important for breeding and recruitment opportunities in floodplain wetlands (Wassens, 2011), and we found that total frog abundance was significantly higher in inundated sites (Littlefair et al., 2021; Ocock et al., 2016). More specifically, the abundance of *Crinia parinsignifera*, *Litoria peronii*, *Limnodynastes tasmaniensis*, and to a lesser extent, *Limnodynastes fletcheri*, and *Litoria latopalmata* were higher in areas with higher inundation, which is consistent with studies in the central and southern parts of the MDB (Amos, 2017; McGinness et al., 2014; Ocock et al., 2016; Wassens and Maher, 2011). Previous studies reported a positive association for these five species with vegetation, rainfall, and temperature (Hoffmann, 2018; Jansen and Healey, 2003; Ocock et al., 2016), however, we did not detect those effects at the species-specific level. This may have been partially due to reduced sample sizes for some species that were less frequently observed as some



**Fig. 5.** (A) Mean chorus duration (in minutes) of the nine frog species detected at the six sites before and after river flows inundated the sites. Each data point is the total chorus duration of each species for a given night at a given site before and after flows arrived at a site. See Table 2 for abbreviation used for species names and sites. Arrival of river flows significantly affected two species (negatively for *Limnodynastes fletcheri* (LF) and positively for *Limnodynastes tasmaniensis* (LT)). (B) Bar plot showing frog richness before and after flow ( $\chi^2 = 14.3$ ,  $P < 0.001$ ). No calling was detected at the Allambie Bridge site before flows arrived. (C) Effect of air temperature on frog richness during the acoustic sampling period and regression line with 95 % confidence interval (shaded area).

of our community-level models did detect significant effects of those factors (though less consistently than inundated area).

Consecutive overnight chorusing varied among species and sites upon arrival of river flows. This may reflect differential behavioural (breeding) responses of different species among habitats or could be due to limited spatial sampling at our sites. For example, if the recorder was not in the direct location of inundation, we may have missed call data. The increase in chorusing duration in *Limnodynastes tasmaniensis* after inundation from river flows is consistent with previous findings (Heard et al., 2015; McGinness et al., 2014). The negative effect of arrival of flow on *Limnodynastes fletcheri* was surprising and one possible explanation is that *Limnodynastes fletcheri* has good dispersal ability and calling males can move to nearby low-lying vegetated shallow waterbodies which allowed them to disperse beyond the recorders in response to inundation of nearby habitats (Bishop-Taylor et al., 2015; Ocock et al., 2014). Future acoustic sampling would benefit from pairing trail cameras with acoustic recorders to allow researchers to gauge the specific spatial layout of inundation at the site. Our results from acoustic monitoring were still hindered by low sample size and an inability to assess the movement of frogs in relation to the recorders, but these trends will become clearer with additional recorders to expand the recording radius across the entire site and advancement of automatic detection of frog calls.

Over the five-year period, in addition to examining the effect of percentage of area inundated from river flows, we documented diverse frog communities, including twelve species, two of which (*Cyclorana cultripes* and *C. verrucosa*) remain taxonomically indistinct. However, some burrowing species had been previously recorded from this region were not detected during our study (e.g., *Neobatrachus sudelli*, *Notaden bennetti*, *Uperoleia rugosa*, and *Platyplectrum ornatum*) (Southwell et al., 2014; Wilson et al., 2009). This may be a result of low rainfall at the time of surveys (cumulative rainfall of past four days from frog survey dates: 2.2 mm in 2018, 34.1 mm in 2017, 25.4 mm in 2016, 10 mm in 2015) as burrowing species are responsive to heavy rainfall (Ocock et al., 2016; Read, 1999). In addition, some of the missing species are explosive breeders that are only active at a specific time for a very brief period, sometimes in response to heavy rainfall, and are, therefore, not detected during surveys when conditions were not favourable. However, 2019 was a drought year with no rainfall before or during frog surveys and no water was present in the survey sites (BoM, 2020), resulting in 87.86 % lower detection of frog abundance compared to the highest abundance in 2017 with the record of the highest cumulative rainfall (34.1 mm) over the five-year surveys. Though we found statistically insignificant association of frog abundance and richness with rainfall, low detection of frogs during severe drought in 2019 suggests that rainfed wetlands are important for some wetland dependent frog species (Wassens et al.,



2013).

Our results of the overall effect of inundation on frog populations help to fill the knowledge gap in the sub-tropical climatic zone in northern MDB and reflect the findings in other studies in semi-arid and temperate regions in Australia (e.g., Littlefair et al., 2021; Hoffmann, 2018; Ocock et al., 2016) and worldwide (e.g., Kupferberg et al., 2012; Vignoli et al., 2007).

## 5. Conclusion

Our results suggest an overall positive effect of wetland inundation on abundance and species richness, especially on the abundance of five frog species. Our results imply that inundation from river flows including small environmental water deliveries can be an important strategy to mitigate the negative impact of river regulation, a potentially threatening process for frogs occurring in the sub-tropical region in the northern MDB. Future research should focus on understanding interrelationships in species composition, occurrence, and more refined measures of environmental watering (e.g., flow velocity, increasing water depth on arrival of flow) to better understand the effects of inundation.

## CRediT authorship contribution statement

**Mohammad Abdur Razzaque Sarker:** Conceptualization, Data curation, Writing – original draft, Investigation, Formal analysis, Methodology. **Donald T. McKnight:** Supervision, Conceptualization, Formal analysis, Methodology, Funding acquisition. **Darren Ryder:** Supervision, Conceptualization, Formal analysis, Methodology, Funding acquisition. **Amelia Walcott:** Investigation, Methodology, Data curation, Funding acquisition. **Joanne F. Ocock:** Investigation, Methodology, Data curation, Funding acquisition. **Jennifer A. Spencer:** Investigation, Methodology, Data curation, Funding acquisition. **David Preston:** Investigation, Methodology, Data curation, Funding acquisition. **Sheryn Brodie:** Formal analysis. **Deborah S. Bower:** Supervision, Conceptualization, Formal analysis, Methodology, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109640>.

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