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ARTICLE

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Environmental influences on chorusing patterns in an Australian tropical savanna frog community

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Abstract

Ecoacoustic methods provide opportunities for ecological studies of vocalizing species within the context of the natural habitats and communities in which they occur. Continuous acoustic monitoring of species assemblages can reveal patterns in breeding phenology, behavior, and interactions. We used long-duration false-color spectrograms derived from acoustic indices to detect the nightly chorusing of a community of anurans in a tropical savanna in north Queensland. We described the chorusing patterns of each species over two wet seasons at three breeding sites, and used conditional random forest analysis to investigate the influence of various environmental factors. Frogs in these habitats form multispecies aggregations at water bodies during breeding periods when males form large choruses to attract females. The chorusing patterns revealed the species have different breeding periods, which could be broadly categorized as explosive or prolonged. While rain events were often a trigger for the commencement of the breeding period, species responded differently to environmental conditions. Choruses of explosive breeding species occurred only on the night of, or night after, the first high rainfall event of the wet season. The prolonged breeding species showed idiosyncratic patterns of chorusing, which were generally consistent across sites. Fine-grained nightly data on patterns of chorusing and the relationship with environmental conditions allow us to understand the detectability of the presence, or absence, of the frog species in these habitats, and provide baseline data for monitoring and management programs.

KEYWORDS
acoustic monitoring, amphibians, animal choruses, breeding phenology, rainfall

INTRODUCTION

The reproductive cycles of most vertebrates are seasonal and influenced by environmental conditions. The timing of breeding activities should occur when conditions, especially weather and resource availability, are favorable to maximize offspring survival and fitness (Foster & Kreitzman, 2010). Temperature and rainfall, in particular, are factors that drive primary productivity and food availability, place constraints on animal activity, and affect growth and development (Brown & Shine, 2006; Helm et al., 2013; Visser et al., 2006). Understanding the specific environmental factors associated with breeding activity within populations contributes to our knowledge of the factors that are important for species' reproductive success.

Studying the breeding activity of animals in their natural habitats brings particular challenges in detecting the onset of breeding periods and observing behavior over time. Species that use vocal behavior during breeding periods are good model organisms for examining the influence of weather on breeding, as the vocalizations are easily detected, and sound recorders allow monitoring the behavior remotely over whole seasons and multiple years. Male frogs call to attract females to breeding sites, and many species aggregate to form large choruses, which are reliable indicators of breeding events. In addition, the advertisement calls of male frogs are a reproductive isolating mechanism, used by females to locate and choose mates of the same species (Gerhardt, 1994; Littlejohn, 1959), and so the calls and choruses of most frog species are readily identifiable in acoustic surveys.

Anuran activity is highly influenced by weather conditions, in particular rainfall and temperature. Frogs rely on moist living conditions at all life stages, having permeable skin and being susceptible to desiccation. Moisture is a particular requirement for egg and larval development, which takes place in ponds, streams, nests in moist burrows, or leaf litter of rainforests (Crump, 2015). Environmental temperature is an important factor for ectotherms and restricts activity to within thermal limits (Navas et al., 2008; Pough et al., 2001). Anuran breeding activity is therefore strongly associated with seasonal rainfall and temperature patterns. In tropical regions, breeding peaks during periods of higher rainfall. In temperate regions, where temperatures are highly seasonal but rainfall is relatively constant throughout the year, breeding activity typically occurs in spring and summer (Wells, 2007). However, these generalizations do not reflect the variability in the timing of breeding periods that occur within species assemblages.

There are many examples that show there is considerable interspecific variation in breeding periods and responses to abiotic conditions within anuran species assemblages. Anuran communities in temperate climate regions typically exhibit a degree of temporal partitioning of breeding periods, including some species that begin calling in winter, and breeding periods ranging from explosively short (1–2 days) to prolonged (several months) (Oseen & Wassersug, 2002; Saenz et al., 2006; Steen et al., 2013; Yoo & Jang, 2012). In tropical rainforest climates, where rainfall may be seasonal but remains high throughout the year, differences in calling phenology have also been observed (Donnelly & Guyer, 1994), and even closely related species which call all year show different responses to weather conditions (Ospina et al., 2013). Tropical rainforests are high in frog species richness, and frogs in these habitats show a variety of reproductive modes, including terrestrial oviposition and direct development of embryos (Crump, 2015). Anuran species within particular communities, but with different reproductive modes, also exhibit different breeding periods and associations with abiotic factors (Crump, 1974; Gottsberger & Gruber, 2004). In addition to rainfall and temperature, factors shown to influence frog breeding activity or calling include humidity (Hauselberger & Alford, 2005; Yoo & Jang, 2012), atmospheric pressure and wind speed (Henzi et al., 1995; Oseen & Wassersug, 2002), moon light (Underhill & Höbel, 2018), and day length (Both et al., 2008; Canavero & Arim, 2009). The moisture and temperature requirements of frog breeding temporally constrain breeding activity, which creates intense competition for resources, such as calling and oviposition sites, food and habitat for tadpole development, as well as acoustic competition in advertisement calling (Allen-Ankins & Schwarzkopf, 2021). The temporal variation in breeding periods that is often observed within species assemblages, and the evolution of different reproductive modes, may be adaptations that result in species-specific responses to environmental conditions.

Anurans in tropical savanna regions experience highly seasonal rainfall with extended dry seasons, and yet many frog species persist in these habitats. Anurans in tropical savannas are expected to breed explosively or opportunistically following rain events that are unpredictable (Lamotte, 1983; Wells, 2007), but some species chorus through the dry season (Brodie et al., 2020). Consistent with studies in other climatic regions, frog populations in savanna habitats include both explosive and prolonged breeding species (Moreira & Barreto, 1997; Prado et al., 2005).

There have been few studies of the abiotic factors influencing seasonal calling patterns of anurans in the tropical savanna region of northern Australia. Dostine et al. (2013) investigated the environmental factors influencing the detectability of frogs using calling surveys near Darwin. Tyler et al. (1983) detailed the calling and breeding periods of a frog assemblage over one wet season in the Northern Territory but did not investigate environmental influences in detail. Information about the timing and environmental drivers of chorusing periods of anurans is required to optimize species monitoring programs. The length of a species' chorusing period within a season will affect its detectability in acoustic surveys. Explosive breeding species may chorus on only a few nights in a breeding season, and therefore be less easily detected than prolonged breeding species calling for many months. This directly influences conclusions about a species' presence or absence at a location. The importance of weather conditions to anuran activity is also useful for understanding the detectability of calling males in acoustic monitoring surveys (Steelman & Dorcas, 2010). Knowledge of the environmental factors that influence male frogs to chorus, along with their breeding periods, tells us when choruses are expected to occur. The chorusing patterns also reveal information about species' breeding ecology, community composition, and species interactions.

The aims of this study were to describe the chorusing patterns of a community of frogs in an Australian tropical savanna and investigate the influence of weather variables on the chorusing activity of each species detected. Frogs in these habitats form multispecies aggregations at water bodies during breeding periods when males form large, loud choruses at night to attract females. Our objective was to collect nightly data on the chorusing activity of frog populations at multiple sites using a method of visualizing long environmental recordings that allowed us to collect more data than traditional sampling methods. Continuous sound recordings contain a wealth of information about the vocal behavior of species, but coarse sampling regimes result in considerable data loss. By taking advantage of all the information contained in continuous sound recordings, we aimed to reveal detailed patterns of the chorusing behavior of the anuran species present and the influence of daily weather factors.

METHODS

Acoustic recordings and species detection

This study used sound recordings obtained at three frog breeding sites at Hervey Range, near Townsville, Queensland (19.37° S, 146.45° E; Figure 1) from October 2012 to April 2014. The location has a tropical savanna climate with a wet–dry rainfall regime, hot, humid

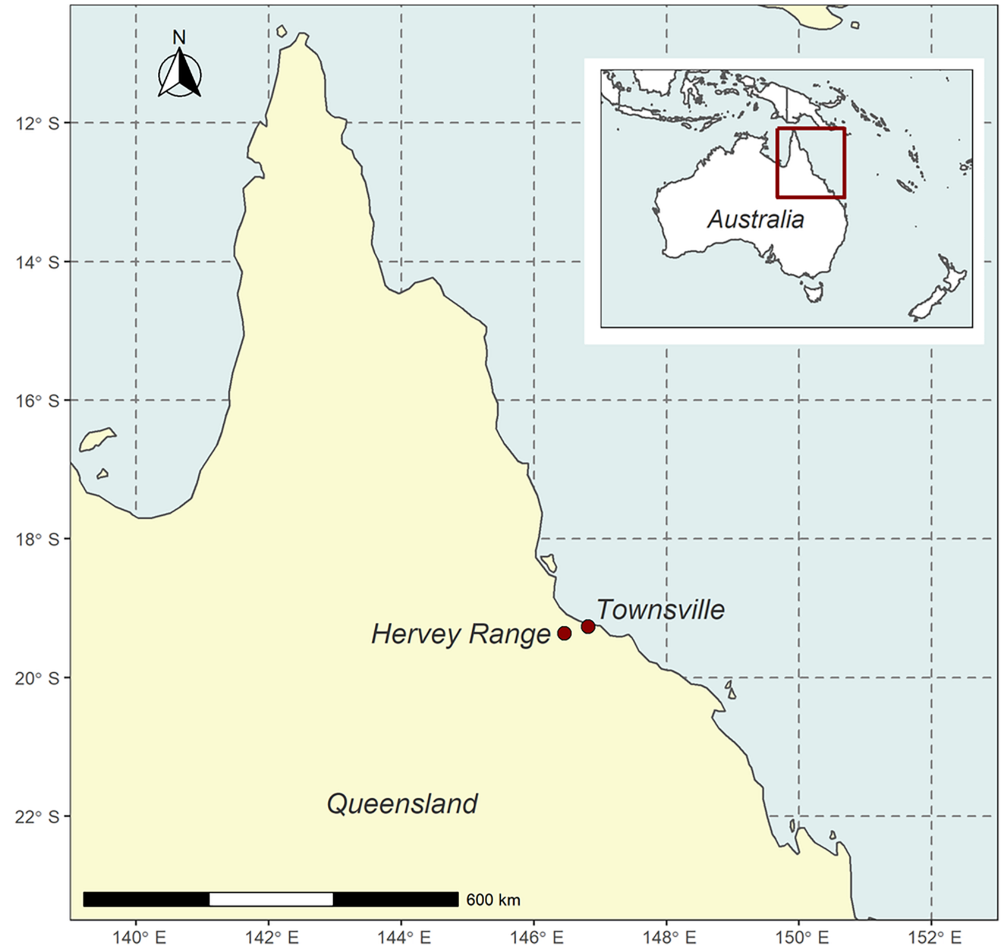

FIGURE 1 Map of northern Queensland, Australia, showing the location of Hervey Range where the study sites were located. The inset shows the map location within the southwestern Pacific region.

summers, and cool, dry winters. The wet season is from December to April, with approximately 80% of the yearly rainfall total typically occurring in these months. The study sites were artificial dams on cattle grazing properties where frogs aggregated during breeding periods, forming large choruses. (The sites are referred to here by their specific location names: “Tearooms,” “Three Mile Creek,” and “Freestun.”) The dams retained water permanently during the study period, although the extent of the water bodies retracted marginally during the dry season. The habitat surrounding the dams was eucalypt open woodland with grass understory and the dams had low-sloping banks, sparse tree cover, and vegetation consisting of emergent grasses and sedges and some floating vegetation.

Sound recorders (HR-5, Jammin Pro, USA) were placed at the edge of each dam, with the microphone facing the center of the water body, and were set to record continuously each night (32,000 Hz sampling rate, MP3 format, 128 kbps bit rate). Anurans in this tropical savanna habitat are nocturnal, and so recordings were only made at night. While the start of some choruses may occasionally have been missed, recording start times were consistent. The majority of recordings commenced at 19:00, but for the first two months of the study period (late dry season 2012) recording commenced earlier at either 18:00 or 18:30. In these early recordings, there were instances when a species commenced chorusing before 19:00, but this was only a few minutes prior to 19:00, or sporadic early calling of individuals; therefore, the earlier survey start did not meaningfully affect the total count of minutes. A total of 1265 nights were recorded at the three sites. All nights, except one, were recorded for at least 717 min (11 h 57.7 min) to a maximum of 786 min (13.1 h). The shortest recorded night was 464 min (7.73 h), and recording ceased at 02:44 a.m., so still captured most of the chorus activity during the night.

Each recording was analyzed to identify any anuran species calling and to record the number of minutes each species was vocally active on each night. Frog calls and choruses were detected using a visualization method based on acoustic indices, which condenses long-duration recordings into single images to highlight different sound sources in the audio (Brodie et al., 2022; Towsey et al., 2014). The images, or “false-color spectrograms,” are composed of three acoustic indices calculated for each one-minute segment in each frequency bin of the standard spectrogram, and combined using three color channels (red, green, and blue). The false-color spectrograms were used to navigate each recording and identify the start and end of choruses, and species were then confirmed by analyzing the raw recordings. Refer to Brodie et al. (2022) for a detailed description of the protocol using the false-color spectrograms for audio analysis.

Chorus activity was measured as the number of minutes of chorusing detected each night for each species. Commonly used measures of frog chorus intensity are number of calling males (e.g., Moreira & Barreto, 1997; Saenz et al., 2006), the average number of calls per minute (e.g., Hauselberger & Alford, 2005), and an estimate of calling intensity based on the level of call overlap (e.g., Bridges & Dorcas, 2000; Nelson & Graves, 2004). All these measures are made at fine temporal resolution, such as per minute or per survey, then averaged or summed over longer time frames. Collecting data at this scale was not feasible for this study, but the start and end times of chorus activity could be determined using the false-color spectrograms. The total number of minutes of chorus activity can be regarded as an indicator of the chorus intensity of the population—longer choruses reflect more individuals and a higher intensity of chorusing (Friedl & Klump, 2002; Llusia et al., 2013).

Choruses were observed to start with intermittent, low-rate calling by one or few individual frogs, before increasing in the number of calling individuals and intensity through the night. The start and end times of choruses were determined when calling was detected in two or more consecutive minutes. This method disregarded single, isolated vocalizations early or late in the night outside the core chorusing period. Our measure of chorusing activity may include times when only one individual was calling, which is difficult to determine from passive acoustic monitoring, but the vast majority of recordings included choruses of more than one, and typically many, individuals. The start and end times of a chorus were recorded for each night and the number of minutes calling was calculated as the difference. If a break in chorusing of greater than 20 min occurred, then the periods of chorusing were calculated separately and summed for the night. We explored the chorusing patterns of individual species at each site during the study period graphically and assessed the synchrony of chorusing between sites by calculating Pearson’s correlation coefficients of chorusing activity between each pair of sites for each species.

Weather and environmental data collection

Weather data were obtained from the Bureau of Meteorology (www.bom.gov.au) and recorded at the nearest weather station (“Woolshed” 19.42° S, 146.54° E), which was approximately 10 km from each of the sites. Three-hourly data were obtained for rainfall, air temperature, relative humidity, air pressure (at station altitude,

~500 m), and wind speed. Rainfall was measured as the cumulative total since the last observation. Wind speed was measured as the average over the 10 min leading up to observation time. Nightly values for air temperature, air pressure, and wind speed were calculated by averaging the three-hourly data for the period 18:00–03:00. Total rainfall on the night of recording was calculated as the cumulative rainfall total from 18:00 to 06:00. In addition to total rainfall on the night, the 3-day cumulative rainfall and 7-day cumulative rainfall totals up to and including the night of observation were derived from the 3-hourly observations to explore the effect of rainfall on chorusing at different time scales. There may be a delay in the response of anurans to rainfall, and so total rainfall during the day leading up to the night of recording (6:00–18:00) and 24-h rainfall total for the previous day (1-day lag) were also calculated. Localized rainfall was likely to vary on occasion from the rainfall observed at the weather station, and so an observer rating of the rainfall intensity during the recording was made from the audio. Rain events were visually apparent on the false-color spectrograms, and the rain intensity at the sound recorder was rated as one of: none, light (drizzle for short periods), moderate (light rain for a large portion of the night, or heavy rain for short periods), or heavy (heavy rain for large portions of the night). Moon illumination data, as the fraction of moon illuminated at midnight, were obtained from the USNO Astronomical Applications Department data repository (United States Naval Observatory, 2017). Day length was calculated as hours of daylight from sunrise to sunset for the study location (lat 19.37° S) using the R package "geosphere" (Hijmans, 2021).

Random forest analysis

We used an interpretable machine learning approach (Molnar, 2022) to investigate the influence of environmental variables on the level of chorusing activity for each species. Random forest models are nonparametric models that provide good predictive power and do not rely on distributional assumptions. Random forests also provide a method of interpretable machine learning through variable importance measures. Random forest analyses were performed for each species separately, with number of minutes of calling each night as the response variable, and environmental covariates as predictors. Our data covered two wet seasons, but some species were only detected in one wet season. We delineated the anuran breeding seasons at the middle of the 2013 dry season (winter solstice 22 June 2013) and excluded data for a season if a species was not detected at a site in that season, which may reflect the species' absence from the breeding site. Nine nights were omitted from the data set of environmental covariates because of missing weather observations. All analyses were performed using R Statistical Software (v4.1.2, R Core Team, 2021).

We fitted random forest models for each species using the "cforest" function in the R package "party," which implements a conditional inference framework to produce random forest models based on unbiased trees (Hothorn et al., 2021; Strobl et al., 2007). Conditional inference trees reduce the bias toward selection of variables with more cut points or categories (Hothorn et al., 2006). Several parameters that regulate the random forest learning process are user-defined, and so model tuning was performed to find the optimal values of the "mtry" parameter (number of randomly selected candidate variables at each node) and the "mincriterion" parameter (controlling tree depth). The range of the "mtry" parameter considered was 2–14 variables, and the values of the "mincriterion" considered were 0.95 and 1. The optimal set of these two parameters was determined from the model with the lowest mean absolute prediction error on out-of-bag observations (i.e., those not used in training the tree) on 2000 trees (Breiman, 2001; Probst et al., 2019).

Variable importance can be calculated for random forest models by calculating the change in prediction error on the out-of-bag observations when the values of the predictor variable of interest are randomly permuted (Breiman, 2001). However, variable importance measures show a bias toward correlated predictors (Strobl et al., 2008). We calculated variable importance using the conditional permutation importance procedure implemented in the R package "permimp" (Debeer et al., 2021). Conditional permutation importance reduces the bias toward correlated predictors by partitioning the predictor space and permuting the variable of interest conditionally on the other predictor variables, retaining the correlation structure (Strobl et al., 2008). The conditional permutation can be controlled by including only those variables associated with the predictor of interest in the conditional permutation scheme. The "permimp" function applies an association test and selects only those variables that are associated with 1—p value greater than a user-defined threshold (Debeer & Strobl, 2020). We chose an association test threshold of 0.85 to ensure all associated predictor variables were included in the conditional permutation.

To check for stability in the variable importance results, five random forest models of 2000 trees were fitted for each species with different random seeds, using the "mtry" and "mincriterion" parameter values identified in the model tuning. If the rankings of the top ranked variables were inconsistent across the five random forests, the permimp procedure was run again with 3000 trees in each random forest. The random forest model with the lowest mean absolute error (MAE) in the out-of-bag predictions was selected to explore the most important variables for each species. The predictive performance of the final models was assessed by inspecting the agreement between the out-of-bag predictions and the observed responses using graphical exploration and the concordance correlation coefficient (Lin, 1989), as implemented in the R "DescTools" package (Signorell et al., 2021).

To explore the effects of the important variables identified in the random forest models, we calculated and plotted accumulated located effects. Accumulated local effects (ALEs) are estimated effects of the predictors in supervised learning models and can distinguish the main effects when there are multiple correlated predictors present in a model (Apley & Zhu, 2020). They achieve this by calculating the average differences in predictions across quantile intervals of the predictor (i.e., local effects), which avoids extrapolation of the response outside of the multivariate predictor space, and isolates the main effect of the predictor of interest from the effects of other predictors (Molnar, 2022). The ALEs of selected individual predictors were calculated using the R "iml" package (Molnar & Schratz, 2020).

RESULTS

Temporal patterns of chorusing

We detected 17 anuran species from four families in the sound recordings across the three study sites. These included 10 Pelodryadids (*Litoria* sp. and *Cyclorana* sp.), four Limnodynastids (*Limnodynastes* sp. and *Platyplectrum ornatum*), two Myobatrachids (*Crinia deserticola* and *Uperoleia mimula*), and one Bufonid (*Rhinella marina*). Eleven species were detected at all three sites, three species were detected at two sites, and three species were detected at only one site.

The nightly chorusing activity of the anuran community at our study sites was concentrated in the wet season, January–March, of both years, but the patterns were highly variable among species (Figures 2 and 3). *Limnodynastes peronii* was the only species not detected in January or February, instead calling through the late wet and dry seasons (Figure 2e). There was a wide range of breeding period lengths, and some variability among sites and between years. There were high correlations in the measured chorusing activity among sites for many species, revealing species-specific chorusing behavior (Figure 4).

Most species detected could be characterized as having either prolonged or explosive breeding periods (Wells, 1977). Eight species were detected calling for more than one month in at least one study year (Figure 2). *Litoria fallax* (Figure 2a) and *Litoria nasuta* (Figure 2c) had the longest calling periods. *R. marina* chorusing was episodic but occurred in every month of the year (Figure 2b). *C. deserticola* (Figure 2d) and *Litoria rubella* (Figure 2h) had shorter chorusing periods in 2013 than in 2014, but the timing and duration of these periods were remarkably synchronous across sites. The calling patterns of *Litoria rothii* (Figure 2g) and *Limnodynastes convexiusculus* (Figure 2f) were inconsistent across sites, with a chorusing period of 2–3 months at Freestun Dam, but shorter periods at other sites. The remaining nine species detected during the monitoring period exhibited explosive breeding behavior, with very short chorusing periods of only one to several days, either on successive nights or intermittent throughout the wet season (Figure 3). The nights of highest chorus activity for species in this group occurred on or around the same dates across sites in each wet season. While the categorization of species into the two groups was not definitive, all the species in the explosive group had calling periods of less than one month.

Weather patterns during the study period

The observed daily temperatures (Figure 5a) and rainfall (Figure 5b) during the study period were characteristic of a tropical wet–dry climatic regime (McGregor & Nieuwolt, 1998). Temperatures were high in summer, with low seasonal variation in daily minimum and maximum temperatures. Rainfall was highly seasonal with low daily rainfall until the first major rain events of the wet season (23 January 2013 and 30 January 2014). Most rainfall occurred from January to March, with very little rainfall in the cool, dry season months. In all months during the study period, monthly rainfall was below historical mean rainfall, except for January 2013 in which an extreme rainfall event occurred (24-h total: 269.2 mm on 23 January 13). Air pressure (at weather station altitude) was lower during the wet season than the dry, and decreased markedly during rain periods (Figure 5c). Day length ranged from 10.96 h of daylight at the winter solstice, to 13.30 h at the summer solstice (Figure 5d). Average nightly wind speed showed a slight seasonal trend of lower values during the dry season in 2013 (Figure 5e).

Effects of environmental variables on chorusing activity

The onset of chorusing activity for most species coincided with the first major rain event in both wet seasons, but

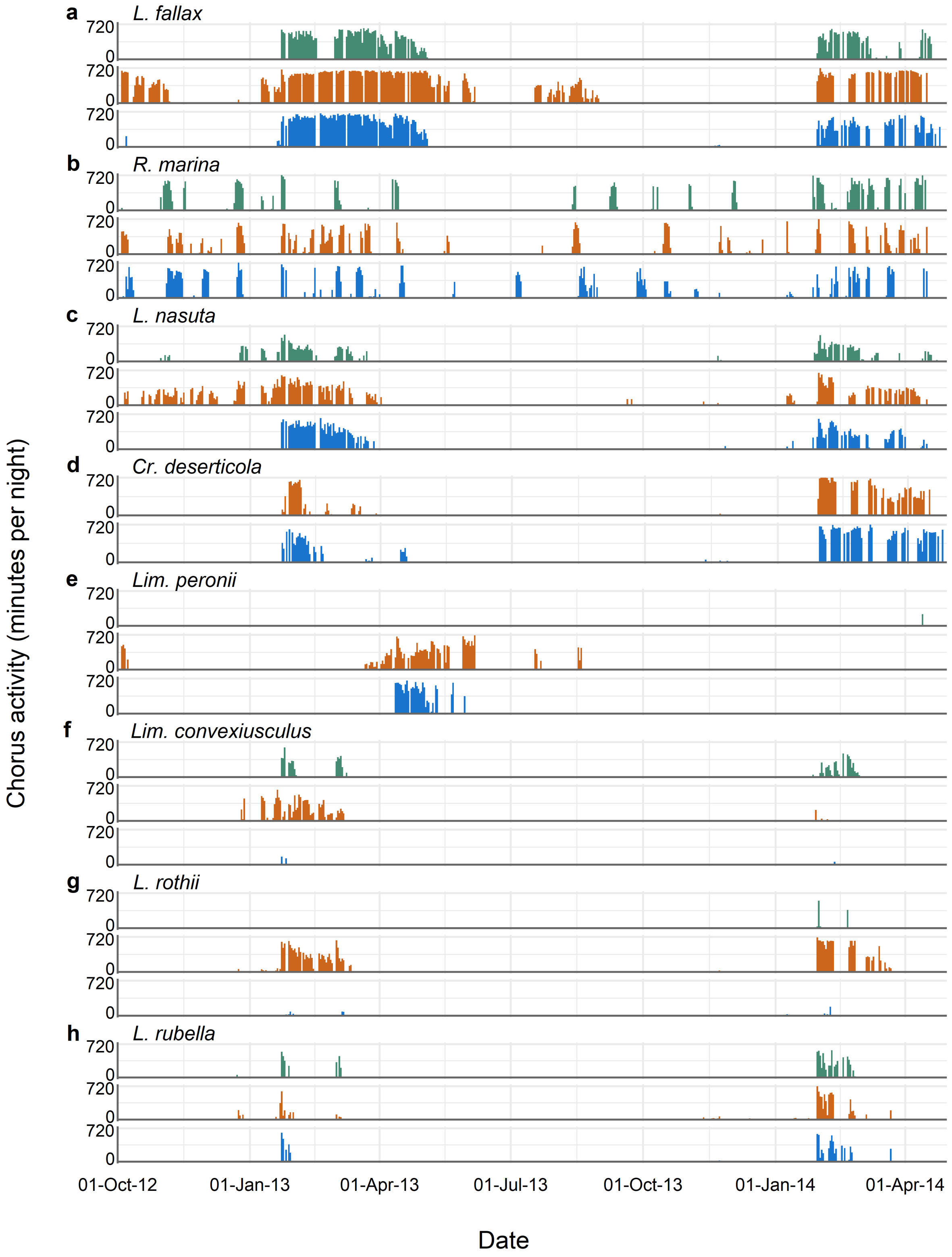

FIGURE 2 Nightly chorus activity of eight frog species with the most prolonged calling periods at our dry tropics study sites. The *y* axis represents the number of minutes of chorus activity measured each night from the analysis of continuous sound recordings. Colors represent the three study sites and are only shown if the species was detected at the site (green, Three Mile Creek; brown, Freestun; blue, Tearooms).

there was some species-specific behavior. *L. fallax* was vocally active at the Freestun site at the start of the study period (late dry season), but high, consistent chorusing commenced at the onset of the wet season in both years (Figure 2a). *R. marina* choruses were detected in all months during the study period, but the frequency of the

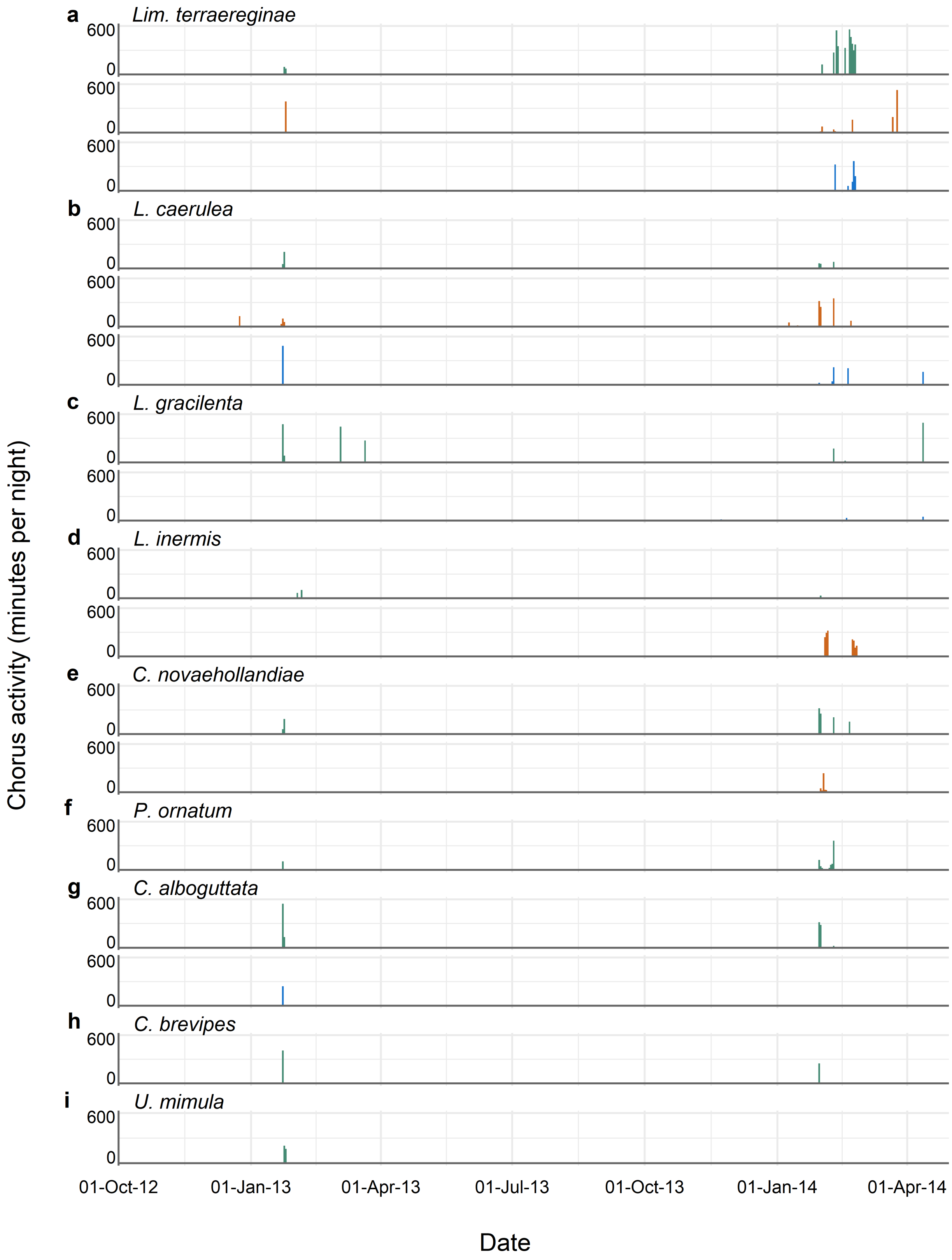

FIGURE 3 Nightly chorus activity of nine frog species with the shortest calling periods at our dry tropics study sites. The *y* axis represents the number of minutes of chorus activity measured each night from the analysis of continuous sound recordings. Colors represent the three study sites and are only shown if the species was detected at the site (green, Three Mile Creek; brown, Freestun; blue, Tearooms).

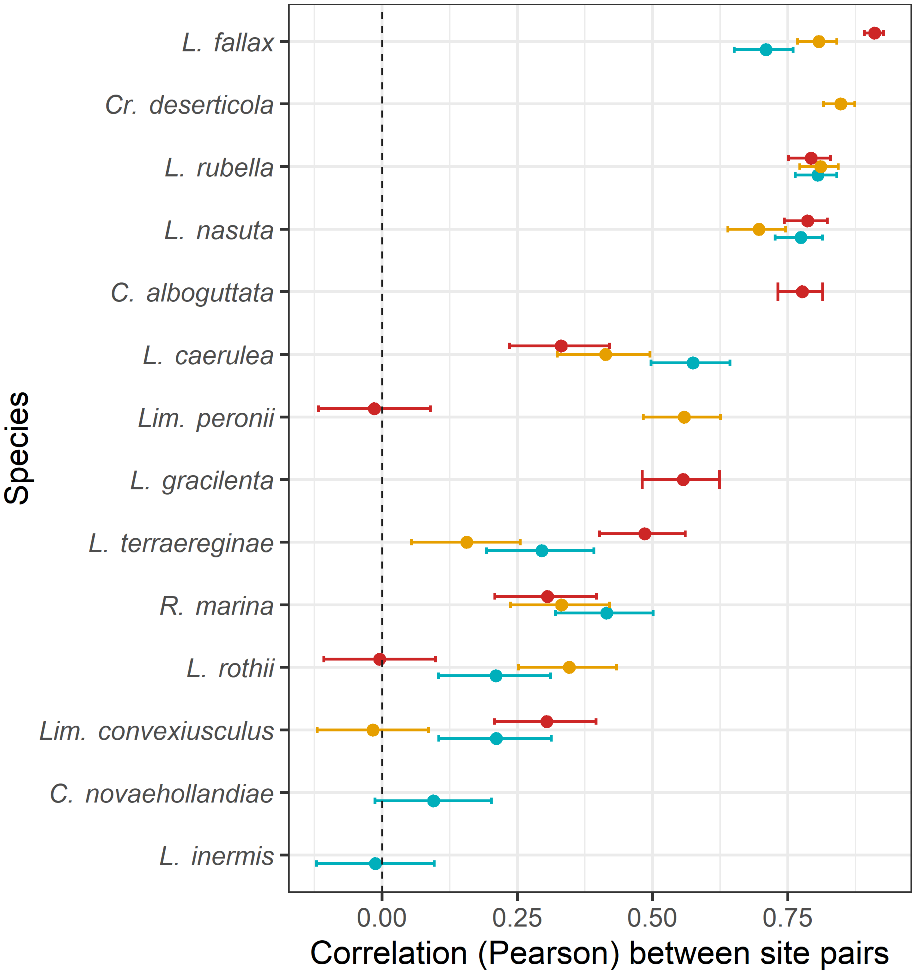

FIGURE 4 Pearson correlations of chorusing activity (measured in minutes per night) between each pair of sites for species detected at more than one site. Dots represent the correlation estimate and bars show the 95% CI. Site pairs are represented by colors (red, Tearooms-Three Mile; yellow, Tearooms-Freestun; blue, Three Mile-Freestun).

episodic choruses increased in the months after the onset of the wet season (Figure 2b). *L. nasuta* was often vocally active in the months before the onset of the wet season, but highest chorusing activity occurred following the first major rain event (Figure 2c). *Lim. peronii* was detected in the late dry season of 2012, and then not again until the end of the wet season in 2013, not apparently in response to any rain events (Figure 2e). With the exception of some early calling by *Litoria caerulea* and *Litoria gracilenta*, the first choruses of the explosive breeding species occurred on the night of, or night after, the first significant rainfall event (24-h total >40 mm) in each wet season (Figure 3).

The number of species detected calling each night was positively associated with all rainfall variables, but most strongly with the 7-day rainfall total ($r^2 = 0.34$, df $= 1263$, $p < 0.001$; Figure 6a). Species richness was also positively associated with average night air temperature ($r^2 = 0.18$, df $= 1242$, $p < 0.001$; Figure 6b) and negatively associated with average night air pressure ($r^2 = 0.25$, df $= 1246$, $p < 0.001$; Figure 6c). No species were detected calling on nights when the average air temperature was less than 13.25°C. At least one species was detected calling on any night when rainfall was greater than 9 mm (Figure 6d).

The predictive performance of random forest models for predicting nightly chorusing activity from environmental covariates varied with the number of nights a species was detected chorusing. The models with the highest concordance correlation coefficient tended to be for those species with the highest chorusing detections in the data (Table 1). All models tended to underpredict chorusing activity on nights when chorusing occurred, but also predicted some chorusing on nights when the species did not call (Appendix S1: Figures S1–S17). Our aim in this study was not to maximize the predictive performance of the models, but to include only relevant environmental variables and explore which were most influential in

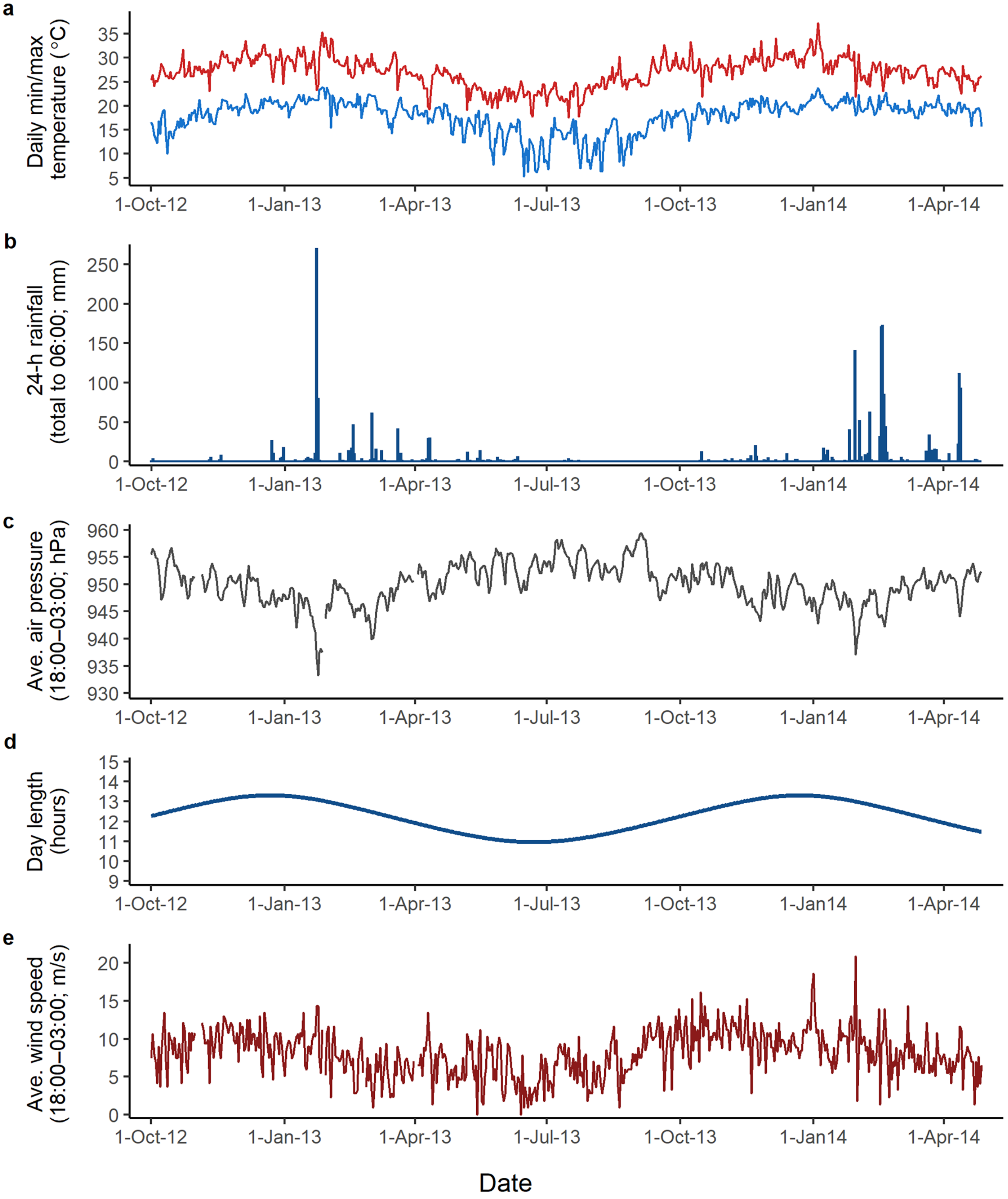

FIGURE 5 Environmental conditions during the study period: (a) daily minimum (blue) and maximum (red) temperatures; (b) 24-h rainfall totals to 06:00; (c) average nightly air pressure at station altitude; (d) day length as number of daylight hours; (e) average nightly wind speed. Weather observations were made at the Woolshed weather station, approximately 10 km from the study sites (data from Bureau of Meteorology, www.bom.gov.au).

driving chorusing activity. All models, even those with relatively poor predictive performance, did predict chorusing through the observed calling periods and no or low chorusing in periods when species did not chorus. In this regard, the random forest models did learn a degree of information from the input features, and

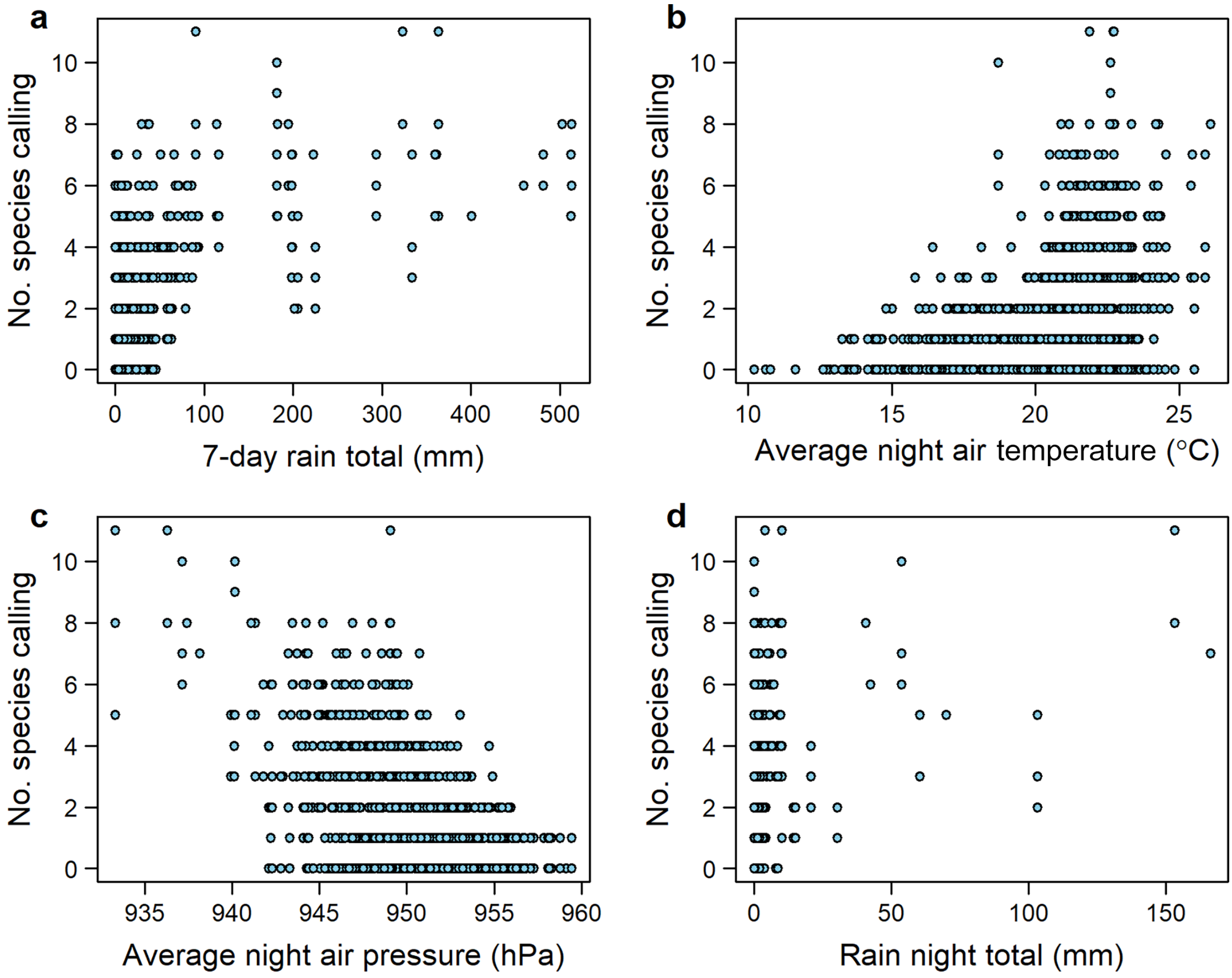

FIGURE 6 Relationships between weather variables and richness of species detected calling each night.

variable importance is an informative measure of which variables contributed most to the predictive power of the models.

Variable importance estimates for the random forest analysis show that the environmental variables influenced species with prolonged and explosive breeding patterns differently (Figure 7; Appendix S1: Figure S18). Rainfall variables were generally the only important variables for predicting chorusing of explosive callers, with short-term rainfall conditions the most influential. Two exceptions to this were *Limnodynastes terraereginae* and *Litoria inermis*, which exhibited explosive chorus patterns in our data, but were only influenced by the 7-day rainfall total. In contrast, the 7-day rainfall total, air temperature, and day length were the most influential variables for prolonged callers. *L. rubella*, *L. convexiusculus*, and *L. rothii* were most influenced by the 7-day rainfall total. However, rainfall was not the most important variable for the species with the longest calling periods. Average nightly wind speed and day length were the most important predictors of *L. fallax* chorusing activity, moon fraction was the most important variable for *R. marina*, and day length was the most important variable for *L. nasuta*, *C. deserticola*, and *L. peronii*.

ALE plots are shown in Figure 8 for the most important variables determined in the random forest analysis. ALE plots are also included for variables ranked close to the most important variable. The ALE for *L. gracilenta*, *U. mimula*, and *Cyclorana brevipes* were not calculated, as these models had low prediction performance. The local effects of a predictor variable are the difference in the predicted response, calculated within intervals, when the predictor variable is set at the lower and upper limits of each interval (as implemented in the R "iml" package, Molnar & Schratz, 2020). Plotting the centered, cumulative effects across the range of the predictor allows for graphic interpretation of the effects within the envelope of the training data (Apley & Zhu, 2020). Note that the

TABLE 1 Performance metrics of random forest models predicting the chorusing activity of each species from environmental variables.

Species	N	N instances	CCC	R^2	MAE
Litoria rubella	1244	168	0.818	0.697	14.74
Litoria fallax	1244	517	0.800	0.669	97.48
Litoria nasuta	1244	370	0.753	0.614	59.72
Crinia deserticola	854	175	0.745	0.607	60.21
Limnodynastes peronii	829	98	0.674	0.499	40.94
Litoria caerulea	1244	44	0.396	0.284	3.30
Limnodynastes terraereginae	1030	25	0.388	0.223	8.41
Rhinella marina	1244	438	0.387	0.240	124.35
Cyclorana novaehollandiae	603	12	0.338	0.191	3.60
Litoria rothii	1081	136	0.337	0.181	37.49
Cyclorana alboguttata	779	7	0.285	0.181	3.09
Limnodynastes convexiusculus	1244	92	0.262	0.098	26.75
Litoria inermis	603	10	0.253	0.116	4.73
Platyplectrum ornatum	390	8	0.190	0.104	3.39
Uperoleia mimula	163	2	0.138	0.059	4.24
Litoria gracilenta	1244	25	0.116	0.041	2.91
Cyclorana brevipes	390	2	0.114	0.076	3.06

Abbreviations: CCC, concordance correlation coefficient; MAE, mean absolute error of predictions; N instances, number of nights species chorus was detected; N, number of observation nights in the study period; R^2, coefficient of determination.

ALE plots show the main effects of each predictor and do not include the effects of any second- or higher-order interactions with other variables. Also note that local effects were calculated for quantiles of the predictor variable (i.e., intervals of equal size), and so the intervals have varying range. Therefore, the ALE plots for the rainfall variables have longer intervals in the range of high rainfall values, reflecting the right-skew in the observed rainfall distribution.

Rainfall at various scales was associated with higher predicted chorusing activity of most species when rainfall was above a certain threshold (Figure 8a–d). Rainfall during the day before recording commenced had a positive effect on predicting the chorusing of *Cyclorana alboguttata* and *Cyclorana novaehollandiae* when the recorded rainfall was more than approximately 10 mm. *L. caerulea* responded to a lower threshold, with daytime rainfall of more than 2 mm having a positive effect (Figure 8a). The 3-day cumulative rainfall total also had a positive effect on the predicted chorusing of *C. novaehollandiae* and *L. caerulea* when the total was above 25–50 mm (Figure 8c). The rain intensity at the site (observer rating from the audio) was the most important predictor for *Playtplectrum ornatum*, rather than measured rainfall at the weather station, and predicted chorusing for *P. ornatum* was higher when rain was moderate or heavy (Figure 8b). The 7-day cumulative rainfall total had a positive effect on chorusing of the several species shown in Figure 8d when it was above 30–60 mm.

The effect of day length was strongest for *Lim. peronii* chorusing activity, which was predicted to be highest on the shortest days, and below average on days longer than 11.75 h (Figure 8e). For *C. deserticola* and *L. fallax*, day length greater than about 13 h was associated with lower chorusing activity. For *L. nasuta* and *L. rubella*, predicted chorusing activity was higher on longer days. Average nightly air temperature had a positive effect on the chorusing activity of species for which it was identified as an important variable in the random forest models (Figure 8f). Chorusing for *C. deserticola* and *L. fallax* was predicted to be above average when the average air temperature was higher than 20°C and below average at lower temperatures. *L. peronii* chorusing was also predicted to be lowest at low air temperatures and increase when air temperature reached about 17°C. Air temperature had a positive effect on *L. convexiusculus* chorusing above 22°C. Average nightly wind speed had a negative effect on chorusing activity for *L. fallax* (Figure 8g). Moon illumination had a negative effect on chorusing activity for *C. deserticola*, *L. nasuta*, and *R. marina*, with higher chorusing activity predicted when moon illumination was low (Figure 8h).

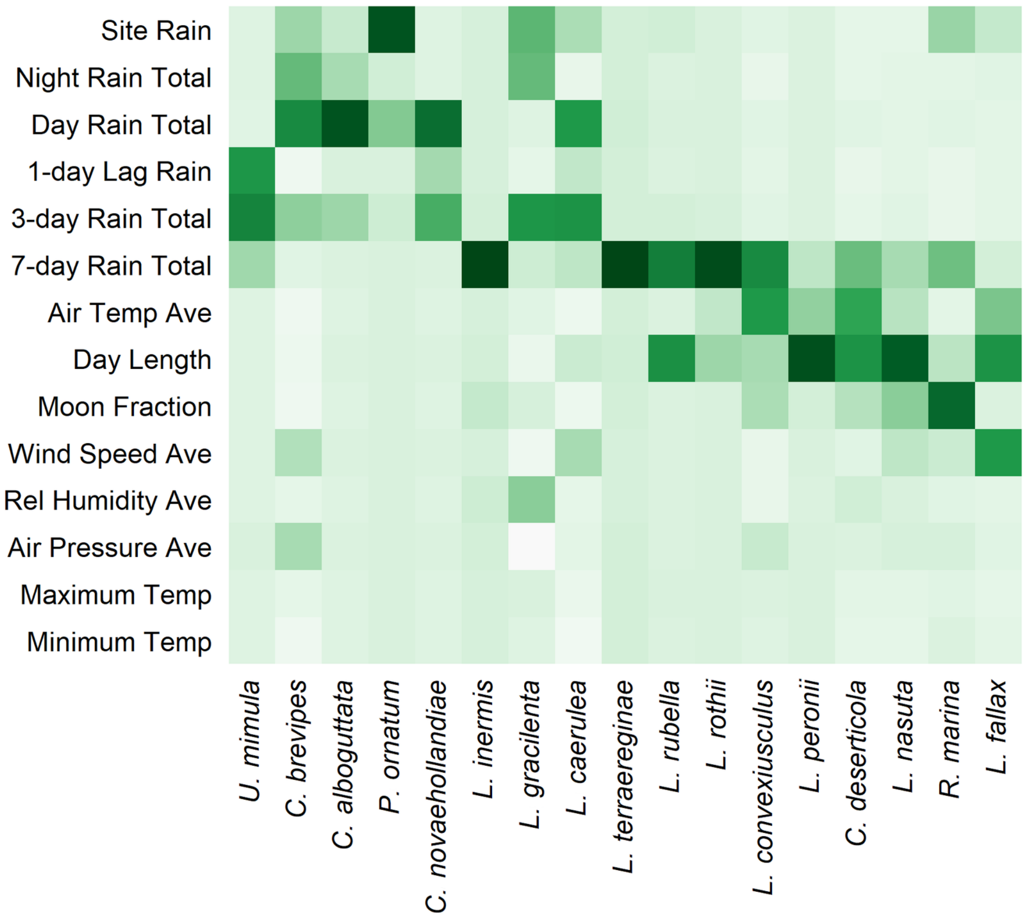

FIGURE 7 Heatmap of variable importance in predicting chorusing activity for the best performing model for each species in random forest analysis using conditional permutation importance. Darkest green indicates the most important variable and lightest green/white indicates the least important variable. The importance values (increase in prediction mean square error) were centered and scaled separately for each species. Species have been ordered left-to-right on the heatmap in order of shortest to longest calling periods (taking into account the length of the calling periods within each breeding season). The variable importance results for individual species are presented in Appendix S1: Figure S18.

DISCUSSION

Anurans in tropical savanna habitats require humid conditions to support activity and breeding pools that persist long enough for larval development (Lamotte, 1983). The high seasonality and variability of rainfall in wet–dry tropical savannas suggest that anuran breeding activity would be restricted to the wet season and breeding events would track rain events. Therefore, it is not surprising that the chorusing periods of most species detected in our study were aligned with the rainy season. This was not the whole story, however. Using continuous acoustic recording and an acoustic visualization tool to detect and measure the duration of choruses on each night allowed us to obtain data on chorusing behavior at a nightly resolution. This allowed us to reveal, in detail, the seasonal chorusing patterns of each species, and show that the start of core chorusing periods coincided with the first major rain event of each wet season. There were some exceptions, such as *R. marina*, which exhibited episodic chorusing throughout the study period, and *Lim. peronii*, which started calling at the end of the wet season. The high synchrony of initial choruses at all sites and in both wet seasons of the study period clearly indicates that the breeding periods of most species were stimulated by the onset of the wet season.

Temporal patterns of chorusing

Although chorusing of the majority of species was synchronized with the start of wet season, there was considerable variation in the length of chorusing periods among species. The length of anuran breeding periods is an important characteristic to consider, as it has implications for many ecological processes, including mating

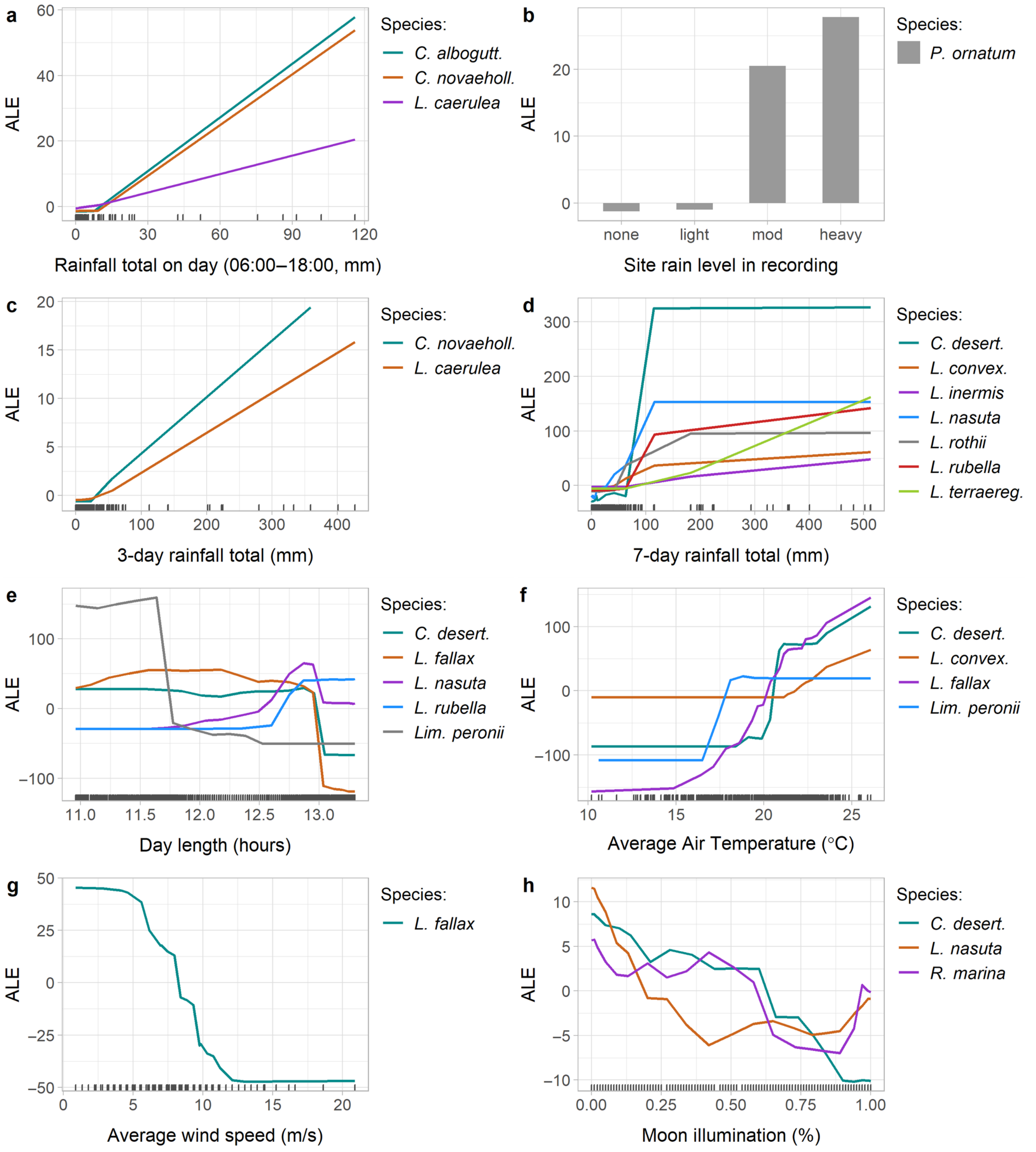

FIGURE 8 Accumulated local effects (ALEs) plots for most important variables predicting nightly species chorusing activity in random forest analysis using conditional permutation importance. ALEs are the accumulated average differences in predictions calculated for local quantiles of the predictor variable, and are in units of the response (i.e., in minutes per night). Effects are presented if the variable was ranked as the most important variable or close to the most important variable, for that species' model. Raw data of the continuous variables are plotted on the *x*-axis rug plots. See Table 1 for full species names.

systems, sexual selection, species interactions, and community composition (Wells, 2007). The characterization of breeding periods as explosive or prolonged is useful for describing this facet of anuran breeding behavior, but, more practically, these terms describe the opposite ends of a continuum. A wide range of breeding periods was evident in our study community, from explosive chorusing on only one night, to chorusing periods of several months, and there were several species within these extremes that cannot be definitively characterized. For example, chorusing by *L. convexiusculus* and *L. rothii* was detected for 2–3 months at Freestun Dam in 2013, but shorter periods at other sites and times. *R. marina*, on the other hand, was detected chorusing in all months of the year but has also been described as an opportunistic breeder (Wells, 1977; Zug et al., 1975), and it exhibited many short chorusing periods throughout the breeding season consistent with this characterization. The wide range of chorusing patterns observed, around the limitations imposed by the timing of rainfall events, indicates that a variety of factors other than rainfall also drive breeding activity.

Effects of environmental variables on chorusing activity

We found different environmental factors influenced the nightly chorusing activity of species. In particular, explosive and prolonged breeding species responded to rainfall at different timescales. Among the variables tested in the random forest analysis, only short-term rainfall factors, up to the 3-day cumulative rain total, were important for the explosive breeders, except for *L. inermis* and *Lim. terraereginae*. Only *P. ornatum* responded to the immediate rainfall conditions (i.e., the level of rain as observed in the recording). Other species in the explosive breeding group responded to rain during the day (i.e., in the 12 h 6:00–18:00 before recording started), the 1-day lagged rain total (total rainfall for 24 h of the previous day), or the 3-day cumulative rainfall total (total rainfall for 72 h up to and including the night of recording) or a combination of these. *L. inermis* and *Lim. terraereginae* responded only to the 7-day rainfall total. This indicates that there is a lagged response to rainfall by these species, likely because individuals must leave their refuges and move to the breeding site at night to call (Saenz et al., 2006). There may also be social factors influencing chorus formation, and chorus activity may increase on the nights following rain, as more individuals join choruses in response to initial calling (Bee, 2007; Fouquet et al., 2020). In contrast, the nightly chorus activity of most prolonged calling species was influenced by the cumulative 7-day rain total, but not rainfall at shorter timescales (Figure 8d). This was not a lagged effect as these species began chorusing when high rain events occurred, but then continued for many nights after. Further, rainfall was not a strong predictor in the random forest models for *L. fallax*, *R. marina*, and *Lim. peronii*. Rainfall during the study period was intermittent, with several events of high rainfall, but many days with low or no rainfall (Figure 2b). Once initiated, choruses of the prolonged breeders continued for extended periods regardless of rainfall, and other factors were more influential in driving chorusing at the nightly scale.

Day length (or photoperiod) has been linked to anuran reproductive cycles (Pancharatna & Patil, 1997; Rastogi et al., 1976) and suggested as the main driver of seasonality in anuran breeding activity (Both et al., 2008; Canavero & Arim, 2009; Medeiros et al., 2016). Day length is expected to be a strong cue for the onset of breeding in predictable, seasonal environments where increasing daylight hours reliably indicate future environmental conditions (Bradshaw & Holzapfel, 2007; Wingfield et al., 1992). Following this, in areas where rainfall is unpredictable but is a limiting resource, such as in tropical savannas, day length is not expected to be as important as weather conditions in triggering anuran breeding activity (Helm et al., 2013). Day length is also not considered a strong cue at tropical latitudes where the number of daylight hours does not vary greatly (Bradshaw & Holzapfel, 2007). At our study sites (Latitude 19.36° S), day length ranged from 11.0 to 13.3 h between each solstice—a small difference relative to higher latitudes. Nonetheless, day length was the most important variable in the random forest models for *L. fallax*, *C. deserticola*, *Lim. peronii*, and *L. nasuta*, and was also influential for *L. rubella*. Previous studies that have argued for photoperiod as the main seasonal driver of anuran breeding were in temperate or subtropical climates, where breeding occurs mainly in spring and summer (when days are longest), and found positive correlations between day length and species richness or abundance (Both et al., 2008; Canavero & Arim, 2009; Medeiros et al., 2016). In our results, chorusing activity was not linearly correlated with day length and, for some species, lowest chorusing was predicted on the longest days (Figure 8e). Day length had a negative effect on the chorusing activity of *Lim peronii*, which mostly occurred from April to August (austral autumn and winter). Prolonged breeding in anurans is driven by asynchrony in female reproductive cycles and arrival at breeding sites, which sustains choruses of calling males for several months (Wells, 1977). The predictive strength of day length, over the other weather variables, for chorusing activity of prolonged breeders, likely reflects the seasonality of breeding and its association with the time of year, rather than direct causality.

Temperature has a strong influence on anuran metabolic processes and activity, and lower temperatures require more energy to maintain activity (Pough et al., 2001). Calling is energetically costly for male frogs (Ryan, 1988), and species with long breeding seasons are expected to reduce calling effort when conditions are less favorable to conserve energy. Individual calling activity is positively associated with temperature (Brepson et al., 2013), as is individual chorus participation in tropical, prolonged breeding species (Townsend & Stewart, 1994). Several of the prolonged breeding species were positively influenced by air temperature in our study (Figure 8f). Air temperature was likely not a factor at the start of the wet season, as this was also the warmest month of the year (Figure 5a). But later in the breeding season, cooler overnight temperatures may have reduced individual calling effort and therefore chorus duration on some nights.

We considered several other meteorological variables with potential associations with anuran activity in the analysis. Relative humidity and air pressure can act as stimuli for anuran calling (Llusia et al., 2013; Steelman & Dorcas, 2010), but these were not strong predictors for chorusing in the community in our study. This was likely because relative humidity was consistently high at night, particularly during the wet season, and air pressure was negatively correlated with both air temperature and day length. Average nightly wind speed was ranked as the (approximately equal) most important variable for *L. fallax* in the random forest analysis (Appendix S1: Figure S18b). The estimated ALEs revealed a negative effect of wind speed on predicted chorusing activity of *L. fallax* (Figure 8g). Consistent with this result, we observed no calling activity on some nights with persistent strong wind, and breaks in *L. fallax* chorusing when strong wind occurred in the recordings (Sheryn Brodie, personal observation). Wind could inhibit calling activity as it exposes frogs to higher evaporation rates or to acoustic interference, and previous studies have also found a negative effect of wind speed on calling (Oseen & Wassersug, 2002; Steelman & Dorcas, 2010). *L. fallax*, the Eastern Sedge Frog, was the smallest of the tree frog species in our study (male body length range 22–26 mm, Tyler & Knight, 2020), and males call from elevated positions on vegetation or shrubs (Hoskin et al., 2015). These traits combined may explain why wind speed was a top predictor for *L. fallax* calling, but not for other species. Wind increases air evaporation rates and smaller frogs desiccate faster than larger frogs (Nevo, 1973). Calling from elevated positions likely makes *L. fallax* males more susceptible to desiccation than other small frogs that call from the ground, or in or near the water, such as *C. deserticola* and *L. rubella*. The larger tree frogs, *L. caerulea* and *L. rothii*, also call from elevated positions but were unaffected by wind speed. Although, it should be noted, wind speed was ranked third or fourth in predictor variable importance for *L. caerulea* (Appendix S1: Figure S18i), this further supports the role of wind conditions in influencing frog calling behavior.

Moon illumination (as fraction of the moon) was detected as the most important variable for *R. marina*, and also influential for *C. deserticola* and *L. nasuta*. Several studies have detected negative effects of moonlight on anuran calling activity, but others have found positive effects (Grant et al., 2012), indicating the effect of nocturnal light levels is species specific. In our study, moon illumination had a negative effect, with chorusing activity predicted to be higher at low levels of moonlight, that is, around the new moon (Figure 8h). Muller et al. (2018) observed a negative effect of moonlight on the trapping rates of *R. marina* in the post-wet season, indicating that light conditions affect the activity of this species generally. Breeding activity exposes individuals to predation, and some males may be inhibited from calling on nights of high light intensity (Grant et al., 2012). Although in our results the estimated effects of moon illumination were not strong, the ALEs include only the first-order effects. The effects of any second-order interactions with other important variables, particularly rainfall (which reflects cloud conditions) and day length (representing a seasonal effect), may also contribute to the importance of moon illumination as a predictor in the random forest models. Further, the fraction of moon illuminated is a coarse approximation of moon light at the ground during a given night, and does not take into account factors that affect the level of light perceived by anurans, such as cloud cover, vegetation cover, and the variation in moon rise and set times during the different phases of the lunar cycle (the moon is visible in the early evening during the waxing phases, but rises later when waning). Measuring ambient light levels directly when frogs are active would help elucidate the nature of the effect of nocturnal light intensity on anuran activity (Onorati & Vignoli, 2017).

The timing of anuran reproductive activity is plastic and responds strongly to abiotic conditions (Wells, 2007). The patterns we observed in our study community were likely affected by multiple factors that we did not measure. Other site variables may have affected the community composition and population size of certain species at the study dams. Site features such as elevation, dam structure, or hydrology may not be favorable for some species that were rarely detected, such as *P. ornatum* and *L. inermis*. The breeding of some species may appear explosive if they were present in small population sizes, and therefore choruses were detected on only a few nights.

Geographical comparisons

Anuran activity is strongly influenced by environmental conditions, and so their breeding periods are expected to vary geographically. Many of the species detected in this study are widespread, with ranges extending south into subtropical and temperate regions of eastern Australia. (The exceptions are *L. convexiusculus* and *U. mimula*, which, while also having broad ranges, are restricted to northern Australia.) Our results add to the knowledge of the breeding patterns of these widespread species as most documented information comes from surveys in the southern extent of their ranges. Reference information about the breeding periods of our study species refers generally to the months in which breeding or calling has been documented, and many are described as breeding in spring (September–November) and summer (December–February) (Clulow & Swan, 2018). We demonstrate that the majority of species in our study breed during the wet season, which occurs mid- to late summer, and lowest chorus activity occurs in the late dry period, which aligns with the austral spring. These regional differences largely reflect the latitudinal variation in rainfall patterns in Australia. In subtropical regions, rainfall is less seasonal, and in temperate latitudes is highly uniform throughout the year. In northern Australia, rainfall patterns are driven by the Australian monsoon, which is less predictable—the wet season typically occurs from December to February, although there is variability from October to April (Bureau of Meteorology, 2023a). The timing of anuran breeding in northern Australia is expected to occur in response to the onset of the wet season each year, but there may be additional factors, such as temperature or rainfall thresholds, necessary to initiate breeding activity. Larger scale studies, over multiple years and locations, would clarify the complex interactions among abiotic factors driving anuran breeding.

Most studies of chorusing in anuran assemblages in Australia are from temperate or subtropical zones. To our knowledge, there are only two studies from northern Australia with which we can compare our results. Tyler et al. (1983) surveyed an anuran assemblage at Jabiru, Northern Territory (NT), over two wet seasons and documented the reproductive behavior of 22 species. The start of calling activity of most species coincided with the onset of the wet season, which occurred in November of each year, and most species had extended calling periods for several months until March or April. These included *L. caerulea* and *P. ornatum*, which we detected calling on only occasional nights at Hervey Range. Rainfall is considerably higher at Jabiru than Hervey Range, and also more consistent—rainfall is typically recorded on most days in January to March—compared with our study site where rainfall is more intermittent (Bureau of Meteorology, 2023b). The more persistent pattern of wet-season rainfall likely drives breeding seasons to be longer in the NT tropical savanna. Dostine et al. (2013) investigated the influence of several weather variables on the detection probabilities of 14 anuran species near Darwin, also in the NT. Although they did not collect nightly data and could not detail the seasonal chorusing periods, similar to our results they found a variety of responses among species, with rainfall as a primary driver of calling. Water temperature and the number of days since the start of the wet season were the most influential variables across species, and both these factors are associated with cumulative rainfall.

Corresponding with the less seasonal rainfall in southeast Australia, several species detected in our study had quite different calling periods in their southern ranges. Studies in southeast Queensland (Plenderleith et al., 2018) and New South Wales (Lemckert & Mahony, 2008) documented calling periods of numerous species, including seven species detected in our study: *L. caerulea*, *L. fallax*, *L. gracilenta*, *L. rubella*, *Lim. peronii*, *Lim. terraereginae*, and *P. ornatum*. In both studies, calling periods began in September or October (austral spring) and *L. fallax* and *Lim. peronii* were detected calling in all months surveyed, including winter. *Lim. peronii* in particular exhibited a noticeably different chorusing pattern in our study. In its southern range, calling is detected year-round in response to rainfall and temperature (Lemckert & Grigg, 2010; Lemckert & Mahony, 2008; Plenderleith et al., 2018). In contrast, at Hervey Range, *Lim. peronii* was the only species we did not detect calling in the peak wet season, and chorusing began at the end of wet season. A potential reason for the later chorusing activity of *Lim. peronii* is avoidance of acoustic competition. This species has a short, relatively soft advertisement call that overlaps in frequency with several other species, and may be masked during periods of high-intensity choruses of other species (Allen-Ankins & Schwarzkopf, 2021). Alternatively, high temperatures may constrain the calling activity of *Lim. peronii* in our study region, which is at the northern extent of the species' range (Tyler & Knight, 2020). Further studies of *Lim. peronii* in its northern range would be of interest and add to the knowledge of the geographical variation in anuran breeding behavior more broadly.

The random forest model for *R. marina* was not a strong predictor of nightly chorusing activity of this species, despite the large amount of data we obtained (Table 1), indicating that *R. marina* chorusing activity is not strongly influenced by environmental factors, which is consistent with previous findings (Plenderleith et al., 2018). Reproductive cycles are regulated by endogenous hormonal activity, but there is an established association between anuran reproductive cycles and external environmental conditions (Duellman & Trueb, 1986).

The seasonal reproductive cycle of *R. marina* is linked with rainfall, but at any time of year, there is a proportion of mature toads capable of breeding (Yasumiba et al., 2016). Although rainfall was not a predictor of nightly chorusing activity for *R. marina*, chorusing was more frequent in the wet season, indicating more favorable conditions for breeding activity. The episodic pattern of chorusing we have documented suggests other factors are driving *R. marina* chorusing activity at breeding sites. Calling is an indicator of breeding activity generally, but not necessarily that spawning has occurred. The pattern of chorusing may be influenced by more males arriving at the breeding site and joining the choruses on consecutive nights, rather than the arrival of females. Additionally, *R. marina* are known to switch from advertisement calling to active searching or scramble competition (Vargas-Salinas, 2007), and the density of toads or the arrival of females may affect the level of calling activity.

Consistent with our results, Plenderleith et al. (2018) also determined daily rainfall was the best predictor for the explosive breeders *L. terraereginae* and *P. ornatum*. However, in their study, several other species were influenced by minimum temperature (*L. caerulea* and *L. rubella*) or air pressure (*L. gracilenta*) rather than rainfall, in contrast to our results. Clearly, species may respond differently to weather conditions in different parts of their climatic ranges. A recent broadscale study of drivers of anuran calling also found evidence of this. Thompson et al. (2022) based their analysis on a citizen-science dataset of anuran call occurrence across Australia, and found that day of the year and temperature were the most influential factors associated with calling on a continental scale. However, they were able to analyze and compare the responses of several species across climatic zones, and found rainfall was more important for some species in their tropical ranges.

Concluding remarks

The requirement of moisture for anuran activity and larval development drives competition for food resources and breeding sites, as well as acoustic competition among males when calling. Temporal partitioning is considered the most important niche dimension for aquatic anuran larvae, through interspecific differences in predation risk and intense competition for food among tadpoles (Toft, 1985). Following this, seasonal temporal partitioning in adult anuran breeding activity is widely observed in assemblages in various climatic zones (Blair, 1961; Donnelly & Guyer, 1994; Heard et al., 2015; Oseen & Wassersug, 2002; Richter-Boix et al., 2006). Seasonal tropical savanna and semiarid climates place more stringent constraints on anuran breeding and activity in general. Consequently, anurans in these environments are largely restricted to being nocturnal and aquatic, wet-season breeders (Lamotte, 1983). These constraints are expected to reduce opportunities for partitioning resources temporally (Toft, 1985). Nonetheless, several studies, including ours, have revealed a degree of temporal partitioning of breeding activity in anuran assemblages in seasonal tropical environments (dos Santos Protázio et al., 2015; Moreira & Barreto, 1997; Prado et al., 2005; Schalk & Saenz, 2016).

Passive acoustic monitoring affords opportunities to study animal behavior in complex ecological assemblages at a greater scale using improved analysis tools. Using a visualization method to survey a large set of continuous sound recordings, we obtained nightly data on the chorusing patterns of an anuran community at multiple breeding sites over two wet seasons. Our results are important for understanding the detectability of frog species in acoustic monitoring programs in northern Australia. The tropical savanna bioregion of northern Australia is vast, largely undeveloped and remote, and therefore many species are under-surveyed (Pintor et al., 2019). Monitoring of ecological communities over time is important for detecting the impacts of disturbance, and baseline information is essential to detect changes in populations (Magurran et al., 2010). Further, the Cane Toad, *R. marina*, is an introduced species, and a better understanding of the breeding ecology of this species will inform management and control efforts. The chorusing and breeding patterns of the frog species of northern Australia have been rarely documented. Continuous monitoring over multiple breeding seasons and multiple sites was essential for obtaining baseline data on species-specific calling patterns. Prolonged breeding species have high detectability for a large part of the breeding season, but explosive breeding species may only be detected on several nights during the year and would be missed if recorders were deployed after the onset of the wet season. Anuran populations vary in time and space, and monitoring multiple breeding sites highlighted that some species may exhibit different patterns of chorusing at different sites within a localized area. Breeding periods also vary geographically, and knowledge of the breeding patterns of anurans in their local ranges is required for effective monitoring, and for increasing knowledge of species distributions and behavior.

AUTHOR CONTRIBUTIONS

All authors conceived the study. Sheryn Brodie designed the sound analysis methodology and collected the data. Sheryn Brodie performed the statistical analysis and

Slade Allen-Ankins and Lin Schwarzkopf advised on the analyses. Sheryn Brodie wrote the draft manuscript and finalized the manuscript, with editorial input from Slade Allen-Ankins and Lin Schwarzkopf.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Brodie et al., 2023) are available from the Research Data JCU repository: https://doi.org/10.25903/bpkv-gf77.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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