Science of the Total Environment 878 (2023) 163080

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Soundscape phenology: The effect of environmental and climatic factors on birds and insects in a subtropical woodland

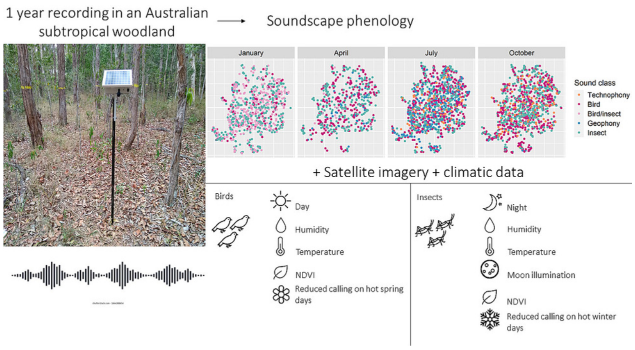
Marina D.A. Scarpelli *, Paul Roe, David Tucker, Susan Fuller

Queensland University of Technology, Brisbane, Australia

HIGHLIGHTS

- Calling activity is affected by different environmental factors depending on the taxonomic group.
- Higher-than-average temperatures affect birds and insects in different seasons.
- Phenology shows impacts of climate change on animal communication.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Rafael Mateo Soria

Keywords:
Biophony
Acoustic indices
Ecoacoustics
Climate change
Remote sensing
Temporal scales

ABSTRACT

Climate change and biodiversity loss are significant global environmental issues. However, to understand their impacts we need to know how fauna respond to environmental and climatic variation over time. In this study, remote sensing techniques (satellite imagery and passive acoustic recorders) were used to investigate the variation in biophony over different timescales, ranging from one day to one year, in a sub-tropical woodland in eastern Australia. The prominent sources of biophony were birds at dawn and during the day, nocturnal insects at dusk and during the night, and diurnal birds and insects (mainly cicadas) over the summer period of December, January, and February. While different environmental factors were found to be key drivers of phenological response in different faunal groups, temperature, humidity and the interactions between temperature, humidity, moon illumination and vegetation greenness were most important factors overall. Using observed temperatures relative to the historical mean for each day of the year, we evaluated the impact of higher-than-average temperatures on calling activity. We found that nocturnal insects call less frequently on days when the temperature was hotter than average in winter months (June, July, and August), and birds call less frequently in hot spring days (September, October, and November) meaning these groups can be susceptible to temperature increase as consequence, for example, of climate change. This study demonstrates how animal calling behaviour is affected by different environmental variables over different temporal scales. This study also demonstrates the utility of remote sensing techniques for assessing the impacts of climate change on biodiversity. It is highly recommended that monitoring schemes and impact assessments account for phenological changes and environmental variability, as these are complex and important processes shaping animal communities.

---

* Corresponding author.
E-mail address: ninascarpelli@gmail.com (M.D.A. Scarpelli).

http://dx.doi.org/10.1016/j.scitotenv.2023.163080
Received 13 November 2022; Received in revised form 17 March 2023; Accepted 22 March 2023

1. Introduction

Globally we are in a zone of uncertainty with respect to biodiversity loss and climate change (Steffen et al., 2015), and therefore it is critical that we better understand the impacts of changing environmental conditions on biodiversity. Phenological events can affect animal behaviour resulting in temporal cycles such as diurnal rhythms, seasonal responses or even patterns repeated every two to seven years (e.g.: linked to the La Niña–El Niño southern oscillation). As the relationships between animal behaviour, phenology and the environment are complex and intertwined, studies on how fauna respond to environmental conditions are required if we are to assess and predict climate change impacts.

Phenology is the study of recurrent biological phenomena and in the context of the current study, we interpret phenology as an integrated concept that includes ecological, evolutionary and chronobiological perspectives. In this sense, phenological events occur over short (e.g. hourly, daily) and long (linked to seasons and life-cycles) timeframes (Visser et al., 2010). Although many factors may be responsible for driving phenology, in Australian ecosystems climatic factors are particularly important (Chambers et al., 2013). While direct phenological response to changes in environmental conditions may occur, sometimes the effect is not immediate. For example, temperature in the previous three months may be an important trigger of plant fruiting events (Rawal et al., 2015). When there is a lag between environmental changes and phenological events, fauna rely on cues to predict future conditions (Visser et al., 2010). The precise mechanism of how environmental cues translate into specific behavioural actions is not completely clear, but it relies on calendar-internal clock dynamics (for example, interpreting day length as a cue for seasonal change) (Visser et al., 2010). Research on faunal responses to phenological events can provide insight on how the calendar-clock dynamic works, but also importantly can provide better understanding of seasonal and sporadic events (Moore et al., 2016) and their effects on biodiversity and animal behaviour.

There are numerous underlying factors that drive and affect animal behaviour, including intrinsic (e.g.: hormones and physiological reasons); environmental (e.g.: light intensity, temperature, habitat structure, etc.); and social factors (e.g.: mate attraction, territory defence, avoidance behaviour). As the earth rotates around the sun, the variation in sunlight (day/night and seasonal variation) influences environmental parameters. As a result, animal communities organise around these cycles (Brandstätter, 2003). Rainfall and associated environmental changes are known to affect the breeding season of many bird species (Karr, 1976) as well as trigger a delayed increase in calling activity for some Australian frogs (Heard et al., 2015). Evidence also suggests that temperature affects calling behaviour for amphibians with varied effects across different geographic locations and seasons (Llusia et al., 2013). Vegetation phenology is documented to be a very important factor influencing the behaviour of phytophagous insect species (Lowman, 1982). Temperature is also known to affect insect behaviour, with increased activity on warmer days (Alexander, 1968; Rebaudo and Rabhi, 2018). These studies demonstrate how phenology and environmental factors can influence animal behaviour, including communication through signal transmission.

Communication is a critical animal behaviour influencing reproductive success, fitness and a species evolutionary potential (Bradbury and Vehrencamp, 2011). Sound production is one mode of communication used to maintain social interaction among groups, individuals and species (Brumm and Slabbekoorn, 2005; Mathevon et al., 2004). Birds, for example, are well known for their song use, and there are several behaviours associated with it such as mate attraction, territory defence, and contact calls to maintain group cohesion (Slabbekoorn and Halfwerk, 2009). Frog choruses have the ultimate goal of attracting females, but there are several other types of calls emitted depending on other ecological and anthropogenic factors (Narins et al., 2007). Cicadas produce a congregation type of call, that is used to attract females but also reduce predation risk (Moulds, 1990) and the success of these calls varies with environmental factors (e.g.: cloud cover, rain and wind) (Alexander and Moore, 1958). Crickets also use sound production to attract mates (Beckers and Wagner, 2011). Therefore, among both vertebrates and invertebrates, acoustic communication is an important behaviour and evidence suggests that temporal separation in acoustic activity may be linked to circadian rhythms on a nocturnal/diurnal cycles, and environmental and phenological patterns across longer timeframes.

Traditional biodiversity surveys involve trapping and manual observation making them expensive to implement in terms of personnel and equipment, over long timescales. Moreover, the presence of humans in the field on a regular basis can influence animal behaviour and therefore bias the results (Sugai and Llusia, 2019). Remote sensing approaches for monitoring fauna using autonomous sensors can address these issues because they can be left unattended for long periods to record continuous data, while providing a permanent record (Sugai and Llusia, 2019). Biodiversity can be monitored using drones, camera traps and acoustic sensors, while permanent weather stations and satellite imagery can provide information on the environment and vegetation, including phenological events. For example, the Enhanced Bloom Index (EBI) has been used to quantify flowering (Chen et al., 2019) and the Normalised Difference Vegetation Index (NDVI) measures greenness (Asrar et al., 1984), both calculated using satellite images. Remote sensing approaches are now invaluable for many research areas and in the ecological context they have been widely used for investigating patterns in biodiversity across large spatial and temporal scales.

Passive acoustic monitoring is increasingly used to survey biodiversity, but long-term continuous recording generates a lot of data, which can be challenging to analyse. One solution is to use Convolutional Neural Networks (CNN's) and recent studies have shown their utility for detecting anomalous sounds (e.g.: chainsaw, gunfire) across ecosystems (Sethi et al., 2020) and understanding changes in biophonic indicators of ecosystem function (Folliot et al., 2022). Another computational strategy that can be used to summarise large amounts of sound data is the calculation of acoustic indices. Acoustic indices are used to measure different aspects of sound characteristics (frequency, time and/or intensity) and a combination of three indices has been found to provide reliable representation of the soundscape including biological sounds or biophony produced by vocalising fauna (Brodie et al., 2020; Gan et al., 2020; Towsey et al., 2018b). The three indices are: Acoustic Complexity Index (ACI), which measures the differences in sound intensity across adjacent values (Pieretti et al., 2011), the Temporal Entropy Index (ENT), which measures the entropy of acoustic signals across the time dimension (Sueur et al., 2008) and Events Per Second, an index which measures the number of acoustic events present in each second of recording (Towsey, 2018).

In this study, we demonstrate how a combination of acoustic indices analysed using machine learning (motif discovery) and remote environmental sensing, can be used to examine faunal responses and soundscape phenology in the face of escalating human impacts and climate change. We investigated changes in calling activity relative to a range of environmental variables across varying timescales from one day to one year in a woodland in eastern Australia.

2. Material and methods

2.1. Data collection

Continuous acoustic recording data for one year (2020) from a single Australian Acoustic Observatory (Roe et al., 2021) sensor (Solar BAR | Frontier Labs AU [WWW Document], 2020) deployed at the Samford Ecological Research Facility (SERF) (−27.38892, 152.881) were analysed. The sensor recorded in mono channel at 16-bits and 22,050 Hz sampling rate. SERF is located approximately 20 km from Brisbane in South-East Queensland (SEQ), Australia. The region has a subtropical climate (minimum temperatures between −3 °C and +18 °C, fully humid with hot summer (Kottek et al., 2006) and gently undulating topography. The area where the sensor was located consists of a dry sclerophyll forest, dominated by *Eucalyptus tereticornis*, *Eucalyptus crebra* and *Corymbia* species.

2.2. Acoustic indices

Acoustic indices were calculated for each recording minute using *AnalysisPrograms.exe* (Towsey et al., 2018a). Acoustic Complexity Index (ACI) (Pieretti et al., 2011), Temporal Entropy (ENT) (Sueur et al., 2008) and Events Per Second (EVN) (Towsey et al., 2014) were then analysed using time-series motif classification (Scarpelli et al., 2021). The time-series motif classification use wavelets derived from acoustic indices to classify minutes of sounds. The motif discovery algorithm groups subsequent groups of minutes iteratively and search the time-series pattern derived from those minutes in the recording. Each motif was approximately 30 to 40 min long and the sound categories included biophony (birds, insects, frogs), geophony (rain, wind, etc.) and technophony (cars, airplanes, etc.). Because of the length of the motifs (30 to 40 min), more than one sound class could be present within the same motif and therefore more than one sound source was attributed to the label (e.g.: if there are birds and insects present in the same motif, it was labelled as bird/insect). Thirty percent of motifs were manually labelled, and a Random Forest algorithm was used to extrapolate the labels for all the motifs, following the method outlined by Scarpelli et al. (2021). With 30 % manual labelling the training process has an accuracy of >90 %, and 70 % when considering the extrapolation of tags to the non-labelled data. As a result, the motifs provide a verified (through the manual labelling process) metric to quantify soundscapes with the number of motifs being an indication of calling activity (e.g.: an increase in the number of motifs in a given month is interpreted as higher acoustic activity within that month).

2.3. Environmental and temporal variables

Seven environmental and temporal variables were included in the model. Temperature and humidity were collected at SERF using a weather station (Davis Vantage Pro 2 weather station) logging data every 5 min. If data were missing (due to sensor malfunction), temperature and humidity values were averaged on either side of the latest values recorded. There was a total of 19 days when the equipment malfunctioned resulting in missing records that needed averaging (approximately 5 % of the total records). Rainfall was collected using the same sensor, however missing values were not averaged as rainfall data are not autocorrelated. Historic daily temperatures (2009–2019) were obtained from https://www.longpaddock.qld.gov.au/silo/ and the mean temperature for each day was calculated and compared with the mean temperature for the sampled year. Days in the sampled year (2020) were then classified as “lower temperature than average” or “higher temperature than average”.

Planet Scope images were acquired using the Sentinel Hub engine (Sentinel Hub, 2022). Planet Scope is a constellation of satellites that provide almost daily earth images with a 3 × 3 m resolution. Normalised Difference Vegetation Index (NDVI) and Enhanced Blooming Index (EBI) were calculated using the configuration utility from Sentinel Hub. The bands used for the calculation of satellite indices can be found in the supplementary material. Some problems with the satellite images were encountered, such as cloud cover and incomplete images due to the position of the satellite preventing it from acquiring more images. Therefore, the satellite data were not sampled in a standardised manner over the year. Also, due to low sample size, it was not possible to create an auto-regressive model to estimate the values for unsampled months (January and February). Therefore, the available images were averaged per month, and if no images were available, the month was excluded from this analysis that used these variables. These indices were chosen as they provide information on seasonality and flowering/fruiting events on a pixel-by-pixel basis. A 325 m buffer was drawn with the sound recorder in the centre using QGIS (QGIS Geographic Information System, 2022) and NDVI and EBI mean and range were calculated. The buffer was drawn considering the microphone recording radius in additional to constraints to acquire the data since this is derived from proprietary satellite imagery and there were quota limitations. Pearson's correlation tests were then performed in R (R Core Team, 2019) to exclude correlated values. Mean EBI and mean NDVI had a correlation value of 0.71 ($t = 6.0989$, df = 35, p-value = 5.722e−07) and were therefore excluded. EBI range values and NDVI mean values were not correlated and therefore used in the analysis.

Sunrise, sunset, moon rise, moon set, start and end of night information were obtained using the suncalc (0.5.1) (Thieurmel and Elmarhraoui, 2022) package in R. Dawn was the period between “nightEnd” (start of morning astronomical twilight) and “sunrise” (top edge of the sun appears on the horizon) and dusk between “sunset” (start of evening civil twilight) and “night” (dark enough for astronomical observations). “Night” comprised the whole period between “dusk” and “dawn”, while “Day” was the entire period between “dawn” and “dusk”. Moon illumination was calculated using the lunar (0.2–1) (Lazaridis, 2014) package in R and then moon rise and set were matched with recording time. If the moon was in the sky during the recording period, the moon illumination value was used, otherwise a value of 0 was attributed to the moon illumination value. All recording times corresponding to the period ‘day’ were also attributed a value of 0 for moon illumination.

2.4. Statistical analysis

Statistical analysis was performed using two different temporal configurations: by period of the day (dawn, day, dusk, and night) and across months (mean values for environmental variables per period) to account for both daily variability and seasonality. Given that animal behaviour varies greatly depending on period of the day and taxonomic group, the attribution of “periods” was very important for the partition of the analysis. Environmental variables are, by nature, autocorrelated (Legendre et al., 2002), therefore Random Forest classification models were used due to the flexibility of this technique when data are autocorrelated (Breiman, 2001). The models were built to classify the motif labels based on environmental variables. All the variables tested for each model can be found in the Supplementary Material. For example, using values of temperature, humidity, rain, etc. the algorithm would classify each given motif into bird, insect, etc. From that, it was possible to find out which variables were more important to classify the minutes in each sound category. The mean decrease accuracy statistic is used in Random Forest models to evaluate the results. If mean decrease accuracy is negative, random variables are better predictors than the variables included in the model. The mean decrease accuracy values have meaning when compared with other values of the same model, however they should not be applied out of context. Plots were used to evaluate the effects that variables had on each sound category.

After the Random Forest modelling a PERMANOVA (Anderson, 2017) was performed to assess significance levels and explanatory power of the variables indicated by the Random Forest algorithm. PERMANOVA is a permutational analysis of variance that is very flexible in its assumptions and therefore can be used when data are autocorrelated (i.e.: there is no assumption regarding independence of samples). The analyses were conducted firstly between all the taxonomic groups (birds, insects, and bird/insect) and including the periods (dawn, day, dusk, and night) to determine the influence of predictors in the overall calling activity. In a second analysis, taxonomic groups and their predictors were tested separately, without including the period. This was done because of the ecological and behavioural differences in groups, assuming the variables would have different explanatory power depending on the group.

To understand how seasonality influences biophony, a monthly model was created. In this analysis, the environmental variables were averaged by month, meaning that each variable would have one single value for the whole month. Because variables had different sampling schemes (temperature, humidity, and rain were measured every 5 min, whereas EBI and NDVI had a scattered sample size due to the availability of satellite imagery), so to guarantee the same sample size across months, the variables were averaged monthly for this analysis. To investigate how environmental variables influence biophony at different periods of the day, a model was created with temperature, humidity, rain, and moon illumination at each period (dawn, day, dusk and night). A Kruskal-Wallis test was implemented in R to compare the median number of motifs in days when the temperatures were classified as lower or higher than the historical average for that day and a Kruskal-Wallis effect was also calculated in R using the "eta-squared" metric (Tomczak and Tomczak, 2014). This metric reports the percentage of the dependent variable that can be explained by the independent variable.

A dimensionality reduction Uniform Manifold Approximation and Projection (UMAP) (McInnes et al., 2018) was performed for visualisation purposes using the umap::umap in R with the default settings. UMAP were completed using the wavelet data used for the motif analysis and trained with the whole dataset. For visualisation purposes, some of the plots have modelled values using the 'geom_smooth' function in R package ggplot2 (Wickham, 2009).

3. Results

The soundscape varied throughout the year (Fig. 1). There were a total of 10,265 motifs in 7671.97 h (approximately 316 days) over one year of recordings. Motifs containing biophony (alone or with another sound source) dominated the soundscape with 87.7 % motifs (*n* = 9004). <1 % of motifs were exclusively technophony (n = 53) and 60 % of motifs contained technophony along with biophony and/or geophony (n = 6151). Less than 1 % of motifs were composed of geophony only (n = 664) and 0.08 % (n = 863) had geophony along with other sounds.

3.1. Biophony

The soundscape exhibited some clear patterns according to month of the year (Fig. 2). The months of April (22 days recorded) and May (26 days recorded) had smaller sample sizes due to equipment malfunction over the recording period. Therefore, Fig. 2 contains information on how many motifs were identified, how many recording days and the mean number of motifs per day of recording for each month. November had the highest number of motifs per day (n = 34), while April had the least (n = 23). Birds and insects (nocturnal insects, mainly crickets) were predominant throughout much of the year, however during the months of December, January, February and March, the soundscape was more dominated by the bird/insect class (diurnal birds and cicadas) (the hourly distribution of biophony over the year can also be seen in the Appendix 10.7). Geophony increased in April and was largely absent from August onwards. Technophony increased from May and persisted throughout the rest of the year. Frogs were also detected in the recordings, but very infrequently.

3.2. Random forest

Models were constructed to examine the relationship between biophony across different temporal scales and environmental features. While both geophony and technophony were initially included in the models, neither of them were found to be important for classifying any of the biophony classes, and therefore further details are not presented.

3.2.1. Monthly soundscape

For diurnal groups (bird and bird/insect classes), humidity was the best variable to predict the sound classes (Fig. 3B and Fig. 4B). For birds, the

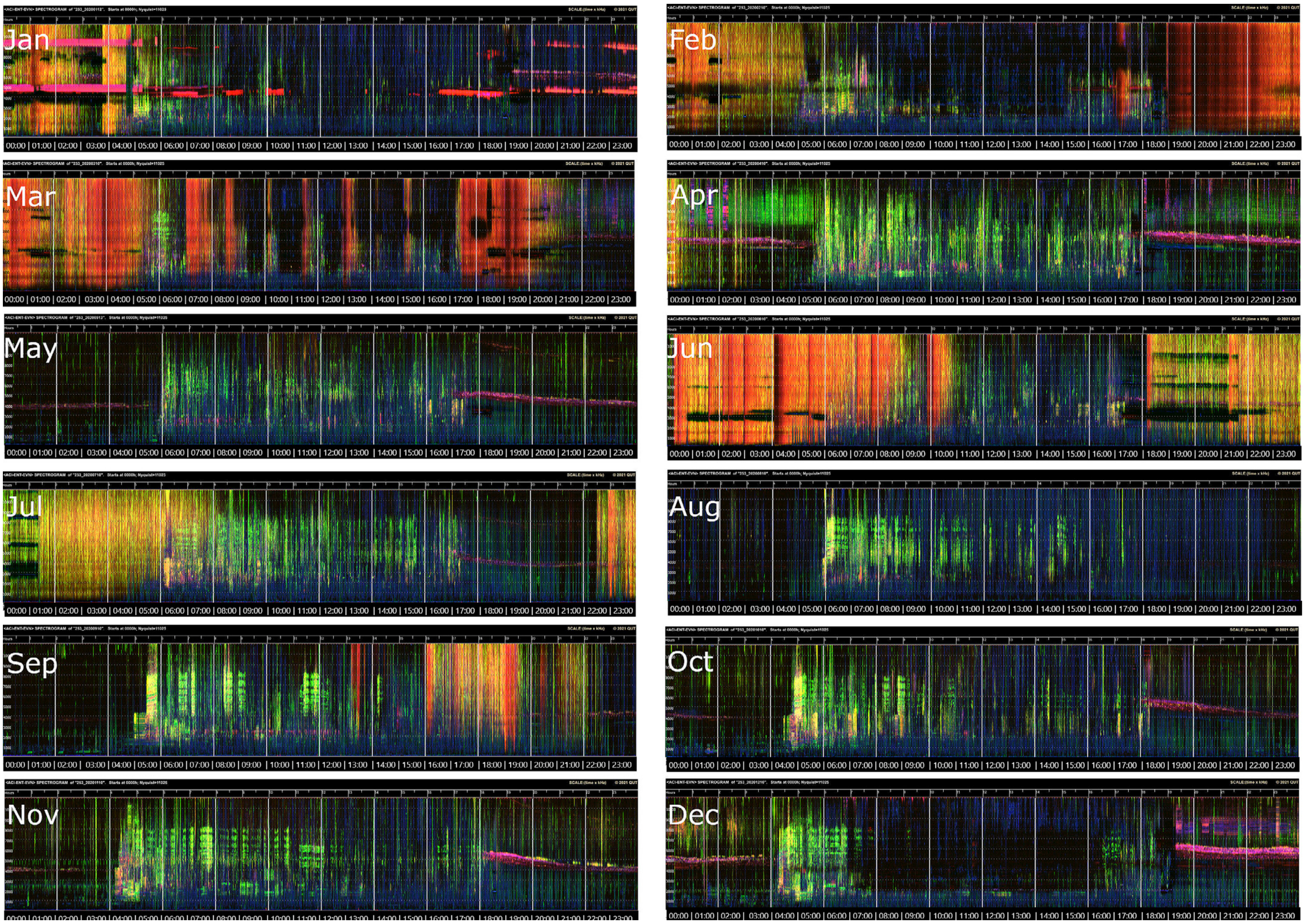


Fig. 1. False-Colour Spectrograms for one day of each month. Orange and yellow colour across all frequency bands is rain. Pink horizontal tracks are insects. Green and some yellow features are mainly birds. Blue features are technophony. Each white vertical bar represents 1-h block of recordings starting at 00:00 (midnight), and the frequency spectrum goes from 0 kHz to 10 kHz.

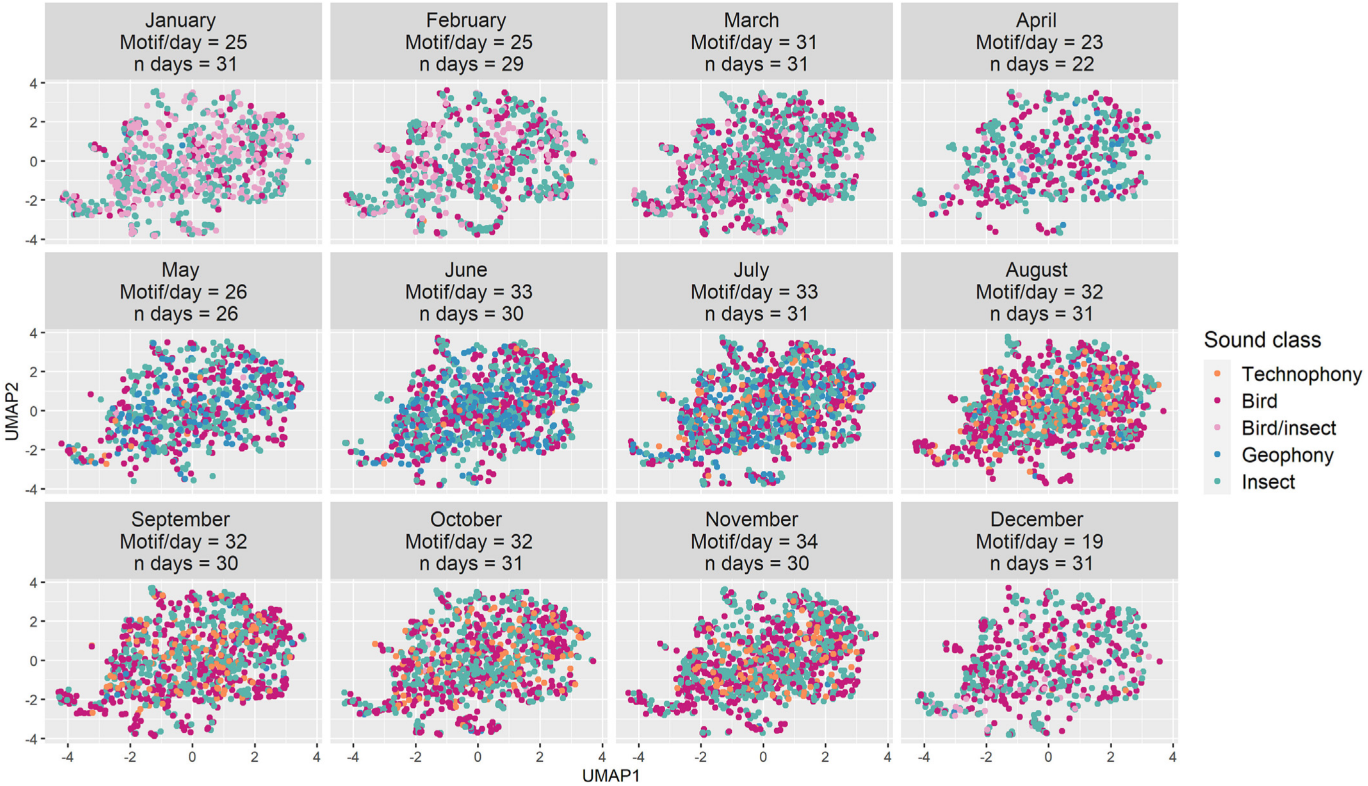


Fig. 2. Soundscape variation over the months with main sound classes.

second-best variable was NDVI (Fig. 4B) and for bird/insects, temperature (Fig. 3B). Temperature and NDVI were the best predictors for the insect (nocturnal insects) class (Fig. 6B). Motifs labelled with bird/frog/insect and frog/insect had a low sample size and therefore it was not possible to draw any conclusions for these classes. The model had an observed error of 0 for birds and insects, and 0.33 for bird/insects. The complete table with results can be found in Supplementary Material.

3.2.2. Bird/insect and dawn soundscape

The dawn soundscape presented a combination of biodiversity sounds, especially during summer and the start of autumn (January, February, and March). The bird/insect class corresponds mainly to diurnal insects (cicadas) sharing the acoustic space with birds. During this period, diurnal classes (bird/insects and birds) shared the acoustic space with most minutes assigned to both classes (Fig. 3A).

The bird classes had a low error rate (0.05) while and bird/insect class had a poor error rate (0.33). The bird class was the most predominant sounds in the period tested presenting a better result. Temperature and humidity were the best predictors for these classes. For insects, the observed error rate was 100 % indicating that the model did not classify any of the motifs correctly. Therefore, the variables indicated here apply only to the bird/insect class. Tables with complete results can be found in the Supplementary Material. Fig. 3 provides visualisations of the relationship between the number of bird/insect motifs and temperature and humidity. Bird/insect sounds were highest in January, February and March, corresponding to very high levels of humidity (80 %+). The number of motifs increased with increasing temperature up until approximately 20 °C and then decreased slightly and plateaued at temperatures >25 °C.

3.2.3. Birds and day soundscape

The day soundscape was dominated by birds and diurnal insects (bird/insect class) sharing the space during summer but for the rest of the year birds dominated the soundscape with an occasional insect occurrence.

The random forest model for biophony during the day performed very well for birds, with an observed error rate of 0.01 and temperature and humidity were the most important variables. The relationship between number of motifs and environmental variables is demonstrated in Fig. 4 and number of bird motifs was positively related with humidity and negatively related with temperature. The model did not perform well for bird/insect, insect, and frog/insect due to low sample size, so no environmental predictors could be identified. Tables with complete results can be found in the Supplementary Material.

3.2.4. Nocturnal insects, dusk and night soundscape

A change in the dominant biophony was found in the dusk and night soundscape compared with the dawn and day, with insects the predominant class throughout the year. Because the dominant biophony is the same, results for dusk and night are presented together.

In summer, again, there was some overlap between birds and insects on the same motifs (bird/insect in Fig. 5A and B) but not as much as was observed during the day and at dawn. Some nocturnal birds were observed, for example the Australasian Boobook. In February, it was also possible to detect the presence of frogs chorusing (Fig. 5B). Moon illumination and humidity were found to be the best predictors for insects at dusk (observed error: 0.004). Fig. 6 summarises the results found for the month analysis, as well as dusk and night.

Observed error for the night model was high for birds (0.68) and bird/insect (0.94), due to smaller sample size. However, the model had a low observed error for insects (0.1). Temperature and humidity were the best predictors for insects at night. Fig. 6 summarise the result of environmental variables and number of insects motifs for dusk, night, and months. Low sample sizes for the frog/insect motifs meant there were insufficient data for the Random Forest to perform accurately.

3.3. PERMANOVA statistics

3.3.1. Taxonomic groups and period

Period of the day (dawn, day, dusk, night) had a strong influence on calling activity – represented here by the number of motifs with biophony (Pseudo $F_{3,696} = 564$, $R^2 = 0.62$, *p*-value = 0.001). Other variables such

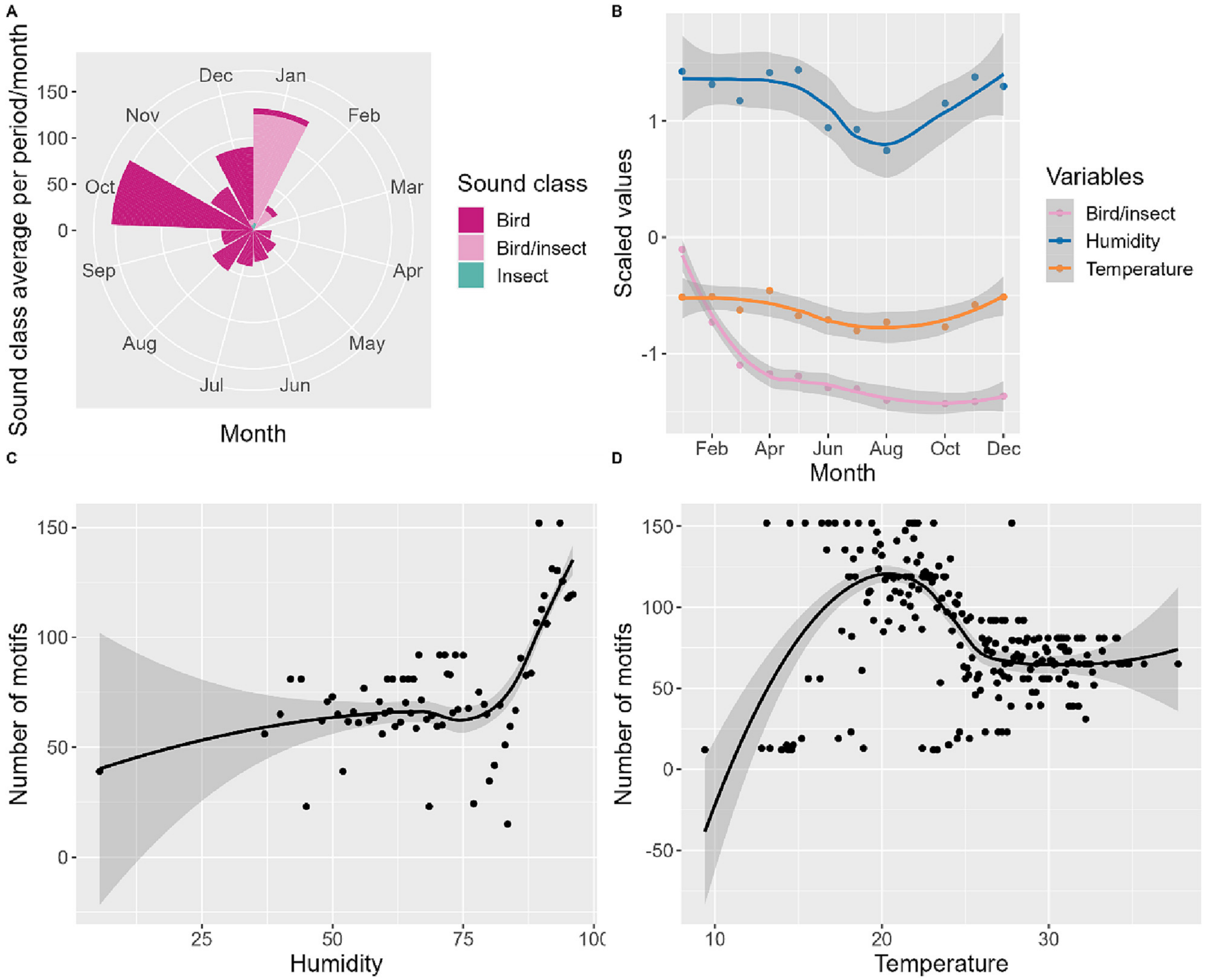


Fig. 3. A: Dawn soundscape biophony. The periods of the day were attributed based on sunset and sunrise information, so the "dawn" hours are variable across the year (earliest start at 3:15/latest end at 06:40). Counts are the number of motifs of each class per month in the dawn period. Due to difference in sampling effort, the average motif per day for each month can be found in Supplementary material. Plots B, C and D refer to Bird/insect, the most dominant sound in the period. B: Humidity, Temperature and number of bird/insect motifs scaled values based on the mean through the year, demonstrating the yearly trends of the number of motifs and the environmental variables that influence the represented sound class. The values were scaled only for visualisation purposes. C and D show the overall relationship between humidity and temperature and the number of bird/insect and bird motifs for the hourly analysis. Plots B, C and D were generated with ggplot2::geom_smooth in R and they were only used for trend visualisation purposes.

as moon illumination, temperature, humidity and their interactions were significant with a lower explanatory power (complete results can be found in the Supplementary Material).

3.3.2. Bird/insect

The bird/insect analysis indicated that temperature (Pseudo $F_{1,22}$ = 5.96, R^2 = 0.16, *p*-value = 0.003) and the interaction between temperature and humidity (Pseudo $F_{1,22}$ = 6.12, R^2 = 0.16, *p*-value < 0.05) had a weak, significant impact on calling activity (see complete PERMANOVA results in the Supplementary Material).

3.3.3. Birds

For birds, temperature (Pseudo $F_{1,404}$ = 97.33, R^2 = 0.18, *p*-value = 0.001) had a weak but significant effect on calling activity. Humidity, and the interactions between temperature and humidity, and temperature and NDVI were also significant (*p*-value < 0.05) but with lower R^2 values (<0.1). The complete statistics for the variables presented can be found in the Supplementary Material.

3.3.4. Insects

Temperature (Pseudo $F_{1,318}$ = 63.53, R^2 = 0.13, *p*-value = 0.001) and humidity (Pseudo $F_{1,318}$ = 40.80, R^2 = 0.08, *p*-value = 0.001) had a weak, significant influence on insect calling activity. Moon illumination was also statistically significant as well as the interaction between moon illumination and humidity, temperature and humidity, moon illumination and NDVI and humidity and NDVI but with a lower R^2 (<0.05). The complete statistical results can be found in the Supplementary Material.

3.4. Climate change effects on biophony

Given the importance of temperature on the calling activity of all the taxonomic groups, the median number of motifs/day for each sound category (bird, insect and bird/insect) were compared at temperatures lower and higher than average. Birds (Kruskal-Wallis x^2 = 44.172, df = 23, *p*-value < 0.05; Fig. 7A) exhibited a small to moderate effect caused by temperature (lower or higher than average), with effect size depending on the month. Nocturnal insects (Kruskal-Wallis x^2 = 45.747, df = 23, *p*-value < 0.05) exhibited a significant difference between groups (temperature lower or higher than average) with a small effect size (Fig. 7B). There was no

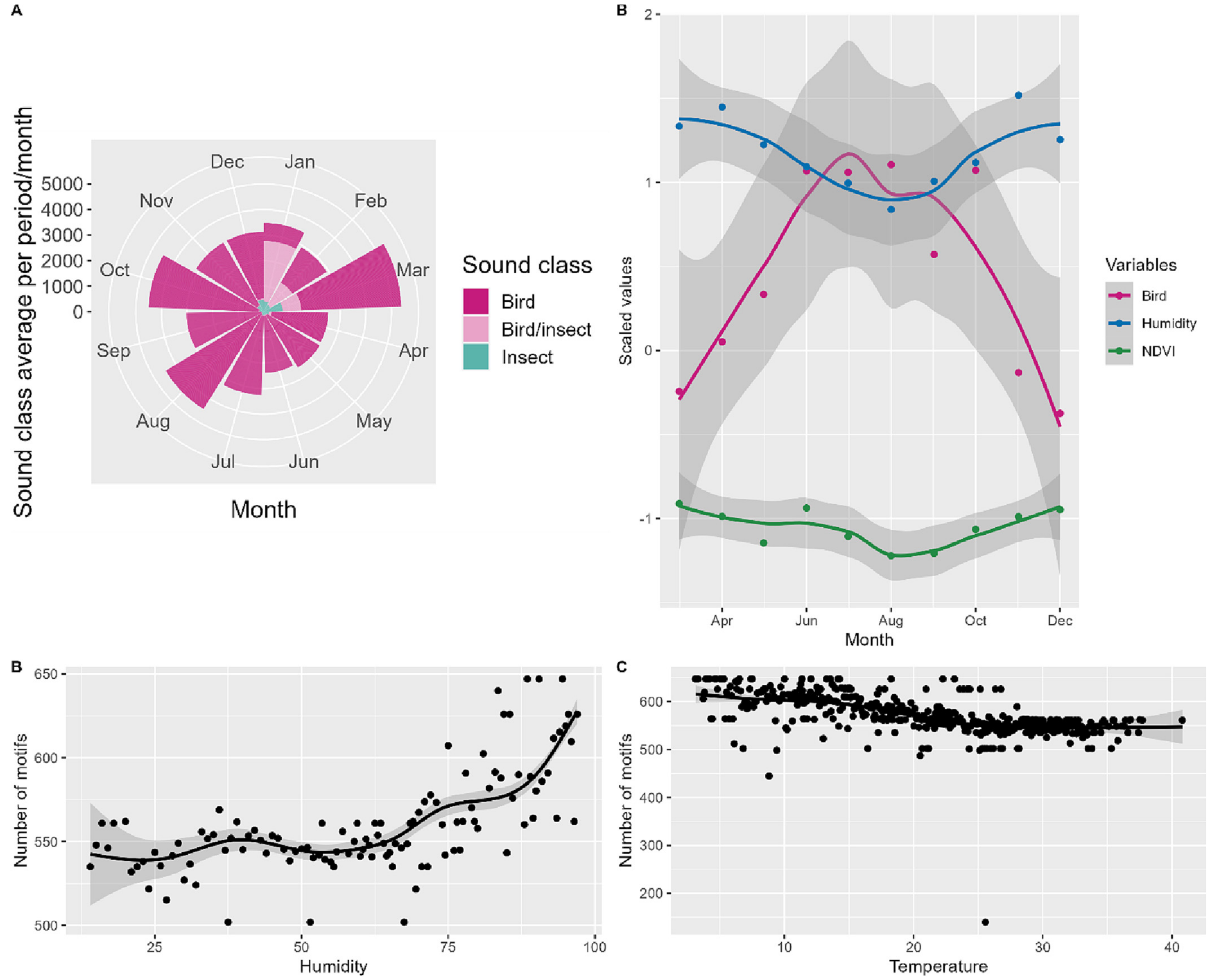


Fig. 4. A: Day soundscape for biophony. The periods of the day were attributed based on sunset and sunrise information, so the "dawn" hours are variable across the year (earliest start at 04:45/latest end at 18:49). Counts are the number of motifs of each class per month in the day period. Due to different in sampling effort, the average motif per day for each month can be found in Supplementary material. Plots B, C and D refer to Bird, the most dominant sound in the period. B: Humidity, temperature and number of bird motifs scaled values based on the mean through the year, demonstrating the yearly trends of the number of motifs and the environmental variables that influence the represented sound class. The values were scaled only for visualisation purposes. C and D show the overall relationship between humidity and temperature and the number of bird motifs for the hourly analysis. Plots B, C and D were generated with ggplot2::geom_smooth in R and they were only used for trend visualisation purposes.

significant difference in the number of bird/insect motifs between days with temperatures lower and higher than average (Kruskal-Wallis $x^2 = 26.638$, df = 19, p-value = 0.1134). The complete tables with the detailed effect size for birds and insects can be found in the Supplementary material.

Fig. 7A shows bird/insect with higher number of motifs with hotter days, although the difference between hotter and colder days were not statistically significant for this class. In Fig. 7B reveals that there was no clear difference in bird motifs between groups for most of the year, except for spring (September to November), where there are more motifs in the days with temperatures lower than average. Fig. 7C shows that there was a higher number of insect motifs in the days with temperatures lower than historical averages in autumn and winter (March to September) and the trend changes in the months corresponding to spring and summer (September to February).

4. Discussion

This study has demonstrated how remote sensing of acoustic biodiversity and the environment can be used to investigate phenology across long temporal scales. Our data have revealed the environmental cues that dictate the diurnal and seasonal phenology of birds and insects in a sub-tropical forest and how the predicted increase in temperatures due to climate change may affect those taxonomic groups.

4.1. Daily phenology of birds and insects

For most of the year, birds dominated the soundscape during the day whereas insects (mainly crickets) dominated the soundscape during the night. Results of the current study have revealed a typical pattern of bird activity over a 24-h period, i.e. higher activity at dawn and dusk, and lower activity at night (due to most birds in this study being diurnal) and during the middle of the day when temperature and humidity were highest. Acoustic signals are used by fauna for communication and are subject to natural selection pressures to increase their efficacy. This can result in changes to the properties or timing of transmissions (Krause, 1987). The cacophony of the dawn chorus, for example, is well-known and many hypotheses have been investigated to understand the preference for singing at this

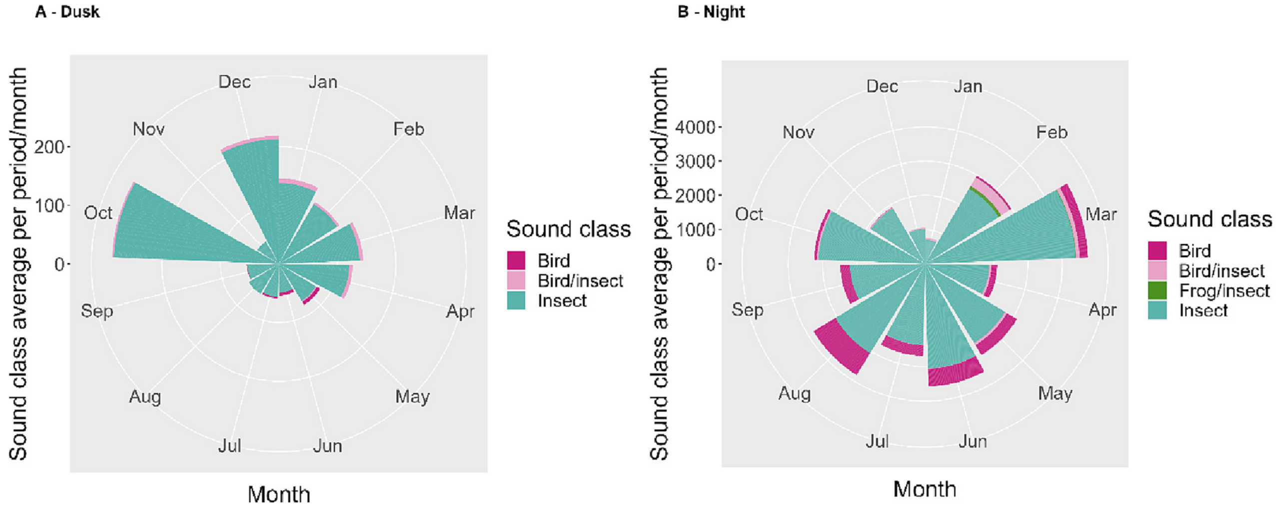


Fig. 5. (A) Dusk and (B) night soundscape for biophony. Counts are the number of motifs of each class per month in the dusk and night periods. The periods of the day were attributed based on sunset and sunrise information, so the "dawn" hours are variable across the year (earliest start at 17:02 and latest end at 20:20 for dusk and earliest start at 18:25 and latest end at 05:17 for night). Due to different in sampling effort, the average motif per day for each month can be found in Supplementary material.

time of the day. Explanations include good condition for sound transmission, lower predation risk and hormonal cycles (for a review see Gil and Llusia, 2020). The result is that the possible advantages for calling at dawn surpasses the masking effect caused by so many species calling at the same time. There is also evidence indicating that acoustic signalling might be driven by phylogenetic relationships and evolutionary constraints (Tobias et al., 2014). Cicadas, for example, call in choruses to avoid predation (Moulds, 1990; Young, 1981). In this study, the night soundscape was dominated by insects and insects generally call more at night to avoid birds, their main predator (Naumann, 1991; Rentz, 1996). The main abiotic factors responsible for interference in acoustic signal transmission are sound attenuation (e.g.: temperature, humidity and wind (Henwood and Fabrick, 1979)) and background noise (Haupert et al., 2022) so animals benefit if they avoid signal mitigation by these factors.

4.2. Seasonal phenology of birds and insects

The patterns found in the present study with less bird activity during hotter hours of the day and months of the year may be explained by their behaviour of decreasing activity to prevent overheating and water loss. The majority of birds are diurnal and have small body size, and this makes them extremely susceptible to overheating (McKechnie and Wolf, 2010). Insects also had higher calling activity with lower temperatures. Research documenting the relationship between insect activity and

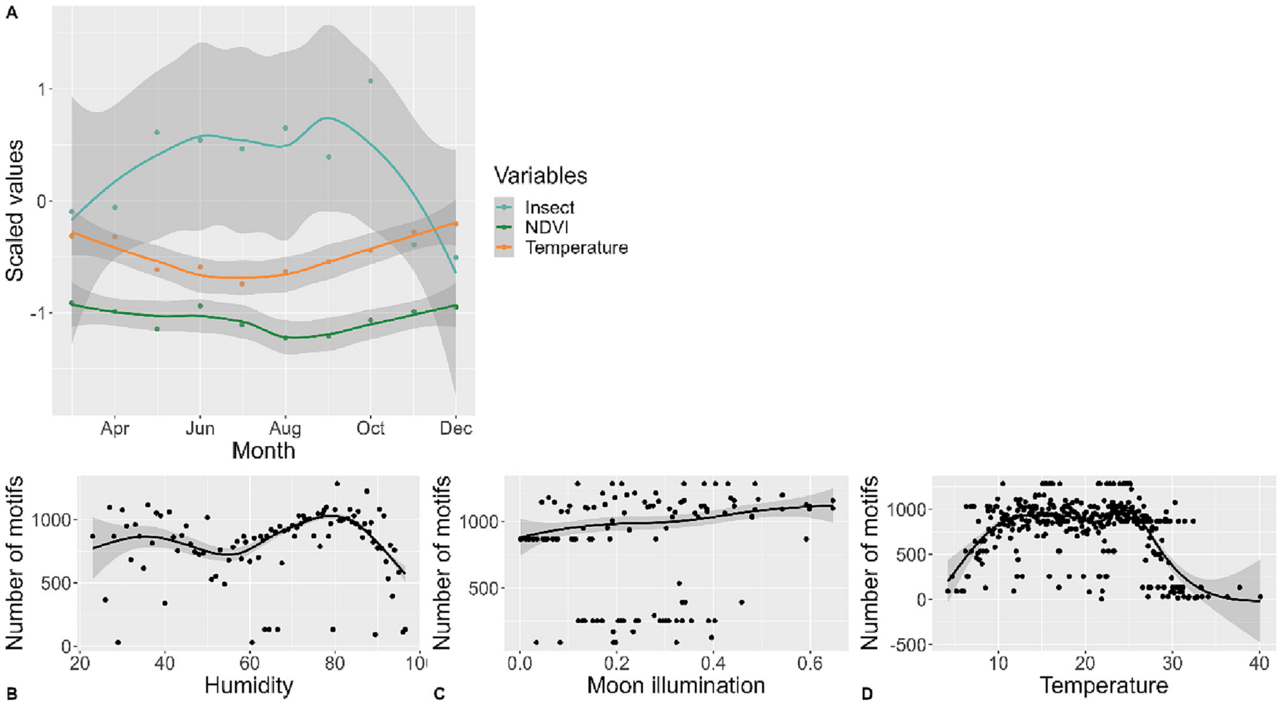


Fig. 6. Summary of environmental variables and soundscape variation for nocturnal insects. A: NDVI, Temperature and number of insect motifs scaled values through the year, demonstrating the yearly trends of the number of motifs and the environmental variables that influence the represented sound class. The values were scaled based on the mean only for visualisation purposes. B, C and D show the overall relationship between humidity, moon illumination, temperature, and the number of insect motifs throughout the day. Plots B, C and D were generated with ggplot2::geom_smooth in R and they were only used for trend visualisation purposes.

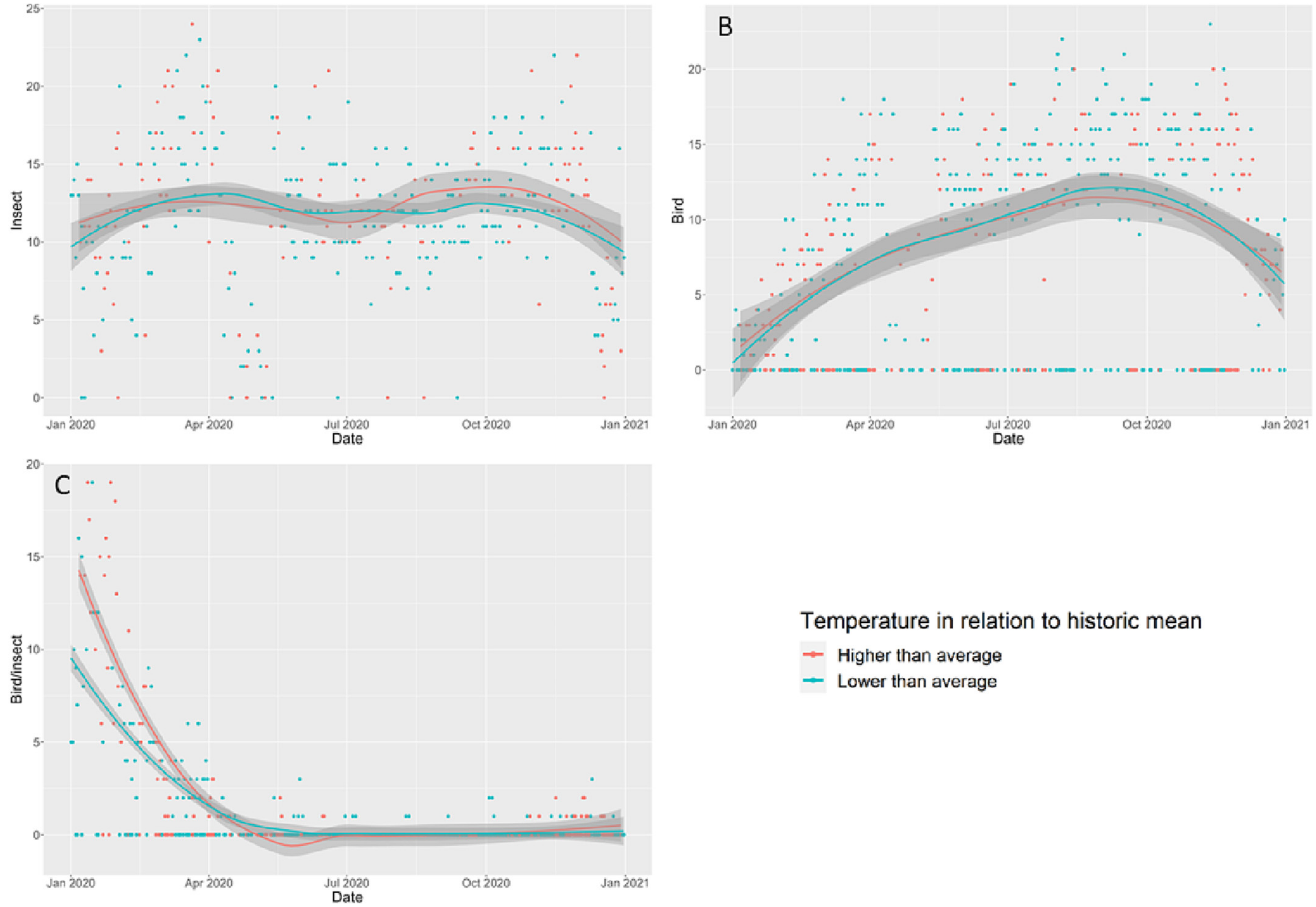


Fig. 7. The points and lines show the distribution of motifs over the year, coloured by temperatures higher or lower than average for that day. (A) demonstrates the distribution for birds; (B) for insects and (C) for bird insects. These plots were generated using "geom_smooth" function in R.

temperature is varied. Some suggests that insect activity (Rebaudo and Rabhi, 2018) and biomass (Bhardwaj et al., 2019) increases with increase in temperatures, whereas another study suggests that lower temperatures might favours insect movement (Campbell, 1976). Although the present research was conducted in winter, it is a subtropical environment, where lower temperatures are around 9 °C (*Graphical climate statistics for Australian locations*, 2020). Models suggest that development rates in insects decrease when temperature is lower than 10 °C (Rebaudo and Rabhi, 2018), evidencing that the winter in South-East Queensland is within a tolerable threshold for the group.

Evidence also suggests that external elements such as light intensity, humidity and temperature are responsible for controlling activity rhythm in crickets (Campbell, 1976). Interestingly, a strong positive interaction of moon illumination and insect activity was found in the current study. While some evidence suggests that insect activity is reduced with increased moon illumination (Campbell, 1976), orthopteran biomass increases during a full moon in Australia (Bhardwaj et al., 2019). No information on cloud cover for the night sky was available and therefore couldn't be included in our model. While this may have had an effect on our results for moon illumination, the relationship we found was very strong and so it would be unlikely to have such a different pattern even with high cloud cover for some nights. The relationship between humidity and insect calling activity was found to be variable in the current study, with different humidity values associated with higher calling activity.

The soundscape during the warmer months of the year (December, January, February, and March) was very distinct compared to the cooler months (June, July and August), mainly due to the presence of cicadas sharing the acoustic space with birds during the summer period (bird/insect class). Cicadas were the dominant insects calling during the day and temperature and humidity were found to be the best predictors of activity for this group. This was unsurprising as cicadas in South-East Queensland are known for their higher activity in summer, when temperature and humidity is higher (Ewart, 2001). In fact, the results found here corroborate previous studies, as we only recorded this group in summer (December, January and February).

Lower NDVI was also found to be linked to higher nocturnal insect calling activity. It is reported that insect seasonality reflects plant phenology (Lowman, 1982) and the activity of herbivorous insects is linked to their food source. Many orthoptera species chew foliage and a study undertaken in Brazil also found that the density of herbivorous orthoptera in a dry forest was higher during the dry season (winter) (Silva et al., 2017). There are several adaptations in dry forest plants so that they can cope with seasonal changes in water availability and sunlight (Lebrija-Trejos et al., 2011), and more research is needed to understand what is the relationship between plant and insect adaptation to environmental conditions. It should be considered that while NDVI was used as a measure of vegetation greenness in the current study, it only corresponds to the canopy in forests with dense tree layer, and many insect species feed on grasses and shrubs, which were not measured. Humidity and NDVI were found in this study to be associated with bird communication. Bird calling activity was higher when humidity and NDVI were lower in winter (June, July and August in Australia). Several, non-mutually exclusive, hypotheses can explain these patterns. First, the low humidity and NDVI values found in winter act as a cue for the following season, which is spring, the reproductive season for most birds. Second, lower remote sensing "greenness" indices have been associated with higher flowering season, when there is a higher reflectance of the flowers instead of green leaves (Dixon et al., 2021). Lower NDVI values and higher bird calling activity could then be associated with more flowering events and consequently food availability for nectarivore species. All the individual mechanisms and assumptions addressed might explain in part the patterns found. However, organisms and their underlying ecology are complex and respond to local and regional scales, hampering the attribution of individual traits and patterns to one driver (Chambers et al., 2013).

4.3. Human impacts on the environment

As humans increase the conversion of natural areas and climatic changes are more and more pronounced, it is very important to understand the natural dynamics of ecosystems with direct impacts on animal survival. The present study suggests alterations in the calling activity of birds and insects at temperatures higher than historical average. The fact that insects call less than average on hotter autumn and winter days suggests that this group are susceptible to higher temperatures associated with climate change. The decrease in the number of motifs associated with birds in spring also demonstrates how these changes might directly impact survival and reproduction, since this is the reproductive season for this group. For terrestrial organisms, temperature is known to affects metabolic rates, and consequently, energy consumption, storage and development rate (Marshall et al., 2020; Williams et al., 2015). It is also known that responses to climate change are species specific, and the responses can vary between and within groups depending on the interactions of environmental variables and adaptive responses (Briga and Verhulst, 2015; Cunningham et al., 2021; Kiritani, 2013).

4.4. Limitations

The element of spatial variability was not addressed in this study, as the goal was to solely focus on temporal dynamics. However, it is very likely that different patterns and relationships would be found in different ecosystems and biomes and for other faunal groups not examined in the present study. Finally, there are several other research angles concerning animal behaviour and phenology that could not be addressed in this study, such as ecosystem health, function, and provision of services (but see Folliot et al., 2022 for recent insights on using ecoacoustics for this purpose). As the last Intergovernmental Panel on Climate Change (IPCC) report predicted ongoing warming for the Australasian region, it is very important that both targeted and broad studies (such as the current one) are conducted for understanding species-specific requirements, as well as holistic patterns in biodiversity.

4.5. Conclusions

From a conservation and monitoring perspective, it is important that biodiversity surveys account for climatic, seasonal, and behavioural patterns and variation. There are still a lot of unanswered questions regarding how the environment affects species and moreover how all these dynamics will be affected by climate change and the many other impacts that biodiversity faces. As demonstrated in this study, soundscapes can be very useful in investigating changes in ecosystems, not only biophonic patterns related to biodiversity, but also patterns related to geophony and technophony. The conclusions and patterns found in the present study are significant in demonstrating the importance of environmental phenology on animal behaviour and how acoustic data can be valuable to understand phenology at large-scales. Finally, identifying acoustic baselines across ecosystems is very important so this technique can be used to detect important environmental changes.

CRediT authorship contribution statement

MDAS, PR, DT, SF: Conceptualization and Investigation; MDAS and DT: Data curation; MDAS: Formal analysis, methodology and writing original draft; MDAS and PR: Funding acquisition; PR, SF, DT: Supervision, review & editing.

Data availability

The recordings used in this study can be found in https://acousticobservatory.org/ and the Landsat images can be found in https://www.usgs.gov/.

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.

Acknowledgements

We would like to thank Marcus Yates for providing climatic data for SERF; Sentinel Hub for sponsorship (ID 162301: Multidimensional terrestrial ecoacoustic assessment), QUT for providing a PhD scholarship to Marina Scarpelli, Dr. Anthony Clarke for sharing knowledge on insects, and Andrew Schwenke for reviewing the first draft of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.163080.

References

Alexander, R.D., 1968. Life cycle origins, speciation, and related phenomena in crickets. Q. Rev. Biol. 43, 1–44.

Alexander, R.D., Moore, T.E., 1958. Studies on the acoustical behavior of seventeen-year cicadas (Homoptera: Cicadidae: Magicicada). Ohio J. Sci. 58, 107–127.

Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef Stat. Ref. Online, 1–15 https://doi.org/10.1002/9781118445112.stat07841.

Asrar, G., Fuchs, M., Kanemasu, E.T., Hatfield, J.L., 1984. Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat 1. Agron. J. 76, 300–306. https://doi.org/10.2134/agronj1984.00021962007600020029x.

Beckers, O.M., Wagner, W.E., 2011. Mate sampling strategy in a field cricket: evidence for a fixed threshold strategy with last chance option. Anim. Behav. 81, 519–527. https://doi.org/10.1016/j.anbehav.2010.11.022.

Bhardwaj, M., Soanes, K., Lahoz-Monfort, J.J., Lumsden, L.F., van der Ree, R., 2019. Little evidence of a road-effect zone for nocturnal, flying insects. Ecol. Evol. 9, 65–72. https://doi.org/10.1002/ece3.4609.

Bradbury, J.W., Vehrencamp, S.L., 2011. Principles of Animal Communication. Sinauer Associates.

Brandstätter, R., 2003. Encoding time of day and time of year by the avian circadian system. J. Neuroendocrinol. 15, 398–404. https://doi.org/10.1046/j.1365-2826.2003.01003.x.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1201/9780429469275-8.

Briga, M., Verhulst, S., 2015. Large diurnal temperature range increases bird sensitivity to climate change. Sci. Rep. 5, 1–9. https://doi.org/10.1038/srep16600.

Brodie, S., Allen-Ankins, S., Towsey, M., Roe, P., Schwarzkopf, L., 2020. Automated species identification of frog choruses in environmental recordings using acoustic indices. Ecol. Indic. 119, 106852. https://doi.org/10.1016/j.ecolind.2020.106852.

Brumm, H., Slabbekoorn, H., 2005. Acoustic communication in noise. Adv. Study Behav. https://doi.org/10.1016/S0065-3454(05)35004-2.

Campbell, G.D., 1976. Activity rhythm in the cave cricket, Ceuthophilus conicaudus Hubbell. Am. Midl. Nat. 96, 350–366.

Chambers, L.E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L.J., Crawford, R.J.M., Durant, J.M., Hughes, L., Keatley, M.R., Low, M., Morellato, P.C., Poloczanska, E.S., Ruoppolo, V., Vanstreels, R.E.T., Woehler, E.J., Wolfaardt, A.C., 2013. Phenological changes in the southern hemisphere. PLoS One 8. https://doi.org/10.1371/journal.pone.0075514.

Chen, B., Jin, Y., Brown, P., 2019. An enhanced bloom index for quantifying floral phenology using multi-scale remote sensing observations. ISPRS J. Photogramm. Remote Sens. 156, 108–120. https://doi.org/10.1016/j.isprsjprs.2019.08.006.

Cunningham, S.J., Gardner, J.L., Martin, R.O., 2021. Opportunity costs and the response of birds and mammals to climate warming. Front. Ecol. Environ. 19, 300–307. https://doi.org/10.1002/fee.2324.

Dixon, D.J., Callow, J.N., Duncan, J.M.A., Setterfield, S.A., Pauli, N., 2021. Satellite prediction of forest flowering phenology. Remote Sens. Environ. 255, 112197. https://doi.org/10.1016/j.rse.2020.112197.

Ewart, A., 2001. Emergence patterns and densities of cicadas (Hemiptera: Cicadidae) near Caloundra, South-East Queensland. Aust. Entomol. 28 (3), 69–84.

Folliot, A., Haupert, S., Ducrettet, M., Sèbe, F., Sueur, J., 2022. Using acoustics and artificial intelligence to monitor pollination by insects and tree use by woodpeckers. Sci. Total Environ. 838, 155883. https://doi.org/10.1016/j.scitotenv.2022.155883.

Gan, H., Zhang, J., Towsey, M., Truskinger, A., Stark, D., van Rensburg, B.J., Li, Y., Roe, P., 2020. Data selection in frog chorusing recognition with acoustic indices. Ecol. Inform. 60, 101160. https://doi.org/10.1016/j.ecoinf.2020.101160.

Gil, D., Llusia, D., 2020. The bird dawn chorus revisited. Coding Strategies in Vertebrate Acoustic Communication.

Graphical climate statistics for Australian locations [WWW Document]. URL http://www.bom.gov.au/jsp/ncc/cdio/cvg/av?p_stn_num=044026&p_prim_element_index=18&p_display_type=statGraph&period_of_avg=ALL&normals_years=allYearOfData&staticPage=. (Accessed 20 April 2020).

Haupert, S., Sèbe, F., Sueur, J., 2022. Physics-based model to predict the acoustic detection distance of terrestrial autonomous recording units over the diel cycle and across seasons: insights from an Alpine and a Neotropical. 2022, pp. 1–37. https://doi.org/10.1111/2041-210X.14020.

Heard, G.W., Canessa, S., Parris, K.M., 2015. Interspecific variation in the phenology of advertisement calling in a temperate Australian frog community. Ecol. Evol. 5, 3927–3938. https://doi.org/10.1002/ece3.1666.

Henwood, K., Fabrick, A., 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. Am. Nat. 114, 260–274. https://doi.org/10.1086/283473.

Karr, J.R., 1976. Seasonality, resource availability, and community diversity in tropical bird communities. Am. Nat. 110, 973–994.

Kiritani, K., 2013. Different effects of climate change on the population dynamics of insects. Appl. Entomol. Zool. 48, 97–104. https://doi.org/10.1007/s13355-012-0158-y.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. Meteorol. Zeitschrift 15, 259–263. https://doi.org/10.1127/0941-2948/2006/0130.

Krause, B.L., 1987. Bioacoustics, habitat ambience in ecological balance. Whole Earth Rev. 14–18.

Lazaridis, E., 2014. lunar: Lunar Phase & Distance, Seasons And Other Environmental Factors.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Poorter, L., Bongers, F., 2011. Environmental changes during secondary succession in a tropical dry forest in Mexico. J. Trop. Ecol. 27, 477–489. https://doi.org/10.1017/S0266467411000253.

Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25, 601–615. https://doi.org/10.1034/j.1600-0587.2002.250508.x (Cop.).

Llusia, D., Márquez, R., Beltrán, J.F., Benítez, M., do Amaral, J.P., 2013. Calling behaviour under climate change: geographical and seasonal variation of calling temperatures in ectotherms. Glob. Chang. Biol. 19 (9), 2655–2674. https://doi.org/10.1111/gcb.12267.

Lowman, M.D., 1982. Seasonal variation in insect abundance among three Australian rain forests, with particular reference to phytophagous types. Aust. J. Ecol. 7, 353–361. https://doi.org/10.1111/j.1442-9993.1982.tb01310.x.

Tomczak, Maciej, Tomczak, Ewa, 2014. The need to report effect size estimates revisited. An overview of some recommended measures of effect size. Trends Sport Sci. 1, 19–25.

Marshall, K.E., Gotthard, K., Williams, C.M., 2020. Evolutionary impacts of winter climate change on insects. Curr. Opin. Insect Sci. 41, 54–62. https://doi.org/10.1016/j.cois.2020.06.003.

Mathevon, N., Aubin, T., Dabelsteen, T., Vielliard, J.M.E., 2004. Are communication activities shaped by environmental constraints in reverberating and absorbing forest habitats? An. Acad. Bras. Cienc. 76, 259–263. https://doi.org/10.1590/S0001-37652004000200011.

McInnes, L., Healy, J., Melville, J., 2018. UMAP: Uniform Manifold Approximation And Projection for Dimension Reduction.

McKechnie, A.E., Wolf, B.O., 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biol. Lett. 6, 253–256. https://doi.org/10.1098/rsbl.2009.0702.

Moore, C.E., Brown, T., Keenan, T.F., Duursma, R.A., Van Dijk, A.I.J.M., Beringer, J., Culvenor, D., Evans, B., Huete, A., Hutley, L.B., Maier, S., Restrepo-Coupe, N., Sonnentag, O., Specht, A., Taylor, J.R., Van Gorsel, E., Liddell, M.J., 2016. Reviews and syntheses: Australian vegetation phenology: new insights from satellite remote sensing and digital repeat photography. Biogeosciences 13, 5085–5102. https://doi.org/10.5194/bg-13-5085-2016.

Moulds, M.S., 1990. Australian Cicadas. New South Wales University Press.

Narins, P.M., Feng, A.S., Fay, R.R., Popper, A.N., 2007. Springer Handbook of Auditory Research: Hearing And Sound Communication in Amphibians. Neuroanatomy.

Naumann, I.D., 1991. Insects of Australia. CSIRO Publishing.

Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). Ecol. Indic. 11, 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005.

QGIS Geographic Information System, 2022. QGIS.org.

R Core Team, 2019. R: A Language And Environment for Statistical Computing.

Rawal, D.S., Kasel, S., Keatley, M.R., Nitschke, C.R., 2015. Herbarium records identify sensitivity of flowering phenology of eucalypts to climate: implications for species response to climate change. Austral Ecol. 40, 117–125. https://doi.org/10.1111/aec.12183.

Rebaudo, F., Rabhi, V.B., 2018. Modeling temperature-dependent development rate and phenology in insects: review of major developments, challenges, and future directions. Entomol. Exp. Appl. 166, 607–617. https://doi.org/10.1111/eea.12693.

Rentz, D.C., 1996. Grasshopper Country: The Abundant Orthopteroid Insects of Australia. 284.

Roe, P., Eichinski, P., Fuller, R.A., McDonald, P.G., Schwarzkopf, L., Towsey, M., Truskinger, A., Tucker, D., Watson, D.M., 2021. The Australian acoustic observatory. Methods Ecol. Evol. 2021, 1–7. https://doi.org/10.1111/2041-210X.13660.

Scarpelli, M.D.A., Liquet, B., Tucker, D., Fuller, S., Roe, P., 2021. Multi-index ecoacoustics analysis for terrestrial soundscapes: a new semi-automated approach using time-series motif discovery and random forest classification. Front. Ecol. Evol. 9, 1–14. https://doi.org/10.3389/fevo.2021.738537.

Sentinel Hub. (n.d.). Retrieved March 31, 2022, from https://www.sentinel-hub.com

Sethi, S.S., Jones, N.S., Fulcher, B.D., Picinali, L., Clink, D.J., Klinck, H., Orme, C.D.L., Wrege, P.H., Ewers, R.M., 2020. Characterizing soundscapes across diverse ecosystems using a universal acoustic feature set. Proc. Natl. Acad. Sci. U. S. A. https://doi.org/10.1073/pnas.2004702117.

Silva, J.O., Leal, C.R.O., Espírito-Santo, M.M., Morais, H.C., 2017. Seasonal and diel variations in the activity of canopy insect herbivores differ between deciduous and evergreen plant species in a tropical dry forest. J. Insect Conserv. 21, 667–676. https://doi.org/10.1007/s10841-017-0009-9.

Slabbekoorn, H., Halfwerk, W., 2009. Behavioural ecology: noise annoys at community level. Curr. Biol. 19, R693–R695. https://doi.org/10.1016/j.cub.2009.07.002.

Solar BAR | Frontier Labs AU [WWW Document]. https://www.frontierlabs.com.au/solar-bar accessed 3.26.22.

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., De Vries, W., De Wit, C.A., Folke, C., Gerten, D., Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Reyers, B., Sörlin, S., 2015. Planetary boundaries: guiding human development on a changing planet. Science 80-, 347. https://doi.org/10.1126/science.1259855.

Sueur, J., Pavoine, S., Hamerlynck, O., Duvail, S., 2008. Rapid acoustic survey for biodiversity appraisal. PLoS One 3, e4065. https://doi.org/10.1371/journal.pone.0004065.

Sugai, L.S.M., Llusia, D., 2019. Bioacoustic time capsules: using acoustic monitoring to document biodiversity. Ecol. Indic. 99, 149–152. https://doi.org/10.1016/j.ecolind.2018.12.021.

Thieurmel, B., Elmarhraoui, A., 2022. suncalc: Compute Sun Position, Sunlight Phases, Moon Position And Lunar Phase.

Tobias, J.A., Planqué, R., Cram, D.L., Seddon, N., 2014. Species interactions and the structure of complex communication networks. Proc. Natl. Acad. Sci. U. S. A. 111, 1020–1025. https://doi.org/10.1073/pnas.1314337111.

Towsey, M., 2018. The Calculation of Acoustic Indices Derived From Long-duration Recordings of the Natural Environment Brisbane.

Towsey, M., Truskinger, A., Cottman-Fields, M., Roe, P., 2018a. Ecoacoustics Audio Analysis Software v18.03.0.41. https://doi.org/10.5281/zenodo.4274299.

Towsey, M., Wimmer, J., Williamson, I., Roe, P., 2014. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. Ecol. Inform. 21, 110–119. https://doi.org/10.1016/j.ecoinf.2013.11.007.

Towsey, M., Znidersic, E., Broken-Brow, J., Indraswari, K., Watson, D.M., Phillips, Y., Truskinger, A., Roe, P., 2018b. Long-duration, false-colour spectrograms for detecting species in large audio data-sets. J. Ecoacoustics 2, IUSWUI. https://doi.org/10.22261/JEA.IUSWUI.

Visser, M.E., Caro, S.P., Oers, K.Van, Schaper, S.V., Helm, B., 2010. Phenology, seasonal timing and circannual rhythms: towards a unified framework. Philos. Trans. R. Soc. B Biol. Sci. 365, 3113–3127. https://doi.org/10.1098/rstb.2010.0111.

Wickham, H., 2009. ggplot2 - Elegant Graphics for Data Analysis. Springer https://doi.org/10.1007/978-0-387-98141-3.

Williams, C.M., Henry, H.A.L., Sinclair, B.J., 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biol. Rev. 90, 214–235. https://doi.org/10.1111/brv.12105.

Young, A.M., 1981. Temporal selection for communicatory optimization: the dawn-dusk chorus as an adaptation in tropical cicadas. Am. Nat. 117, 826–829.