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ORIGINAL ARTICLE

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Diel variation in insect-dominated temperate pond soundscapes and guidelines for survey design

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Abstract

1. Passive acoustic monitoring has been used for decades as a non-invasive tool for quantifying biodiversity in terrestrial and marine ecosystems. Recently, there has been increased interest in the potential for the method to survey freshwater biodiversity. Fundamental aspects of freshwater soundscape phenology, however, often remain poorly understood, despite their importance for suitable survey design.
2. To gain a greater understanding of daily acoustic variation in aquatic insect-dominated temperate pond soundscapes, 840 hr of underwater sound recordings were collected from five ponds in the southwest of the U.K. We calculated six commonly used acoustic indices to investigate diel trends and evaluated the suitability of each acoustic index to identify biologically complex pond soundscapes. In addition, macroinvertebrates were collected from each pond to investigate potential drivers of diel soundscape variation.
3. The ponds studied possessed clear patterns of daily acoustic variation, with acoustic activity typically peaking between 02:00 and 04:00 and around the solar noon. Acoustic Entropy showed the greatest variation between day and night soundscapes and was best suited for detecting overall daily acoustic variation in the study ponds. However, the Normalised Difference Soundscape Index and the Bioacoustic Index captured strong diel variation in aquatic insect-dominated soundscapes. Furthermore, we calculated that a minimum hydrophone deployment time of 24 hr is required to ensure that soundscape variation is adequately captured.
4. This study provides an increased understanding of daily acoustic variation in insect-dominated temperate pond soundscapes, enabling us to provide guidelines for the design and implementation of future passive acoustic monitoring surveys. We suggest that a minimum of 24 hr is required to adequately capture pond soundscape variation. This will increase the chance of detecting key soniferous species in the soundscape and enable more accurate assessments of temperate pond soundscapes.

KEYWORDS
acoustic indices, biodiversity monitoring, freshwater ecoacoustics, pond, soundscape

1 | INTRODUCTION

Freshwater ecosystems are experiencing a greater rate of habitat and species loss than any other ecosystem (Albert et al., 2020). Globally, freshwater vertebrate populations have declined by 84% between 1970 and 2016, and wetlands are disappearing three times faster than rainforests (WWF, 2020). In the U.K., 75% of ponds vanished in the 20th century (Sayer et al., 2012; Wood et al., 2003). There is an urgent need to better understand, conserve, and monitor freshwater ecosystems to minimise, and ideally prevent the loss of freshwater biodiversity. Biodiversity monitoring is a key element of conservation, informing and guiding best practices (Niemelä, 2000). New technologies, such as environmental DNA and drones, are now being used to survey freshwater ecosystems and provide new perspectives on biodiversity. By contrast, the use of audio recordings to describe species-specific sounds and behaviours—bioacoustics—is a fairly well-established area of research (Chesmore, 2004). Recently, however, a shift towards investigating all of the sounds present in an environment at any given time (the soundscape) has occurred, giving rise to the field of ecoacoustics (Greenhalgh et al., 2020; Sueur & Farina, 2015).

Previous studies investigating freshwater soundscapes (Decker et al., 2020; Desjonquères et al., 2015, 2018; Gottesman et al., 2020; Greenhalgh et al., 2021; Karaconstantis et al., 2020; Linke et al., 2020; Putland & Mensinger, 2020) have revealed a large diversity of sounds produced by aquatic insects, plants, fish, amphibians, and also sounds from methane bubbles associated with decomposition. These studies indicate that passive acoustic monitoring of pond soundscapes has the potential to reveal novel information regarding the ecological condition, phenology, and species composition of freshwater ecosystems. Research in tropical freshwater ecosystems has revealed strong diel soundscape patterns (Decker et al., 2020; Gottesman et al., 2020; Karaconstantis et al., 2020; Linke et al., 2020). For example, studies of Australian waterholes (Karaconstantis et al., 2020) and a Costa Rican swamp (Gottesman et al., 2020) have revealed periods of relative quiet during dawn and dusk, and periods around midday and the solar noon, were the most acoustically complex times of day (Gottesman et al., 2020; Karaconstantis et al., 2020). In contrast, relatively little is known about the daily acoustic activity cycles of temperate freshwater ecosystems, although using a sound type classification approach, Desjonquères et al. (2015) described the diel soundscape patterns of three ponds in France, revealing a peak in acoustic activity at a different time of day for each pond. Since pond soundscapes possess clear and varying diel soundscape patterns, it would be useful to understand these causes of these daily soundscape cycles in greater detail.

In this study, we investigated the daily acoustic activity patterns of five temperate ponds by recording and analysing 840 hr of underwater sound recordings from five ponds to determine: (1) if insect-dominated temperate pond soundscapes possess diel variation; and (2) whether macroinvertebrate species composition affects diel soundscape variation. We also calculated six commonly used acoustic indices to investigate diel trends and evaluated the suitability of each acoustic index to identify biologically complex pond soundscapes. In addition, a minimum hydrophone deployment time was calculated to inform the sampling effort required to conduct eco-acoustic monitoring surveys in temperate ponds.

2 | METHODS

2.1 | Study area

This study was conducted at five sites in a temperate southwest region of England, U.K. (Figure S1). Four of the sites were in the vicinity of Bristol, a densely populated urban area with a population of *c.* 463,000, and home to 13 nature reserves (Bristol City Council, 2021). The fifth site was close to Exmouth, a more rural area, and was a reservoir used by anglers targeting common sports fish, such as carp (*Cyprinus carpio*), roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*), and pike (*Esox lucius*). The five study sites ranged between 2,038 and 19,697 m^2 in surface area (mean 9,572 m^2) and were located in nature reserves and reservoirs surrounded by deciduous woodland.

2.2 | Data collection

2.2.1 | Hydrophone deployment schedule

A calibrated HTI-96-Min hydrophone (High Tech Inc) with the following settings: sensitivity −165 dB; re: 1 V/μPa; frequency response 2–40 kHz; flat to ±1 dB, was submerged at least 30 cm beneath the surface of each pond *c.* 2 m from the pond edge. The hydrophone was connected to a SM4BAT FS recorder (Wildlife Acoustics) set at maximum gain (+12 dB) with a sample rate of 192 kHz/32-bit. Each audio file was 15 s long and stored on two 128-GB SD cards (SanDisk) in a .wav format. Each pond was recorded continuously for 1 week from midday to midday (168 hr) between April and June 2020, resulting in 840 hr and 201,600 audio files (Table 1).

2.2.2 | Weather data and water chemistry

Site-specific maximum and minimum air temperatures, and sunrise/sunset time measurements were obtained from the U.K. Met Office (https://www.metoffice.gov.uk/) for each day of recording (Table S1). In addition, total daily rainfall data for the southwest of England were obtained from the Met Office. A calibrated sensION MM 150 water chemistry probe (Hach) was allowed to acclimatise in the pond water until values stabilised, after which nine replicates of pH, conductivity, total dissolved solids, and water temperature were recorded (Table S2).

2.2.3 | Macroinvertebrate sampling and identification

To obtain a snapshot of macroinvertebrate communities present at each study site, a 3-min macroinvertebrate sample was collected using a standard pond net on the start date of each survey (Table 1). The time was divided proportionally between the microhabitats present, as described by Biggs et al. (1998). Macroinvertebrates were preserved on-site in collection boxes with absolute ethanol and later identified in the laboratory using information in Dobson et al. (2012). We chose to focus on macroinvertebrates, as opposed to anurans which can dominate some freshwater soundscapes (Sugai et al., 2021), because temperate pond soundscapes in the U.K. possess low anuran diversity and are typically dominated by aquatic hemipterans in the family Corixidae (Sueur et al., 2011). Due to this focus on Corixidae, they were identified to at least genus level using information in Savage (1990).

2.2.4 | Calculation of acoustic indices

Acoustic indices—Acoustic Complexity Index (ACI), Acoustic Entropy (H), Acoustic Diversity Index (ADI), Acoustic Evenness Index (AEI), and the Normalised Difference Soundscape Index (NDSI)—were calculated for each 15-s audio file using default settings in R v4.0.2 (R Core Team, 2020) using the package *soundsecology* v1.3.3 (Villanueva-Rivera & Pijanowski, 2018). The Bioacoustic Index (BI) was also calculated in *soundsecology* with the minimum frequency set to 2kHz and the maximum frequency set to 30kHz after visual inspection of the data in Audacity (https://www.audacityteam.org/) to identify the bandwidth of the biophony and to ensure the inclusion of aquatic insect stridulation (2–10kHz [Aiken, 1985b]). It is important to note that sounds produced by other taxa, such as anurans and teleosts below 2kHz will not be considered by the BI and NDSI in this study. For a full list and description of the acoustic indices used in this study see Table 2. To ensure that adverse weather

TABLE 1 Study site characteristics and survey dates.

Study site (code)	Decimal latitude, longitude	Survey date (dd/mm/yyyy)	Pond area (m^2)
Abbots Pool (ABP)	51.456, −2.669	08/05/2020–15/05/2020	3,688
Chew Magna Reservoir (CMR)	51.367, −2.622	20/06/2020–27/06/2020	19,697
Eastwood Farm (EWF)	51.444, −2.530	19/04/2020–26/04/2020	2,980
Old Sneed Park (OSP)	51.476, −2.642	09/04/2020–16/04/2020	2,038
Squabmoor Reservoir (SQB)	50.648, −3.359	01/06/2020–08/06/2020	19,462

TABLE 2 A list of the acoustic indices used in this study, details of how to interpret the values generated by each index.

Acoustic index and citation	Interpretation of the values generated by each acoustic index
Acoustic Complexity Index; ACI (Pieretti et al., 2011)	High values indicate increased variation of amplitudes between frequency bands, whereas low values indicate less variation in amplitude between frequency bands. For example, high values indicate insect stridulation and aquatic plant respiration, whereas low values indicate consistent noise that occupies the entire frequency bandwidth.
Acoustic Diversity Index; ADI (Villanueva-Rivera et al., 2011)	High values indicate greater acoustic evenness across the soundscape, whereas low values indicate more acoustic variation across the soundscape. In other words, a high value indicates a constant signal, either noisy or silent, with its energy distributed across frequency bands, whereas a low value indicates a signal with all its energy in one frequency band (pure tone).
Acoustic Evenness Index; AEI (Villanueva-Rivera & Pijanowski, 2018)	High values indicate greater acoustic variation across the soundscape, whereas a low value indicates less acoustic variation. In other words, a high value indicates that the sound intensity is concentrated in a narrow frequency range, whereas a low value indicates little variation between frequency bands. A biodiverse environment can return a low value if the soundscape is saturated with calls occupying a broad frequency range.
Acoustic Entropy; H (Sueur et al., 2008)	High values indicate less amplitude variation among frequency bands across the entire recorded bandwidth, whereas low values indicate more variation in amplitude between frequency bands. For example, an evenly distributed signal across frequency bands (noise or silence) returns a high value (close to 1), whereas a pure tone with all the energy in a single frequency band returns a low value (close to 0).
Bioacoustic Index; BI (Boelman et al., 2007)	High values indicate greater variation between the quietest and loudest 1-kHz frequency bands in the biophony (2–30kHz), where low values indicate less variation between 1-kHz frequency bands in the biophony.
Normalised Soundscape Difference Index; NDSI (Kasten et al., 2012)	High values indicate greater variation and intensity in the biophony (2–11kHz), whereas low values indicate greater variation and intensity in the anthrophony (1–2kHz).

conditions did not affect the values generated by acoustic indices and obscure natural diel acoustic patterns, hydrophone deployment hours affected by rainfall were identified and removed. Rainfall affected hours were removed if they met all the following criteria: (1) occurred on a day with >1 mm total rainfall (Table S1); (2) hourly means of acoustic indices possessed standard deviations at least two times higher than unaffected values; and (3) visual spectrogram analysis confirmed the presence of broadband disturbance typical of rainfall. In total, 18 hr of recordings affected by rainfall were excluded from further analysis (10 from Squabmoor Reservoir, and 8 from Chew Magna Reservoir). Specifically, the hours between 09:00 and 18:00 on 03 June 2020, and 01:00 and 20:00 on 05 June 2020 were removed from Squabmoor Reservoir recordings. Similarly, the hours between 01:00 and 04:00 on 21 June 2020, and 08:00 and 09:00 on 27 June 2020 were removed from Chew Magna Reservoir recordings. All rain-affected hours were replaced with N/As and the missing values were interpolated using the *na.approx* function in the R package *zoo* v1.8.9 (Zeileis & Grothendieck, 2005).

2.3 | Data analysis

2.3.1 | Correspondence Analysis of macroinvertebrate samples

The presence and absence of identified macroinvertebrate taxa for each study site was recorded in a binary format and imported into R. A Correspondence Analysis was then calculated using the package *FactoMineR* v2.4 (Lê et al., 2008). Associated eigenvalues were returned and the biplot was constructed using package *factoextra* v1.0.7 (Kassambara & Mundt, 2020). In addition, tadpoles (Ranidae) and sticklebacks (Gasterosteidae) were identified from pond net samples and were also included in the Correspondence Analysis. No adult anurans were observed during site visits or collected within from macroinvertebrate samples.

2.3.2 | Investigating the relationships between diel period, site, aquatic insect richness, and acoustic indices

To investigate the effect of diel period, site, and aquatic insect species richness on values generated by acoustic indices, we calculated two sets of six generalised linear mixed models (GLMMs) with a Gaussian distribution using the package *lme4* v1.1-30 (Bates et al., 2014). Hourly mean values of each acoustic index were grouped into time blocks of 3 hr and treated as a categorical predictor *Time Block* variable to partially account for temporal autocorrelation within the dataset. Hourly mean values of each acoustic index were also assigned to a categorical *Diel Period* variable, as either daytime or night-time hours, defined by sunrise and sunset times. In a first set of six GLMMs each model consisted of an acoustic index (response variable), study site and *Diel Period* (fixed effects), and *Time Block* (random effect). A Type II Wald Chi-square test was then calculated on the model output to return a Chi-square value (effect size) for the effect of study site and the variable *Diel Period* on each acoustic index.

The source of most acoustic variation between, and within, freshwater soundscapes is often the presence and intensity of aquatic insect stridulation, most notably by water boatmen in the family Corixidae (Hemiptera) (Karaconstantis et al., 2020; Sueur et al., 2011). Water boatmen, such as *Corixa striata*, are known to respond to soundwaves emitted between 2–40 kHz received through tympanal organs (Frings & Frings, 1958). Sound production by water boatmen is well documented, with diel variation in acoustic behaviour, typically stridulating at dusk and during the night (Aiken, 1985a; Decker et al., 2020; Sueur et al., 2011). There are 15 soniferous species of water boatmen in the U.K. (Southwood & Leston, 1959). However, even the presence or absence of a single species, particularly those in the genus *Micronecta* (Sueur et al., 2011), can dramatically alter freshwater soundscape composition. Therefore, we also considered how aquatic insect (Hemiptera) species richness at each study site affected values generated by acoustic indices by including Hemiptera richness as a fixed effect in a second set of GLMMs, which were otherwise calculated as described above.

2.3.3 | Random forest models and variables of importance

To determine which acoustic indices most reliably distinguished diel period, we used a random forest classification approach (Breiman, 2001) with the R package *randomForest* v4.6-14 (Liaw & Wiener, 2002). We constructed a random forest model using mean hourly indices values and the factors *day* and *night*, which were defined based on sunrise and sunset times for each day (Table S1). The model was trained with 30% of the data and tested on the remaining 70%, consisted of 300 trees, and tested all six variables (each acoustic index) at each split.

We also constructed a random forest model using mean hourly indices values and the factors *DominantHemiptera* and *SparseHemiptera*. *DominantHemiptera* was used if more than one species of Hemiptera was identified at a site (Old Sneed Park and Chew Magna Reservoir), and *SparseHemiptera* if one or no Hemiptera species were present (Abbots Pool, Eastwood Farm, Squabmoor Reservoir). The model was otherwise calculated as described above.

2.3.4 | Decomposing time series analysis

The NDSI was selected to visualise daily acoustic variation in biophony for the study sites in further analysis. This is due to the theoretical relevance of NDSI as a proxy for biological sound because it targets the frequency bandwidth in which most organisms produce sound, the biophony (Table 2), and suitability as a proxy for aquatic insect richness (Table 3).

To investigate diel acoustic variation between study sites, the time series was decomposed into four components: (1) observed

TABLE 3 Summary results of generalised linear mixed models investigating the effects of diel period, study site, and Hemiptera richness on values generated by acoustic indices.

Response variable	Term	χ^2	*p*
Bioacoustic Index	Site	237.662	<0.001***
	Hemiptera richness	210.980	<0.001***
	Diel period	57.797	<0.001***
Acoustic Complexity Index	Site	31.993	<0.001***
	Hemiptera richness	28.404	<0.001***
	Diel period	1.344	0.245
Acoustic Diversity Index	Site	499.887	<0.001***
	Hemiptera richness	81.400	<0.001***
	Diel period	2.273	0.131
Acoustic Entropy	Site	19.834	<0.001***
	Hemiptera richness	6.784	0.009**
	Diel period	118.710	<0.001***
Acoustic Evenness	Site	433.386	<0.001***
	Hemiptera richness	70.709	<0.001***
	Diel period	1.763	0.184
Normalised Difference Soundscape Index	Site	689.467	<0.001***
	Hemiptera richness	558.39	<0.001***
	Diel period	25.109	<0.001***

Note: Asterisks indicate the significance of the test: **$p < 0.01$; ****$p < 0.001$.

values, the raw data; (2) trend, an increase/decrease of values over time; (3) daily cycle, the repeating cyclic component within the data; and (4) noise, the random variation within the time series. This was achieved by calculating additive models using the *decompose* function in the *stats* package (v3.6.2) to decompose weekly sound recordings using 24 hourly mean values of the NDSI. An estimate of Phi (φ) was returned by calculating a generalised least squares model to quantify the strength of association between each acoustic index and the hour of day sampled using the *nlme* package v3.1-155 (Pinheiro et al., 2022).

2.3.5 | Estimating a minimum hydrophone deployment time

A data frame for each study site was created by collating the values generated by each acoustic index, resulting in a total of 40,320 rows. Each row in the data frame represented 15 s. Therefore, 240 randomly sequential rows equated to 1 hr of sampling, and 480 sequential rows equated to 2 hr, and so on. For this analysis we defined 14 simulated sampling time periods as 1, 2, 4, 12, and 24 hr, and then 32–96 hr in steps of 8 hr. Median values were then calculated for each acoustic index in each simulated sampling time period across 1,000 permutations to quantify a change in variance over time that is independent of an increasing sample size. We expected that variance in median values would be initially high, after stabilising with increasing sampling effort. Trends were viewed using models fitted with the R package *ggplot2* (v 3.3.5) (Wickham, 2016).

3 | RESULTS

3.1 | Macroinvertebrate sampling and Correspondence Analysis

In total, 28 freshwater macroinvertebrate taxa were identified to species (four), genus (two), family (16), superfamily (one), order (four), and subclass (one). In addition, tadpoles (Ranidae) and sticklebacks (Gasterosteidae) were also sampled and included in further analysis. Chew Magna Reservoir contained the highest species richness, with 21 taxa, Eastwood Farm was the second most species rich (17 taxa), followed by Abbots Pool and Squabmoor Reservoir (11 taxa), and Old Sneed Park was the least species rich site (nine taxa; Figure 1). A full list of macroinvertebrate taxa identified in this study can be found in Table S3.

3.2 | Relationships between diel period, site, aquatic insect richness, and acoustic indices

Generalised linear mixed models showed that differences between study sites explained most variation in values generated by acoustic indices (Table 3). The BI, H, and NDSI differed significantly between diel periods (day and night-time hours). The ACI, ADI, and AEI did not differ significantly between diel periods. Aquatic insect species richness significantly affected the values generated by all six acoustic indices investigated (Table 3).

3.3 | Random forest models and variables of importance

Random forest classification analysis showed that Acoustic Entropy (H) index contributed most substantially to the differences between diel period when all sites are considered (Figure 2). In contrast, the ADI and ACI explained the least diel acoustic variation between all sites.

The mean of the NDSI was by far the most accurate variable for distinguishing between insect-dominated/sparse sites (Figure 2). The BI was also a useful variable for identifying insect-dominated soundscapes. The least accurate variables for identifying insect-dominated soundscapes were the AEI and the ADI.

3.4 | Decomposing time series analysis

The decomposition of the NDSI time series into its components revealed clear diel trends in each study site (Figure 3). In addition, diel acoustic variation varied between each site, with each study site

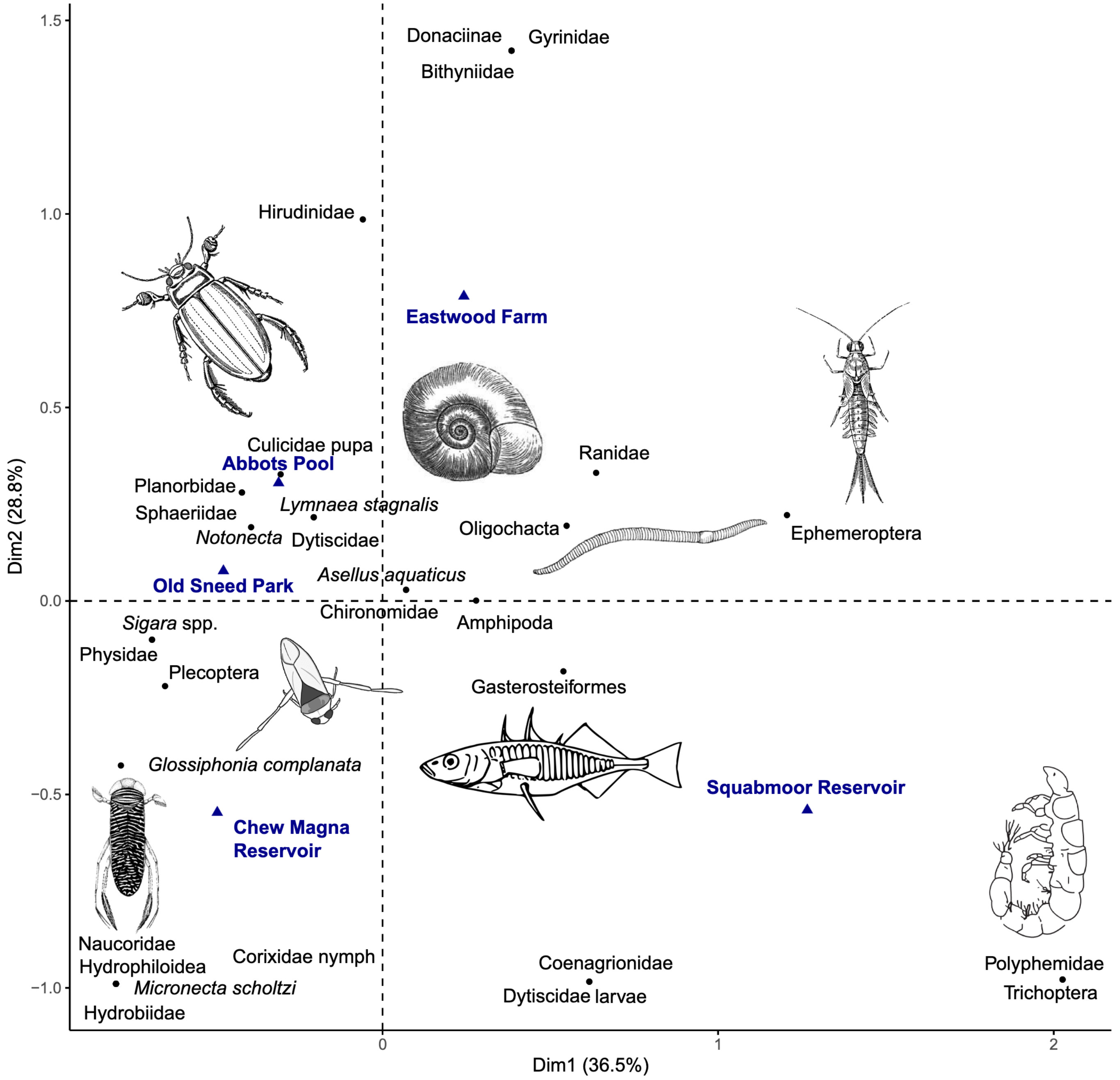


FIGURE 1 Correspondence Analysis applied to macroinvertebrate taxa (black dots) associated with study sites (dark blue triangles) from macroinvertebrate sampling ($n=5$). Illustrations left to right, top to bottom: Dytiscidae, Planorbidae, Oligochaeta, Ephemeroptera, *Sigara*, *Notonecta*, Gasterosteiformes, Trichoptera.

possessing a unique diel cycle. At the study sites Old Sneed Park, Abbots Pool, and Eastwood Farm, acoustic activity peaked around 00:00–04:00, and again around the solar noon. In contrast, Chew Magna Reservoir was most acoustically active during the night and lacked a secondary peak in activity during the solar noon. Squabmoor Reservoir exhibited comparatively little diel variation but is characterised by a distinctive decline in the NDSI just before dawn. The decomposed time series, for all of the other acoustic indices calculated in this study can be found in full in Figures S2–S6.

Estimates of φ indicate the degree of temporal autocorrelation, and therefore the extent of diel variation. Values closer to one indicate a high degree of diel variation, and values closer to zero indicate a low degree of diel variation (Table 4). The ADI, AEI, and H all showed very strong correlations ($\rho > 0.70$) at all study sites. The ACI showed very strong correlations at the study sites Old Sneed Park and Chew Magna Reservoir, and strong correlations ($\rho > 0.50$) at Eastwood Farm, Abbots Pool, and Squabmoor Reservoir. The BI showed very strong correlations at Old Sneed Park, Eastwood Farm, and Chew Magna, and a strong correlation at Abbots Pool. A moderate correlation was observed for Squabmoor Reservoir. The NDSI showed very strong correlations for Old Sneed Park and Chew Magna Reservoir, strong correlations for Eastwood Farm and

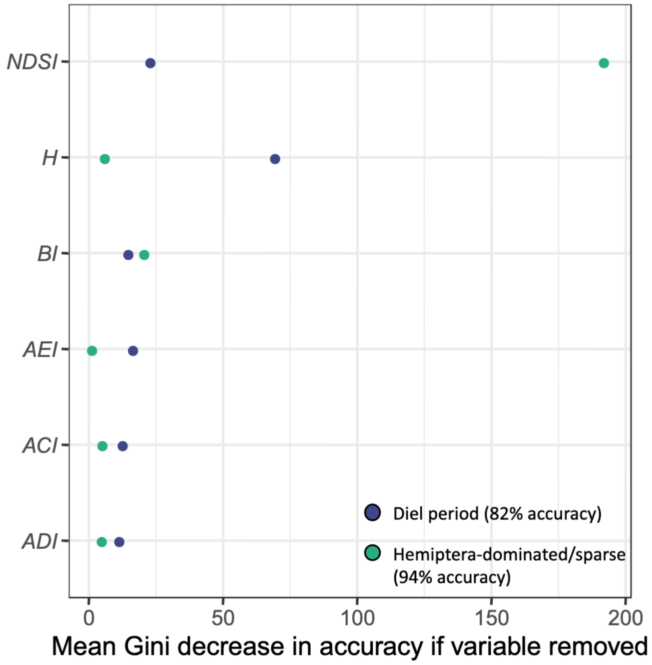


FIGURE 2 Response variables ranked by importance for classifying diel period (dark blue dots), and insect-dominated/sparse soundscapes (green dots), in two random forest models showing decline in predictive model accuracy if a variable is removed. Each random forest was constructed using the hourly mean values of all six acoustic indices. Internally estimated error rate was 17.74% for diel period variables, and 4.39% for Hemiptera variables. The mean decrease in the Gini coefficient quantifies how each acoustic index affects the homogeneity of the nodes in the random forest model. Higher values of a mean decrease in Gini accuracy associated with a variable indicates a greater importance of that variable in the model. ACI, Acoustic Complexity Index; ADI, Acoustic Diversity Index; AEI, Acoustic Evenness Index; BI, Bioacoustic Index; H, Acoustic Entropy; NDSI, Normalised Soundscape Difference Index.

Abbots Pool, while a moderate correlation for Squabmoor reservoir was observed.

3.5 | Estimating a minimum hydrophone deployment time

Variation in the median for each acoustic index was high at low sampling effort (<10 hr) before stabilising in most cases after 20–24 hr of simulated hydrophone deployment time (Figure 4). Typically, stabilisation was achieved after a full daily cycle had been captured by the deployed sampling effort. However, in some cases the variance of ADI, H, and NDSI continued to fluctuate until stabilising after *c.* 72 hr.

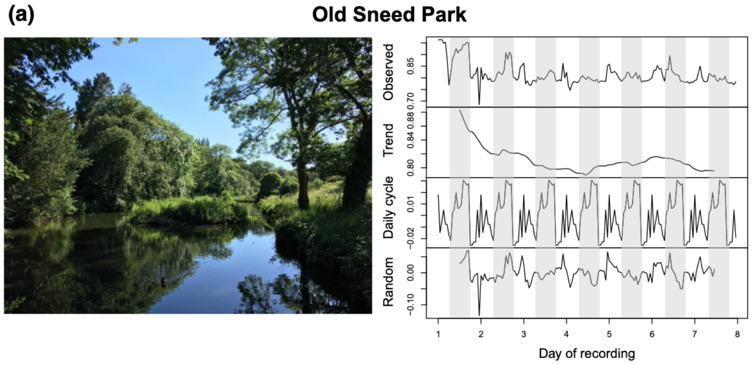
4 | DISCUSSION

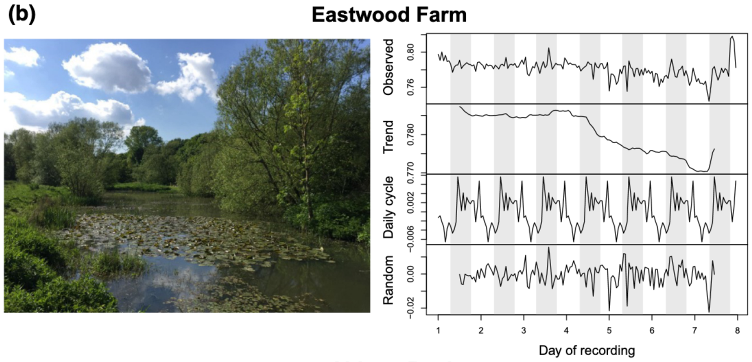
The data gathered in this study support previous work that shows clear diel soundscape patterns in freshwater ecosystems (Decker et al., 2020; Gottesman et al., 2020; Karaconstantis et al., 2020; Linke et al., 2020). This study, therefore, highlights the importance of considering the time of day when designing passive acoustic monitoring surveys in temperate ponds. In agreement with previous research conducted in temperate ponds by Desjonquères et al. (2015), the decomposition of the time series shows that not all pond soundscapes recorded followed the same pattern of diel variation, and that some possessed distinct diel soundscape cycles.

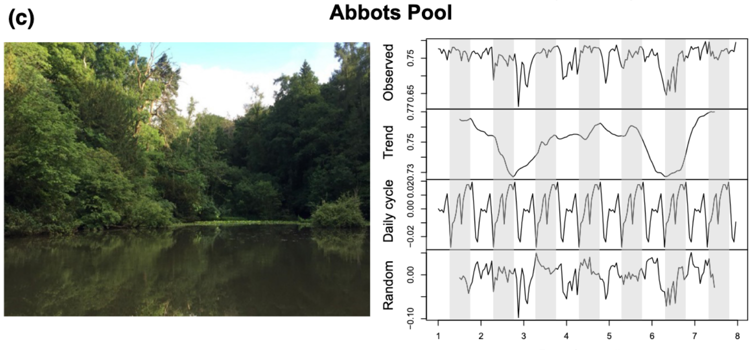
4.1 | Diel soundscape patterns in the biophony of insect-dominated temperate ponds

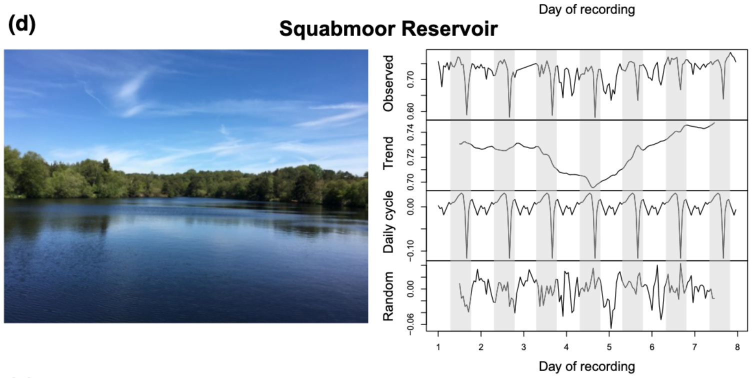
Macroinvertebrate sampling revealed the presence of five species of Hemiptera, three of which were water boatman (Corixidae), at Chew Magna Reservoir, more species than at any other site, and included *M. scholtzi*. Due to the extremely loud sound produced by *M. scholtzi* (Sueur et al., 2011), and other species of water boatman, it is possible that the presence or absence of a single water boatman species could have been responsible for a large degree of variation in soundscapes between sites, and between times of day within sites. A peak in acoustic activity driven by insect-dominated choruses typically occurred between 02:00–04:00, and 20:00–00:00, at Chew Magna Reservoir, Old Sneed Park, and Abbots Pool, driving high degrees of diel variation. Study sites with fewer species of Hemiptera possessed less variation between daytime and night-time hourly means, with most daily acoustic variation probably driven by macrophyte respiration. An increase in acoustic activity during the day at Abbots Pool, Eastwood Farm, and Old Sneed Park is probably due to the presence of macrophytes that produce sound as they respire, perhaps most efficiently around the solar noon *c.* 13:00 (Kratochvil & Pollirer, 2017). It is hypothesised that oxygen concentrations build until a threshold is reached when the oxygen concentration within the leaf structure is greater than that of the surrounding water (C. Desjonquères, personal communication, 14 July 2021). Once this threshold is reached, oxygen bubbles are released along a concentration gradient into the water via the stomata resulting in a series of regularly repeating ticking sounds that gradually dissipate (Kratochvil & Pollirer, 2017). In this study, macrophyte respiration typically occurred between *c.* 4 and *c.* 25.5 kHz. However, little is currently known about the full frequency range of sounds produced by macrophytes and their functional significance. In contrast, the study sites characterised by more open water habitats, Chew Magna Reservoir and Squabmoor Reservoir, lacked a secondary midday peak in acoustic activity due to macrophyte respiration. Interestingly, we also observed evidence of potential acoustic niche partitioning between *Sigara* spp. and *Micronecta* spp. during the night at Chew Magna, presumably to facilitate the simultaneous calling of each species while avoiding competition for acoustic space (Figure 5).

Periods of relative quiet around dawn and dusk were observed in this study at Abbots Pool, Chew Magna Reservoir and Old Sneed Park. Similarly, both Karaconstantis et al. (2020) and Gottesman et al. (2020) reported the lowest values derived from acoustic indices,









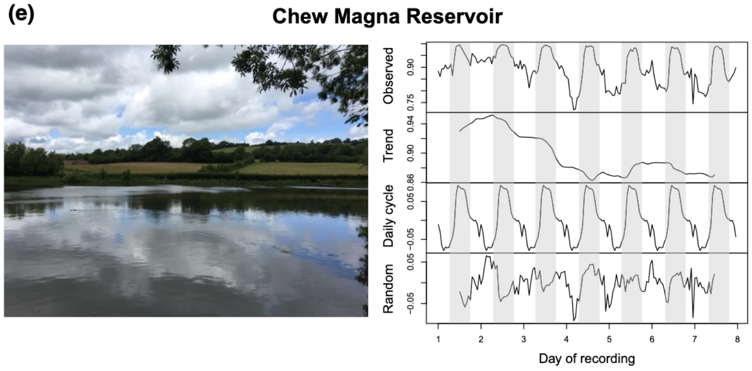


FIGURE 3 Decomposition of time series using hourly mean Normalised Difference Soundscape Index (NDSI), with predicted values from additive model output for each site. (a) Old Sneed Park, (b) Eastwood Farm, (c) Abbots Pool, (d) Squabmoor Reservoir, (e) Chew Magna Reservoir. Light grey boxes indicate night-time hours. Observed = raw data values, trend = increase/decrease in values over time; daily cycle = cyclic component within the time series; random = random variation within the time series.

TABLE 4 Estimates of Phi (φ) from generalised least squares models between each acoustic index calculated (response variable) and hour sampled (explanatory variable) at each study site.

Study site	BI	ACI	ADI	H	AEI	NDSI
Old Seed Park	0.79**	0.72**	0.78**	0.94**	0.81**	0.75**
Eastwood Farm	0.75**	0.64*	0.77**	0.97**	0.70**	0.69*
Abbots Pool	0.66*	0.67*	0.79**	0.99**	0.79**	0.57*
Squabmoor Reservoir	0.38	0.50*	0.80**	0.93**	0.76**	0.45
Chew Magna Reservoir	0.89**	0.70**	0.84**	0.95**	0.82**	0.88**

Note: Estimates of 0–0.19 (no correlation), 0.20–0.29 (weak correlation), 0.30–0.49 (moderate correlation), 0.50–0.69 (strong correlation*), 0.70–1.0 (very strong correlation**) (Frey, 2018).

Abbreviations: ACI, Acoustic Complexity Index; ADI, Acoustic Diversity Index; AEI, Acoustic Evenness Index; BI, Bioacoustic Index; H, Acoustic Entropy; NDSI, Normalised Difference Soundscape Index.

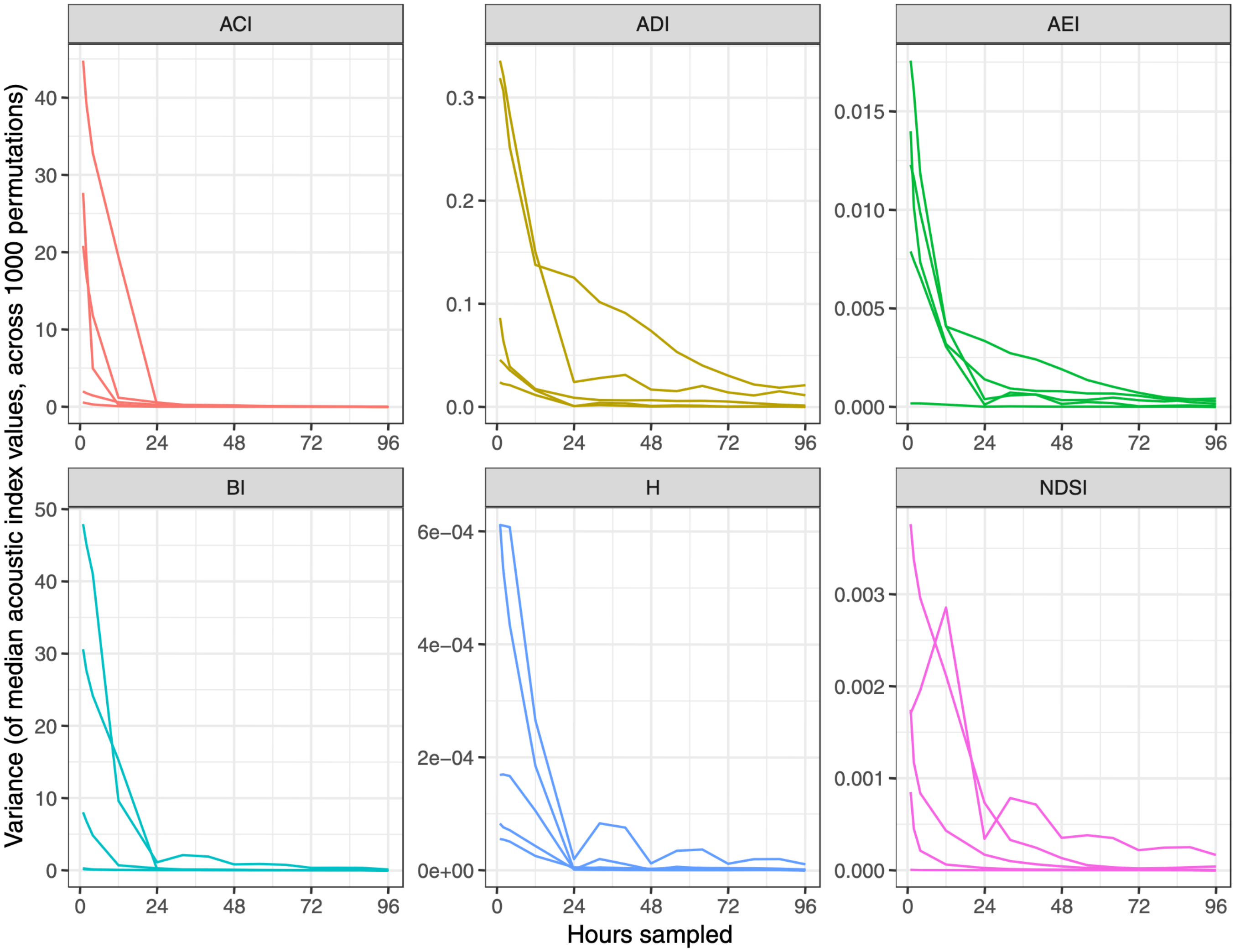


FIGURE 4 Stabilisation of variance of median acoustic index values in each simulated sampling time period across 1,000 permutations. Variation in the median for each acoustic index was high at low sampling effort (<10 hr) before stabilising in most cases after 20–24 hr of simulated hydrophone deployment time. Typically, stabilisation was achieved after a full daily cycle had been captured by the deployed sampling effort. ACI, Acoustic Complexity Index; ADI, Acoustic Diversity Index; AEI, Acoustic Evenness Index; BI, Bioacoustic Index; H, Acoustic Entropy; NDSI, Normalised Soundscape Difference Index.

and therefore acoustic activity, during dawn and dusk. Gottesman et al. (2020) suggested that acoustic inactivity around sunrise and sunset might be due to intermediate levels of light intensity that fail to elicit sound producing behaviour in aquatic insect species that are triggered by extreme light intensities. Temperature has also been shown to regulate aquatic insect stridulation and might also be a contributing factor in determining twilight pond soundscape activity (Jansson, 1968). However, Gottesman et al. (2020) note that the acoustic activity of aquatic insects in a tropical swamp varied without any significant change in light intensity or air temperature, suggesting an additional factor, such as a circadian rhythm governed by an internal biological clock.

Another potential reason for relative quietness during twilight hours could be that stridulating aquatic insects expose their location to predatory freshwater fish, which preferentially forage for prey during twilight hours (Helfman, 1981). Therefore, it is possible that acoustic activity is reduced during twilight hours to reduce the risk of predation (Gottesman et al., 2020). However, Hemiptera stridulation occurring between 2–10 kHz is likely to be undetectable by most species of fish, which are only capable of detecting sounds produced between 0.03 and 1 kHz, and most effectively between 0.03 and 0.05 kHz (Popper & Hawkins, 2019). Nevertheless, fish in the superorder Ostariophysi, such as common carp, possess specialised hearing anatomy (Weberian ossicles) which connect the inner ear to the swim bladder to enable greater auditory sensitivity (Murchy et al., 2016). As a result, ostariophysians are typically capable of detecting sounds produced between 200 Hz and 3 kHz (Ladich & Fay, 2013), and in some cases up to 5 kHz (Lechner & Ladich, 2008). It is worth noting, however, that very few experiments investigating hearing in freshwater fishes have been conducted, and even fewer under suitable acoustic conditions (Popper & Hawkins, 2019). Moreover, the ability of many water boatmen to call as a synchronous chorus has been suggested as a behaviour to make locating and capturing prey items more challenging for predatory fish (Legett et al., 2019). As a result, the potential for the ability of fish to detect Hemiptera stridulation should not be completely ruled out.

4.2 | Evaluating acoustic indices for insect-dominated freshwater soundscape analysis

Despite the intensity of acoustic activity during a synchronous chorus of aquatic insect stridulation, the short repeating phrases that occupy a continuous frequency band with little or no variation in amplitude produced by a single species can be difficult to accurately characterise using some acoustic indices (Desjonquères et al., 2020; Ferreira et al., 2018). For example, the ACI is designed to ignore consistent sounds in the recorded bandwidth to reduce the influence of anthropogenic sounds on calculated values (Pieretti et al., 2011). Karaconstantis et al. (2020) noted that the ACI failed to detect acoustic variation between sites caused by nocturnal aquatic insect choruses. In this study, ACI did not characterise aquatic insect-dominated choruses as well as the BI and the NDSI. However, Linke et al. (2020) were able to successfully detect a nocturnal aquatic insect chorus using the ACI. Because different species of aquatic insect produce calls that occupy different frequency bandwidths, it is therefore

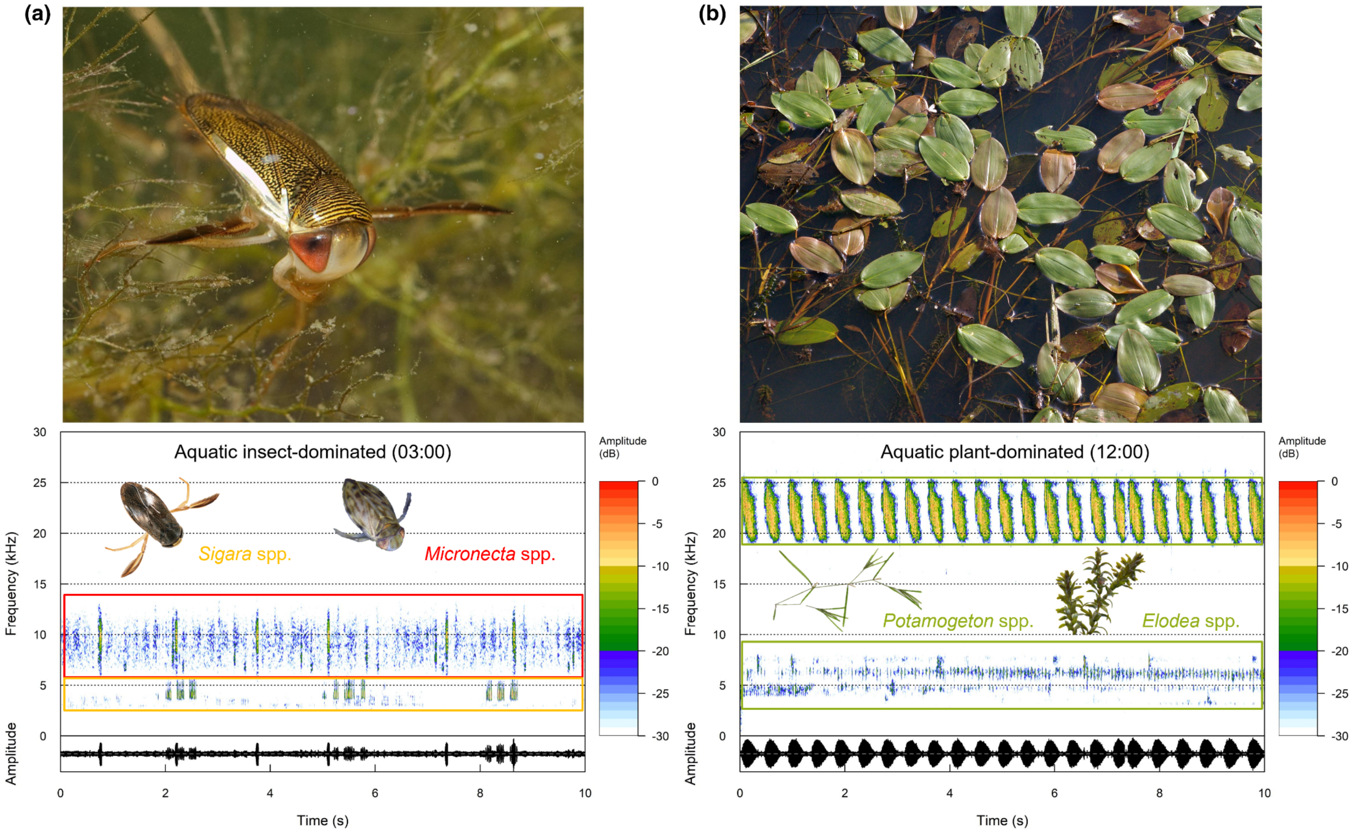


FIGURE 5 Typical night-time (a) aquatic insect-dominated soundscapes, and daytime (b) aquatic plant-dominated soundscape. Coloured boxes show the frequency ranges of sounds produced by taxa of the corresponding colour. Spectrograms were created with an FFT size 2,048.

logical to assume that a chorus composed of multiple aquatic insect species, rather than just one species, is more likely to be successfully detected by the ACI. Karaconstantis et al. (2020) noted that aquatic insect stridulation was clearly identified by H and Median of Amplitude Envelope. In this study, H, together with the ADI and AEI, showed the most significant variation between diel period when all five study sites are considered together. However, these indices consider the entire recorded bandwidth and are therefore susceptible to sounds produced in the geophony, such as wind and rain, the anthrophony, such as road and airplane noise, in addition to the biophony. Values generated by the ADI, the AEI, and H are therefore rarely the result of just biologically produced sounds and should be interpreted as such. More biologically meaningful acoustic indices include the BI, and the NDSI, which specifically target the frequency bandwidth of the biophony and are shown here to be influenced strongly by aquatic insect (Hemiptera) richness. Furthermore, the BI and the NDSI functioned as good proxies for study sites containing a greater species richness of soniferous taxa (e.g., Hemiptera), such as Old Sneed Park and Chew Magna Reservoir compared to study sites containing fewer soniferous taxa, such as Squabmoor Reservoir.

4.3 | Caveats and potential confounding variables

Aquatic insects and plants are known to possess clear seasonal phenologies, with seasonality in breeding periods for Corixidae, and a flowering period for macrophytes (Jansson, 1973; Sayer et al., 2010). Therefore, between-site variability in species compositions and acoustic activity may also be the result of longer-term changes during the survey period (April–June). Survey periods during summer months may have also increased the rates of aquatic insect and plant acoustic activity as a result of increased kinetic energy available for biological processes due to increased light intensity and water temperature (Jansson, 1968; Wright & McDonnell, 1986). Although similar microhabitats, a mix of submerged macrophytes and open water, were selected for hydrophone placement in each study site, the hydrophone was static and sampled continuously at just one location at each site. This lack of spatial replication could be an additional source of between site soundscape variability. In addition, only one macroinvertebrate sample was collected from each study site, therefore, these results should be interpreted with this in mind. Pond depth, substrate type, and submerged macrophyte distribution are also likely to affect the propagation of soundwaves. Adverse weather conditions might also affect the behaviour of organisms producing sound in the biophony.

4.4 | Recommendations for the design of ecoacoustic surveys in insect-dominated temperate ponds

Based on the data presented in this study, we suggest that Acoustic Entropy (H) is the most useful acoustic index for detecting daily acoustic activity cycles in temperate ponds. Acoustic Entropy is less useful, however, when a specific consideration of biologically produced sounds is required in analysis. Therefore, due to strong associations with Hemiptera species richness, the Bioacoustic Index (BI) and the Normalized Difference Soundscape Index (NDSI) are shown here to be good indicators of insect-dominated soundscapes. Although Hemiptera can be responsible for a considerable amount of acoustic variation in pond soundscapes, it is important to note that other soniferous species, such as some Coleoptera, fish, amphibians and aquatic plants also contribute to freshwater soundscape activity and complexity. Therefore, multiple acoustic indices should be calculated in order to accurately capture the diversity of biologically-produced sound in ponds, rather than relying on a single acoustic index.

In addition, we suggest that a minimum of 24 hr should be recorded to ensure that an adequate amount of soundscape variation is captured. Variance stabilised with less sampling effort at study sites with more a clearly defined diel biophony (Old Sneed Park and Chew Magna Reservoir). Whereas study sites with a less clearly defined diel biophony (Eastwood Farm, Abbots Pool, and Squabmoor Reservoir) stabilised after greater sampling effort, potentially due to randomly produced, less predictable sound in the geophony and anthrophony. It is likely, however, that the number of recording hours required to comprehensively capture soundscape variation would increase when more study sites are considered. Furthermore, data collected as part of a long-term monitoring programme spanning multiple seasons and environmental conditions would probably result in greater overall variance, and therefore require a higher sampling effort.

4.5 | Concluding remarks

This study has highlighted the influence of diel period on temperate freshwater soundscapes and therefore the importance of considering diel soundscape variation when designing ecoacoustic surveys in temperate ponds. As a result, we recommend the following when designing and conducting passive ecoacoustic monitoring surveys in temperate ponds: (1) record for a minimum of 24 hr to capture a significant proportion of soundscape variability; (2) conduct initial investigations of the data via spectrogram analysis to define the biophony of surveyed sites; (3) calculate biologically relevant indices, such as the BI and NDSI, to more accurately describe sound produced in the biophony; and (4) calculate multiple acoustic indices to capture all components of the soundscape accurately. Passive acoustic monitoring in ponds has the potential to non-invasively survey aquatic insects, plants, fish, and amphibian activity and diversity in an automated and standardised way. However, more research is required to describe species-specific sounds produced by key species groups. In addition, considerations should be made while designing passive acoustic monitoring surveys for temperate ponds to avoid not capturing the sounds of key soniferous taxa that exhibit diel acoustic behaviour. The data collected in this study provide further evidence that ponds are packed full of sound produced by aquatic insects and plants, highlighting the impressive biodiversity that freshwater ecosystems possess.

AUTHOR CONTRIBUTIONS

Conceptualisation, developing methods, conducting the research, data analysis, data interpretation, preparation of figures and tables, writing: J.G. Data analysis, data interpretation, writing: M.G. Writing, data analysis: G.J.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Diel variation in insect-dominated temperate pond soundscape at https://zenodo.org/record/7307890, reference number 10.5281/zenodo.7307890.

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