Assessing the effects of habitat management practices on vocalizing animals using passive acoustic monitoring

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Declaration of Authorship

I, Richard Beason hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.

Signed: ______________________

Date: ________________________

“The earth has its music for those who will listen”

— Reginald Vincent Holmes, *Fireside Fancies*, 1955

Abstract

There is an urgent need for effective and efficient technologies suitable for assessing the impacts of anthropogenic activity on biodiversity and ecosystem health. This project explores the potential of passive acoustic monitoring (PAM) for investigating the effects of different habitat management types on the activity and diversity of bats and birds. PAM is non-invasive, does not require line-of-sight and can monitor a wide variety of species. In order to record both audible and ultrasonic frequencies, custom recording devices were developed for this study (Chapter 2). The following specific questions were addressed:

Chapter 3. How does the invasion of forest understorey by *Rhododendron ponticum* affect the activity of different bat species in comparison to areas where rhododendron is absent or has recently been removed? I found that effects of invasive rhododendron on native bat species vary according to their respective foraging strategy. In addition, some bat species were negatively affected by the presence of deer.

Chapter 4. How do tree species richness and tree species composition affect acoustic diversity and activity of avian communities in temperate forests? Acoustic indices representing bird diversity demonstrated significant positive relationships with tree species richness, and relationships with some tree species. Some evidence that mixing broadleaves and conifers could benefit bird diversity was also found.

Chapter 5. How do the different types of scrub created by rewilding using free-roaming mammalian herbivores differ in the activity levels of bird and bat communities? Bats with different foraging strategies demonstrated niche separation between the different habitats created by rewilding. Habitat characteristics also had significant effects on bird acoustic indices.

This thesis demonstrates how PAM can be used to monitor the effects of different habitat managements on two different groups of taxa. However, further developments in analysis methods, particularly automated species identification, are necessary to realise its full potential.

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CHAPTER 1

1. General Introduction

1.1 Passive Acoustic Monitoring

Increasing pressure from anthropogenic activity has led to biodiversity loss and the degradation of ecosystems on an unprecedented scale (Pimm *et al.*, 2014; Ceballos *et al*., 2015; WWF, 2018; Díaz, 2019). The need for efficient, reliable survey methods for assessing species diversity, distributions and population trends over large spatial scales and time-frames is therefore both urgent and crucial for assessing the success of conservation and management projects, and informing policy and decision making (Pereira and Cooper, 2006; Sueur *et al*., 2008a; Penone *et al*., 2013). Traditional survey methods, which typically involve either physically trapping or visually observing the species of interest, can be expensive, laborious and impractical or potentially dangerous in some locations (Marques *et al*., 2013; Deichmann *et al*., 2018). Facilitated by recent advances in recording technology, the ability to capture long-term, continuous acoustic data over wide spatial scales has fuelled growing interest in the use of sound as a means of monitoring animal populations and distributions (Servick, 2014; Merchant *et al*., 2015; Pieretti *et al*., 2015). Sound represents an important communication medium and source of information for many animal species that use sounds to perform vital functions such as territory marking, navigation, mate and habitat selection, alarm and social calls, and locating food (Farina, 2018). Although the practice of recording and analysing sounds made by various animals (bioacoustics) is well-established, research in this area has traditionally been limited to studying the behaviour and communication methods of individual species (Lomolino *et al*., 2015). More recently the scope of acoustic monitoring expanded to encompass community and ecosystem level assessments (ecoacoustics) by capturing all the sounds emanating from a particular location (the 'soundscape') (Sueur and Farina, 2015). Soundscape elements are divided into three categories according to their source; anthrophony (anthropogenic noise sources), geophony (abiotic sounds such as wind and rain) and biophony (sounds produced by animals) (Farina, 2014).

Capturing sound with microphones is a passive technique and the use of unattended recording devices, left in-situ, is frequently referred to as Passive Acoustic Monitoring (PAM) (e.g. Blumstein *et al*., 2011; Marques *et al*., 2013; Merchant *et al*., 2015). In addition to allowing monitoring over large spatial and temporal scales, PAM offers several other advantages over traditional surveys. Other than initial set up, and when swapping batteries and data cards, PAM is non-invasive, minimising the amount of disturbance caused by monitoring activities and negating the possibility that the species under observation will be influenced by the presence of surveyors (Mennill *et al*., 2012; Shonfield and Bayne, 2017). PAM inherently creates a permanent digital record that can be shared, re-evaluated, re-purposed or used as baseline data (Riede, 1998; Deichmann *et al*., 2018). While the same arguments could be made for the use of camera traps (Buxton *et al*., 2018a), PAM does not require line-of-sight and can be used in situations that are less favourable for camera traps, e.g. underwater, at night, in dense vegetation (Gasc *et al*., 2013), and for monitoring visually cryptic species (Marques *et al*., 2013). On a per-unit-basis, sound recording devices are capable of monitoring much larger areas than camera traps and can additionally be used to monitor a much greater variety of species (Deichmann *et al*., 2018). While camera traps are most effective when monitoring mid to large-sized mammals and birds at ground level (Buxton *et al*., 2018a; Deichmann *et al*., 2018), PAM has been used to monitor an extensive list of species and species groups including, but not limited to, birds (Shonfield and Bayne, 2017), bats (Newson *et al*., 2015), anurans (Alvarez-Berríos *et al*., 2016), whales (Stimpert *et al*., 2011), dolphins (Brunoldi *et al*., 2016), fish (Ruppé *et al*., 2015), Orthoptera (Riede, 1998), koalas (Hagens *et al*., 2018), primates (Heinicke *et al*., 2015) and elephants (Wrege *et al*., 2017). Furthermore, PAM will inherently capture the vocalisations of all and any species within the frequencies being monitored and can thus be used to simultaneously monitor multiple species and taxa (Heinicke *et al*., 2015; Lacoeuilhe *et al*., 2016; Newson *et al.*, 2017; Figure 1.1).

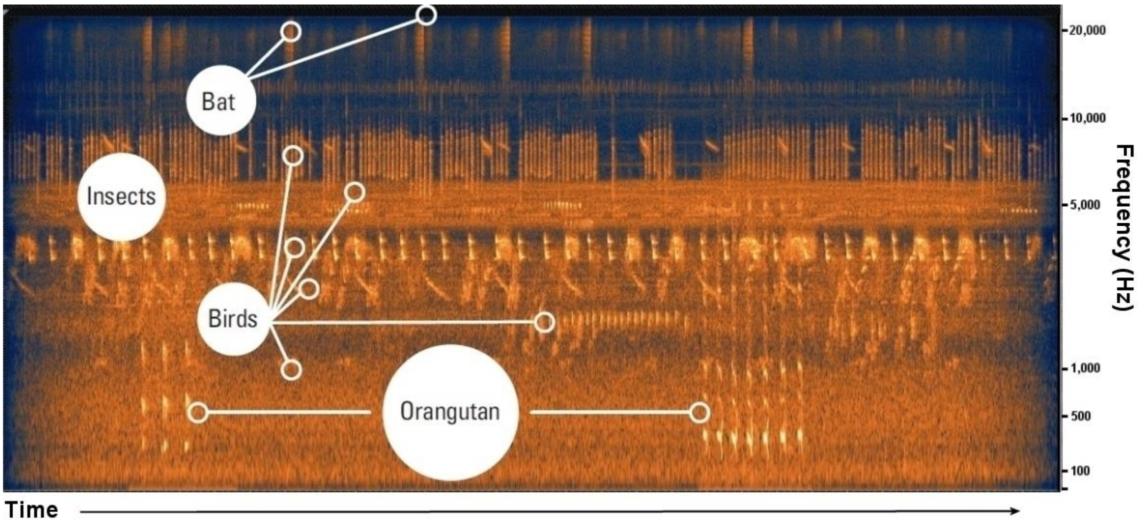


Figure 1.1. The spectrogram of a sound recording made in Sumatran rainforest illustrates how the presence of different species, and different types of species, can be simultaneously detected with passive acoustic monitoring (Servick, 2014).

Apart from the obvious flaw that PAM cannot be used to monitor species that do not vocalise, or otherwise create a recognisable sound, interspecific and intraspecific differences in the detectability of vocalising species can cause additional issues. When comparing activity between different species, interspecific differences in the rate (Alldredge *et al*., 2007), duration (Pohl *et al*., 2013) and loudness (Andreassen *et al*., 2014) of vocalisations could potentially bias results (Johnston *et al*., 2014). Phenology and breeding cycle may also cause variations in detectability; some bird species may vocalise less frequently once paired (Catchpole and Slater, 2008) or when incubating and raising young (Kleindorfer *et al*., 2016) while some anurans (McCauley *et al.*, 2000), Orthoptera (Schmidt and Balakrishnan, 2015) and deer (Pitcher *et al*., 2014) demonstrate distinct peaks in calling activity during, and throughout, the breeding season. Differences in detectability due to phenology could therefore complicate comparisons between surveys performed at different times of the year, even when studying the same species. Additionally, the males of species such as birds (Bibby *et al*., 2000; Collins, 2004), anurans (Gerhardt, 1994; Beebee, 1996), mammals (Hagens *et al*., 2018; Warren *et al*., 2018) and insects (Balenger, 2015; Hartbauer and Römer, 2016) often produce sounds more frequently and/or more loudly than females, particularly when defending territories or attracting mates. For example, although the occurrence of female bird song may be more widespread than previously thought (Odom *et al*., 2014), Webb *et al*. (2016) found that female song was absent in 36% of the 1023 species of songbirds they assessed. Intraspecific differences in vocalising behaviour between the sexes could thus produce misleading estimates of abundance and community health for populations with unequal sex ratios or large numbers of unpaired males, respectively (Bibby *et al*., 2000).

Audio signals can also be degraded by factors such as distance or vegetation cover (Farina, 2014), and sounds of interest may be masked by wind, rain and anthropogenic noise (Francis *et al*., 2011). In the latter situation, the capture of non-biotic sounds can, however, also be potentially desirable for anyone interested in monitoring such sources, e.g. for assessing the effects of anthropogenic noise intrusion (Gil *et al*., 2014; Gentry and Luther, 2017), estimating hunting pressure based on gunshot detection (Astaras *et al*., 2017; Hill *et al*., 2018) or monitoring weather conditions (Erbe *et al*., 2015). PAM generates large amounts of data; for example, recordings for one 24-hour period stored in uncompressed 44.1 kHz, 16-bit, mono wav format will exceed 7 GB in size. For multiple recorders and/or longer timescales, recordings can quickly accumulate into big-data with the associated storage, curation and analysis issues that big-data typically entails (Towsey *et al.*, 2014a). Automated analysis methods, particularly for species-level identifications, have improved somewhat, but are still subject to limitations and can be complex and time-consuming (Deichmann *et al*., 2018; Section 1.3). Acoustic recording devices are also susceptible to the same hazards (e.g. theft, vandalism, extreme weather and animal damage) as camera traps (Farina, 2014) and, similarly, longer term field studies typically require regular equipment revisits to replenish batteries and download data (Pijanowski *et al.*, 2011a).

Previously, portable devices used to record sound typically had high power consumption and required human operation, which limited the spatial and temporal scales over which acoustic data could be collected (Suer *et al.*, 2012; Lomolino *et al*., 2015; Merchant *et al*., 2015). In addition, such devices used magnetic tape as their storage medium, which made them susceptible to hardware failure in hostile environments, limited the frequencies and amplitudes that could be captured and meant the quality of recordings degraded over time (Bradbury and Vehrencamp, 2011). The introduction of digital storage media (e.g. SD cards, external hard drives) and advances in sound recording technology over the last couple of decades have expedited the development of small, cost-effective, programmable Autonomous Recording Units (ARUs) capable of continuously capturing acoustic data over extended time periods (Merchant *et al*., 2015; Farina and Gage, 2017). The availability of ARUs has enabled researchers to simultaneously capture and store high-quality recordings from multiple locations and has underpinned the rapid expansion of acoustic monitoring studies (Lomolino *et al*., 2015; Merchant *et al*., 2015).

1.2 Autonomous Recording Units

A typical ARU usually consists of a microphone(s), electronics enabling the acquisition and storage of digital data, digital storage media, an internal clock to enable scheduled recordings and a power source (usually batteries), all of which are enclosed within some kind of weatherproof casing (Merchant *et al*., 2015; Farina and Gage, 2017; Figure 1.2).

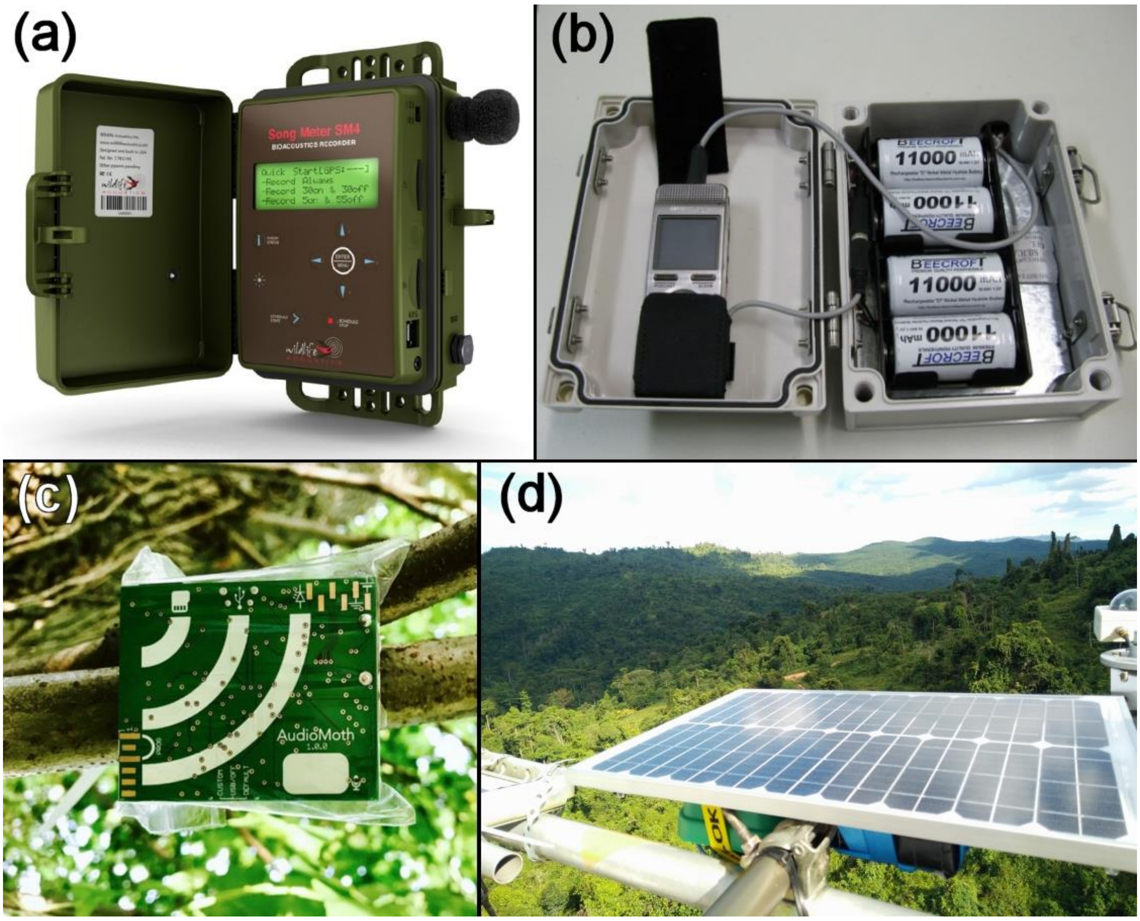


Figure 1.2. Examples of different ARUs: (a) Wildlife Acoustics SM4 (Wildlife Acoustics, 2019a), (b) DIY unit based on a handheld voice recorder (Roe and Wimmer, 2014), (c) AudioMoth (Hill *et al*., 2018), and (d) Raspberry Pi-based, solar-powered ARU with network connectivity (Sethi *et al*., 2018).

Sound is propagated as changes in particle density within an elastic medium (gas, liquid or solid) resulting in alternating regions of low (rarefaction) and high (compression) pressure (Everest and Pohlmann, 2009). Microphones are essential sensors for studying sound as they are able to detect these variations in pressure and convert them into an electrical signal, either by displacement of a physical diaphragm or, as in the case of hydrophones and accelerometers, through a piezoelectric transducer (Bradbury and Vehrencamp, 2011). Different microphones have different frequency responses and the most suitable type will largely depend on the frequencies produced by the animal species being studied (Blumstein *et al*., 2011). Some animals, notably bats, produce sounds above the upper range of human hearing (~20 kHz) and thus require microphones that are sensitive to ultrasonic (>20 kHz) frequency ranges (Obrist *et al*., 2010; Altringham, 2014). In addition to variations in frequency response, microphones also vary in their directional response with different types being more sensitive to sound from 100° (hypercardioid) frontal arc, 120° frontal arc (cardioid) or 360° (omnidirectional) (Audio-Technica, 2009). While the ability to digitise acoustic data has no doubt been crucial to the development of ARUs, the increased availability of small, low-cost yet high-performance, microphones has also been important (Farina and Gage, 2017); electret condenser capsules with low self-noise, such as the Primo EM172 (Primo Co. Ltd, Tokyo, Japan), and MEMS (micro-electro-mechanical systems) microphones, which are capable of recording ultrasonic frequencies (Hill *et al*. 2018).

As mentioned above, the ability to digitize electrical signals produced by microphones has led to the widespread adoption of digital recorders for acoustic monitoring due to the greatly extended recording times and frequency ranges that can be achieved (Bradbury and Vehrencamp, 2011; Browning *et al*., 2017). Analogue signals are converted to digital format by sampling the signal at regular time intervals, known as the sampling rate. The sampling rate determines the Nyquist frequency, which is equal to half the sampling rate and represents the highest sound frequency that can be stored; for example, a 22 kHz sampling rate can only capture audio frequencies up to 11 kHz. Higher sampling rates are thus required when recording higher frequencies, particularly when monitoring in the ultrasonic range, which increases the file sizes of any data generated. Storage capacity is an important consideration for recording devices and one way of increasing the amount of storable data is to use compressed file formats, such as MP3, WAC or FLAC. Compressing audio data with 'lossy' formats, such as MP3, can create false artefacts (e.g. spectral clipping, pre-echoes and tone modulation; Liu *et al*., 2008) and does not preserve the same level of detail as original recordings (Villanueva-Rivera *et al*., 2011). Any use of compression will, therefore, require careful consideration beforehand, to ensure detail and frequency ranges suitable for analysis are maintained.

In addition to data storage capacity, battery life will also determine the length of time over which an ARU can collect data before requiring intervention (Merchant *et al*., 2015). Many commercial ARUs use regular AA or D-cell batteries; expanding the battery capacity or using external batteries can extend the time between replenishment (Sueur *et al*., 2012) but larger battery capacities tend to increase the mass and size of the unit (Hill *et al*., 2018). Some studies have managed to bypass power and data storage limitations using solar panels, wireless data transmission or even both (e.g. Mason *et al*., 2008; Aide *et al*., 2013; Sethi *et al*., 2018). However, such examples are typically set in established locations where suitable infrastructure could be installed on a long-term basis. Alternative strategies for extending data capacity and battery life include limiting recording to specific periods of interest (e.g. dawn, night-time) with timed schedules (Abrahams and Denny, 2018), the use of sampling schemes that record at regular intervals rather than continuously (Pieretti *et al*., 2015) or using triggering algorithms that initiate recording based on the detection of specific sound events e.g. gunshots or bat calls (Prince *et al*., 2019). The situation may further improve with recent developments in open-source devices, which have shown that it is possible to significantly reduce the amount of energy required by ARUs (Hill *et al*., 2018).

Although commercially produced ARUs (e.g. Figure 1.2a) have been available since 2007 (Wildlife Acoustics, 2017), the cost of these devices (>£1,000) meant that only a limited number of units could be deployed in a given study (Sueur *et al*., 2012). To overcome these limitations, some researchers developed their own ARUs based around handheld voice recorders (Wimmer *et al.*, 2013; Towsey *et al*., 2014b; Figure 1.2b) and smartphones (Mason *et al*., 2008; Planitz *et al*., 2009). Despite the recent development of several more reasonably priced, mass-produced options such as the Swift (Cornell Labs, New York, USA) and Soundscape Explorer (Lunilettronik, Fivizzano, Italy), researchers have continued to produce low-cost, open-source alternatives. The AudioMoth (Figure 1.2c), for example, was specifically designed and built from raw electronic components as an inexpensive alternative to commercial options for use in large-scale deployments (Hill *et al*., 2018). Other custom-developed ARU solutions have adapted existing micro-processors such as Arduino and Raspberry Pi to develop their own low-cost, monitoring alternatives (e.g. wa Maina *et al*., 2016; Whytock and Christie, 2016). The potential for developing custom ARUs that are solar powered with wireless data transmission, thus negating the need for regular battery and data storage replacements, has also been demonstrated (Sethi *et al*., 2018; Figure 1.2d). A summary of some commercial and open-source ARUs currently available is presented in Table 1.1. Due to the lack of affordable ARUs capable of recording both audible and ultrasonic frequencies when this project began, it was necessary to design and construct devices specifically for this purpose. This process, as well as ARU design in general, is discussed in more detail in Chapter 2.

Table 1.1. Comparison of specifications for a selection of ARUs that are currently available. Data from Titley Scientific (2019)[1], Hill *et al*. (2018)[2], Wildlife Acoustics (2019a)[3], Wildlife Acoustics (2019b)[4], Whytock and Christie (2016)[5], IInstEco (2018)[6] and Koch (2016)[7].

Device name	Supplier	Max. sampling rate (kHz)*	Data capacity (GB)**	Power supply	Guide Price***
Anabat Swift[1]	Titley Scientific	500	1024	8 x AA-cell	£1044
AudioMoth[2]	Open source	384	32	3 x AA-cell	$50
SM4[3]	Wildlife Acoustics	96	1024	4 x D-cell	$849
SM4BAT FS[4]	Wildlife Acoustics	500	1024	4 x D-cell	$1099
Solo (Pi A+)[5]	Open source	192	256	Ext. µUSB	£83
Soundscape Explorer[6]	Lunilettronik	48 / 192	64	8 x D-cell	€ 500
Swift[7]	Cornell Labs	96	256	3 x D-cell	$250

* Actual frequencies that can be recorded are half this value.

** Based on maximum recommended SD card sizes where lower than the maximum possible for SDXC cards.

*** Batteries and data cards not included. The cost of a microphone has been added for the SM4BAT FS (SMM-U2) and Solo (Clippy EM172) as one is not included with the basic unit.

1.3 Analysis of Acoustic Data

1.3.1 Spectrograms

Arguably, the most fundamental method of visualising and analysing sound is using spectrograms (Obrist *et al*., 2010; Blumstein *et al*., 2011; Merchant *et al*., 2015). Spectrograms are particularly useful as they simultaneously represent acoustic information in three dimensions, time (x-axis), frequency (y-axis) and signal intensity (pixel colour or brightness), in an intuitive format (e.g. Figure 1.1) and can be depicted using a variety of formats such as 3D and false-colour images (Gage *et al*., 2017).

Spectrograms are produced by dividing sound files into short segments (sometimes referred to as frames or windows) of equal length in time, or the same number of samples, which are then analysed using Fast Fourier Transform (FFT). FFT calculates values for the relative intensity of the constituent frequencies within each frame, which can then be represented by an associated colour, or colour intensity, and displayed as pixels in a vertical line. Placing the lines produced for each segment side by side, in the order they were produced, thus produces a final image of frequency spectra against time for the whole file (Farina and Gage, 2017). The time (x-axis) and frequency (y-axis) resolution of FFT calculations are inherently inversely proportional, i.e. shorter frame sizes reduce the spectrogram's frequency resolution and vice versa, and frame sizes should therefore either be chosen based on the intent of the analysis or as a compromise between these two dimensions (Farina, 2014).

In addition to facilitating the presentation, sharing and discussion of sounds as images in printed and digital reading materials, the ability to transform sound into a visual representation has other advantages and applications. Indeed, spectrograms are important for both main approaches typically used by ecologists to quantify sound: species identification and acoustic indices (Farina and Gage, 2017). Below I describe the use of spectrograms in these two approaches.

1.3.2 Species Identification

Listening to an audio file is a real-time process i.e. it will take one minute to listen to one minute of sound. Spectrograms can provide a meaningful overview of sound over relatively long time periods as a single image, facilitating faster navigation through long recordings and the ability to look for specific events or points of interest (Villanueva-Rivera *et al*., 2011; Gage *et al*., 2017). Visual inspection of spectrograms can thus be used as a method of locating and identifying specific species in recordings (Digby *et al*., 2013; Hagens *et al*., 2018). Use of this approach depends on vocalisations of the target species being visually easy to distinguish and recognise and, being time-consuming, is more suited to looking for one, or a small number of, species (Shonfield and Bayne, 2017). Nevertheless, the manual identification of species by means of observing spectrograms and targeted listening can be considered as an analysis method (Buxton *et al*., 2018b).

For birds at least, reviews of all the studies that have evaluated the performance of manually identifying species from ARU recordings with traditional point counts concluded that, overall, results for both methods were generally similar in terms of the number of different bird species detected (Shonfield and Bayne, 2017; Darras *et al*., 2018). However, the actual species detected by each method may vary to some degree; identification from recordings will fail to detect non-vocalising species or species that are difficult to recognise acoustically, whereas physical point counts are less likely to detect species that vocalise infrequently, have short vocalisations or are sensitive to disturbance by the observers (Celis-Murillo *et al*., 2009; wa Maina *et al*., 2016; Darras *et al*., 2018). Additionally, the distance over which surveys are conducted can influence results. ARU surveys offer better performance over fixed distances compared to unlimited range surveys, where human observers are able to spot more species further away than recorders (Darras *et al*., 2018). As with traditional counts, manual identifications from recordings are potentially subject to observer bias (Mammides *et al*., 2017; Turner *et al*., 2018), although the availability of a permanent record does enable re-evaluation and cross-validation (Shonfield and Bayne, 2017). Access to long-term, continuous recordings additionally enables better estimates of site occupancy (La and Nudds, 2016; Abrahams and Denny, 2018). Manual identification is, however, time-consuming, and, for the big data generated by PAM, manual identifications are not always feasible and some form of automated, or semi-automated, analysis is necessary (Planitz *et al*., 2009; Buxton *et al*., 2018b). The use of automated processes thus offers significant potential for advancing the field of acoustic monitoring by reducing the amount of time required to detect and identify species within large datasets, while also retaining most of the benefits mentioned above (Mammides *et al*., 2017; Darras *et al*., 2018).

Fundamentally, automated species identification must be capable of detecting and separating sounds of interest from background noise in continuous recordings before classifying them to species based on their characteristics (Acevedo *et al*., 2009). This is usually achieved using supervised (specific 'recognizers' are trained using examples of the target species) or unsupervised (features are extracted based on inherent properties within the data) feature learning (Stowell and Plumbley, 2014). A wide range of processing techniques, using both supervised and unsupervised approaches, has been applied to the task including; hidden Markov models (Wildlife Acoustics, 2019c), random forests (Ross and Allen, 2014), spectrogram cross-correlation (Charif *et al*., 2010), binary point matching (Katz *et al*., 2016), support vector machines (Heinicke *et al*., 2015), Gabor time-frequency decomposition (Connor *et al*., 2012) and discriminant function analysis (Parsons and Jones, 2000). While a detailed discussion of the various methodologies and software used for automated identification is beyond the scope of this introduction, brief overviews of the software applications used in this study, BatClassify (Scott, 2017) and Kaleidoscope Pro (www.wildlifeacoustics.com) are provided below.

1.3.2.1 BatClassify

BatClassify is a free, open source software application that was developed as part of a Defra-funded project to facilitate larger scale surveys of UK bat species in woodlands (Scott and Altringham, 2014). The software operates unsupervised and features a simple interface where the only necessary user inputs are the source directory where the WAV or FLAC files for evaluation are stored and an output directory to store the results, in the form of a CSV summary and, optionally, spectrograms of the audio files (Scott and Altringham, 2014). The option to split time-expansion recordings is also provided as BatClassify cannot handle long or large audio files and direct-sampling of files a few seconds in length is recommended (Scott and Altringham, 2014).

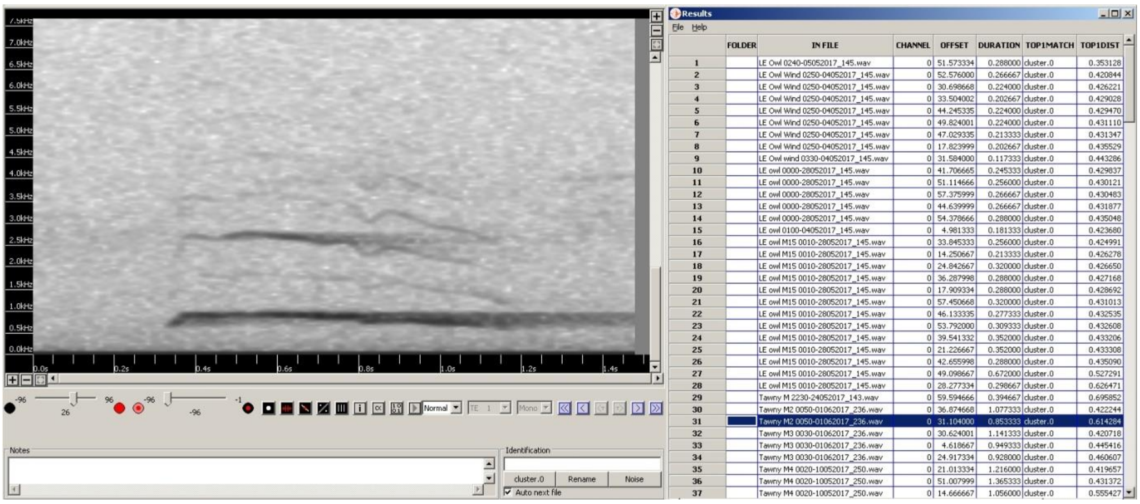
BatClassify uses a two-stage process to perform identifications; first, connected component labelling is used to extract features of interest from log-transformed spectrograms of the input audio files, which are first resampled to 500 kHz and undergo background noise removal, and, second, extracted features are then classified using a tree-based ensemble method, which is capable of handling multiple classes (Scott and Altringham, 2014). Sound files within the input directory specified are analysed sequentially and, for each file, a confidence rating from 0 (very unlikely) to 1 (very likely) is assigned to each species, or species group, to indicate the likelihood of its presence in the recording (Scott, 2017). Additionally, as BatClassify produces confidence ratings for every bat species that could potentially be present, it is able to assign ratings for recordings containing multiple species to more than one species (Scott and Altringham, 2014).

1.3.2.2 Kaleidoscope Pro

Kaleidoscope Pro (v5.1.3) is a commercial software package produced by Wildlife Acoustics (www.wildlifeacoustics.com). The full version of Kaleidoscope Pro costs $399 ($299 for universities) for an annual subscription fee but can also be used for free with functionality limited to viewing and converting files (Wildlife Acoustics, 2019d). The interface for Kaleidoscope Pro is more complicated than BatClassify as it allows the customisation of various signal detection parameters and sensitivity settings for each of its two modes of operation: analysis of bats and analysis of non-bats.

In non-bats mode, Kaleidoscope Pro extracts features that exceed the ambient noise floor, calculated as a rolling average, and splits them into separate sound events based on the specified inter-syllable gap length and frequency parameters (Wildlife Acoustics, 2019c). An FFT analysis of each phrase is transformed into coefficients representing the extracted spectrum, which are then used to construct Hidden Markov Models for each frame (Wildlife Acoustics, 2019c). Hidden Markov Models use time-dependent probability distributions to model statistical representations of the vocalisations present within each frame (Kogan and Margoliash, 1998). Individual phrases are then clustered based on the similarity of their Fisher scores (i.e. maximum likelihood estimations based on an iteratively reweighted least squares algorithm; Fisher, 1925), which range from 0 (phrases are identical) to 2 (phrases are orthogonal) (Wildlife Acoustics, 2019c). Basic clustering is used to examine batches of files (WAV or Wildlife Acoustics' proprietary formats WAC and W4V) and group any sounds it finds based purely on the user-specified signal parameters (Wildlife Acoustics, 2019c).

Following basic clustering (Figure 1.3), any sound events detected can be reviewed, labelled and subsequently used to create classifiers (e.g. for bird songs or calls) that can then be used to search other batches of files for sounds with similar characteristics (Wildlife Acoustics, 2019c).



	FOLDER	IN FILE	CHANNEL	OFFSET	DURATION	TOP1MATCH	TOP1DIST
1		LE Owl 0240-05052017_145.wav	0	51.573334	0.288000	cluster.0	0.353128
2		LE Owl Wind 0250-04052017_145.wav	0	52.576000	0.266667	cluster.0	0.420844
3		LE Owl Wind 0250-04052017_145.wav	0	30.698668	0.224000	cluster.0	0.426221
4		LE Owl Wind 0250-04052017_145.wav	0	33.504002	0.202667	cluster.0	0.429028
5		LE Owl Wind 0250-04052017_145.wav	0	44.245335	0.224000	cluster.0	0.429470
6		LE Owl Wind 0250-04052017_145.wav	0	49.824001	0.224000	cluster.0	0.431110
7		LE Owl Wind 0250-04052017_145.wav	0	47.029335	0.213333	cluster.0	0.431347
8		LE Owl Wind 0250-04052017_145.wav	0	17.823999	0.202667	cluster.0	0.435529
9		LE Owl wind 0330-04052017_145.wav	0	31.584000	0.117333	cluster.0	0.443286
10		LE owl 0000-28052017_145.wav	0	41.706665	0.245333	cluster.0	0.429837
11		LE owl 0000-28052017_145.wav	0	51.114666	0.256000	cluster.0	0.430121
12		LE owl 0000-28052017_145.wav	0	57.375999	0.266667	cluster.0	0.430483
13		LE owl 0000-28052017_145.wav	0	44.639999	0.266667	cluster.0	0.431877
14		LE owl 0000-28052017_145.wav	0	54.378666	0.288000	cluster.0	0.435048
15		LE owl 0100-04052017_145.wav	0	4.981333	0.181333	cluster.0	0.423680
16		LE owl M15 0010-28052017_145.wav	0	33.845333	0.256000	cluster.0	0.424991
17		LE owl M15 0010-28052017_145.wav	0	14.250667	0.213333	cluster.0	0.426278
18		LE owl M15 0010-28052017_145.wav	0	24.842667	0.320000	cluster.0	0.426650
19		LE owl M15 0010-28052017_145.wav	0	36.287998	0.288000	cluster.0	0.427168
20		LE owl M15 0010-28052017_145.wav	0	17.909334	0.288000	cluster.0	0.428692
21		LE owl M15 0010-28052017_145.wav	0	57.450668	0.320000	cluster.0	0.431013
22		LE owl M15 0010-28052017_145.wav	0	46.133335	0.277333	cluster.0	0.432535
23		LE owl M15 0010-28052017_145.wav	0	53.792000	0.309333	cluster.0	0.432608
24		LE owl M15 0010-28052017_145.wav	0	39.541332	0.352000	cluster.0	0.433206
25		LE owl M15 0010-28052017_145.wav	0	21.226667	0.352000	cluster.0	0.433308
26		LE owl M15 0010-28052017_145.wav	0	42.655998	0.288000	cluster.0	0.435090
27		LE owl M15 0010-28052017_145.wav	0	49.098667	0.672000	cluster.0	0.527291
28		LE owl M15 0010-28052017_145.wav	0	28.277334	0.298667	cluster.0	0.626471
29		Tawny M 2230-24052017_143.wav	0	59.594666	0.394667	cluster.0	0.695852
30		Tawny M2 0050-01062017_236.wav	0	36.874668	1.077333	cluster.0	0.422244
31		Tawny M2 0050-01062017_236.wav	0	31.104000	0.853333	cluster.0	0.614284
32		Tawny M3 0030-01062017_236.wav	0	30.624001	1.141333	cluster.0	0.420718
33		Tawny M3 0030-01062017_236.wav	0	4.618667	0.949333	cluster.0	0.445416
34		Tawny M3 0030-01062017_236.wav	0	24.917334	0.928000	cluster.0	0.460607
35		Tawny M4 0020-10052017_250.wav	0	21.013334	1.216000	cluster.0	0.419657
36		Tawny M4 0020-10052017_250.wav	0	51.007999	1.365333	cluster.0	0.431372
37		Tawny M4 0020-10052017_250.wav	0	14.666667	1.056000	cluster.0	0.555427

Figure 1.3. Example of cluster analysis results in Kaleidoscope Pro v5.1.3 (www.wildlife.acoustics.com). Spectrograms of any sound events detected are displayed individually for ease of validation (left) and are also listed in a summary results file (right), where they can be labelled according to species or other criteria.

Clustering also works in bat analysis mode, using the methodology described above except that input audio files are first converted to zero-crossing format. However, the use of classifiers is not recommended for bats and automatic identifications are best performed with Kaleidoscope's in-built call reference library (Wildlife Acoustics, 2019c). Bat species classifiers in the library are grouped within different geographical areas, from continent down to country or state, but individual species or custom groups can also be selected for use in analyses (Wildlife Acoustics, 2019c). Input files are first checked against the signal parameters (frequency range, duration and inter-syllable gap) specified in the settings and any sound events that satisfy these criteria are then compared against the reference classifiers for all the species that were selected (Wildlife Acoustics, 2019c). Matches are determined based on user-defined sensitivity settings, labelled and then presented for validation in a similar way to clusters (Figure 1.3). Kaleidoscope Pro ranks species classifications from highest to lowest probability and presents its best estimate (highest probability) with up to two alternate suggestions; however, unlike BatClassify, it is not apparent whether these suggestions represent alternative classifications for the original identification or potentially indicate the presence of additional species in recordings

(Wildlife Acoustics, 2019c). In either case, a maximum of only three suggestions (i.e. different species) can be produced for any single recording. It is also worth noting that both BatClassify and Kaleidoscope Pro base their classifications on search phase echolocation calls and do not account for other vocalisations such as social calls or feeding buzzes (Scott, 2017; Wildlife Acoustics, 2019c).

1.3.3 Acoustic Indices

Despite the numerous approaches that have been tried, the development of automated identification methods remains challenging and results so far have been mixed (Shonfield and Bayne, 2017). Sources of interest in sound recordings may be overlapped by non-target species, smeared by acoustic reflections, degraded by distance attenuation or adverse weather conditions, all of which make them harder to detect (Potamitis *et al*., 2014). Additionally, many studies have focused on automatic ID methods for a small selection of specific species (Stowell and Plumbley, 2014) and, in many cases, insufficient numbers of validated reference libraries of vocalisations are available to build classifiers for species of interest or large numbers of species (Browning *et al*., 2017). Alternative approaches for quantifying acoustic recordings at the community or soundscape level, rather than identifying all the species that occur within them, have therefore been developed and are commonly referred to as acoustic indices (Farina and Gage, 2017). Simply put, acoustic indices are mathematical metrics that have been designed to summarise different aspects (e.g. complexity, diversity, evenness) of acoustic activity within recordings as a whole, rather than focusing on the sounds of particular species (Sueur *et al*., 2014; Doohan *et al*., 2019).

In terms of ecological assessments, the underlying concept of acoustic indices is that the presence of a greater diversity of vocalising species will result in a corresponding increase in the complexity, diversity or intensity of the sounds they produce as a community (Fuller *et al*., 2015; Gasc *et al*., 2016). The Acoustic Niche Hypothesis (ANH; Krause, 1987) proposes that, similarly to physical habitats where limited resources are shared by many species, the medium over which vocalisations are transmitted (sound waves) is also finite, being limited to useable frequencies and hours in the day. ANH suggests it is therefore reasonable to expect vocalising species to partition their limited sonic environment in a similar manner and, over time, to minimise interspecific competition by adapting to occupy vacant frequency and/or temporal niches (Krause, 1987; Figure 1.4). Indeed, some evidence of acoustic niche partitioning has been demonstrated for species of birds, Orthoptera, frogs, Cetaceans and fish (Brumm, 2006; Tishechkin and Bukhvalova, 2009; Amézquita *et al*., 2011; Ruppé *et al*., 2015; Putland *et al*., 2017). Additionally, at least in some bird species, demonstrations of phenotypic plasticity have shown this type of behaviour is not necessarily reliant on evolutionary timescales (Malavasi and Farina, 2013).

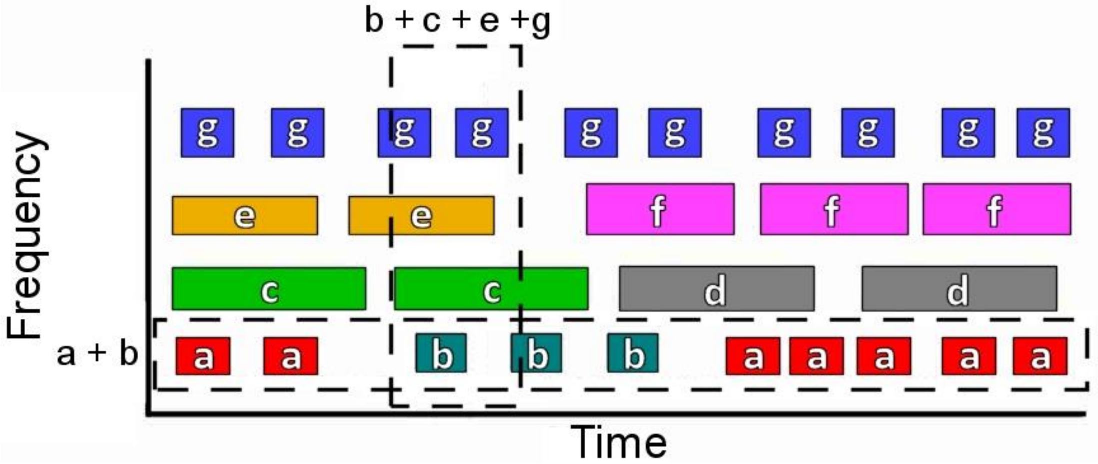


Figure 1.4. Theoretical representation of acoustic niche partitioning for seven hypothetical species (a-g) within the same habitat. The dotted boxes illustrate examples of how species could partition their vocalisation times (a+b) and frequencies (b+c+e+g) in order to minimise interference between them (Farina, 2014).

Along with the acoustic adaptation hypothesis (AAH; Morton, 1975), the theory that a habitat's acoustic characteristics will determine the sounds produced by the vocalising species within it, ANH forms the theoretical basis of ecoacoustics, which is defined as the study of sound to address biological and ecological questions over different spatial and temporal scales (Sueur and Farina, 2015). Acoustic indices, which seek to enumerate various ecological aspects for communities of vocalising species, thus fulfil a similar role to traditional biodiversity indices in ecoacoustics (Eldridge *et al*., 2018) and have become its main tools for analyses (Phillips *et al*., 2018). As acoustic indices consider all the sounds within recordings, they can be susceptible to background noise, wind and rain, and can potentially be influenced by the relative distances, call rates and intensities of vocalising species (Sueur *et al*., 2014; Gage and Farina, 2017). While these issues are similar to those faced by automated species identification, for indices, they could influence the index scores rather than confounding detection and recognition. Nevertheless, they still offer a potentially attractive means of assessing PAM data collected over large spatial and temporal scales as they are computationally-cheap, repeatable, can be processed without specialist skills and can be applied across a range of locations and habitat types (Sueur and Farina, 2015; Farina and Gage, 2017; Buxton *et al*., 2018b). This prospect has encouraged the development of a wide range of acoustic indices and a recent literature review by

Buxton *et al*. (2018b) found 69 unique indices that had been applied to the extraction of biological information in the last ten years. To provide some indication of how indices are calculated and what they represent, four of the more commonly used examples, the Acoustic Complexity Index, Bioacoustic Index, Normalized Difference Soundscape Index and Acoustic Evenness Index, are discussed below.

1.3.3.1 Acoustic Complexity Index (ACI)

The ACI (Pieretti *et al*., 2011) measures the total amount of variability in sound intensity at different frequencies over time within an audio file and is based on the premise that bird songs and other biophonies are more complex than many anthropogenic and geophysical sounds (e.g. traffic noise, running water), which are typically characterised by constant frequencies and intensities. As less complex sounds will produce lower values, ACI therefore aims to minimise the effect of any anthropogenic noise present within the sound file (Pieretti *et al*., 2011). ACI is calculated by dividing the sound file into equally-sized 'boxes' with dimensions in the frequency (y-axis) and time (x-axis) domains and then quantifying the total variation in the audio file based on a matrix of the FFT values for all of the boxes (Pieretti *et al*., 2011; Figure 1.5). As this method produces a cumulative total, longer files will give larger values and it is therefore important to either standardise the length of input files, or to use the ACI/minute value that is also output, when comparing the ACI values of different files (Pieretti *et al*., 2011).

Several studies, predominantly focused on birds, have evaluated whether acoustic indices do indeed offer reasonable representations for any of the ecological aspects they are intended to quantify (Gasc *et al.*, 2016). Generally, these have entailed some form of comparison between index results and typical biodiversity metrics (e.g. species richness, abundance and evenness) that were obtained using traditional methods. Several have found ACI scores were strongly correlated with measures of avian species richness and acoustic community diversity determined by aural inspection of recordings, with higher values where more species were present (Towsey *et al*. 2014b; Buxton *et al*. 2016; Hilje *et al*. 2017). However, it was not always possible to rule out the presence of higher numbers of a dominant species having some influence on results (Buxton *et al*. 2016; Hilje *et al*., 2017). Pieretti *et al*. (2011) and Buxton *et al*. (2018c) also found ACI values were correlated with the number and diversity of avian vocalisations, respectively, when compared to manual counts performed on the same recordings. In comparison to point counts using direct observation, ACI has demonstrated a significant correlation with species richness and even outperformed manual inspection of recordings (wa Maina *et al*., 2016). However, Retamosa Izaguirre *et al*. (2018) found a significant positive relationship between ACI and manual point counts for avian abundance but not necessarily avian diversity.

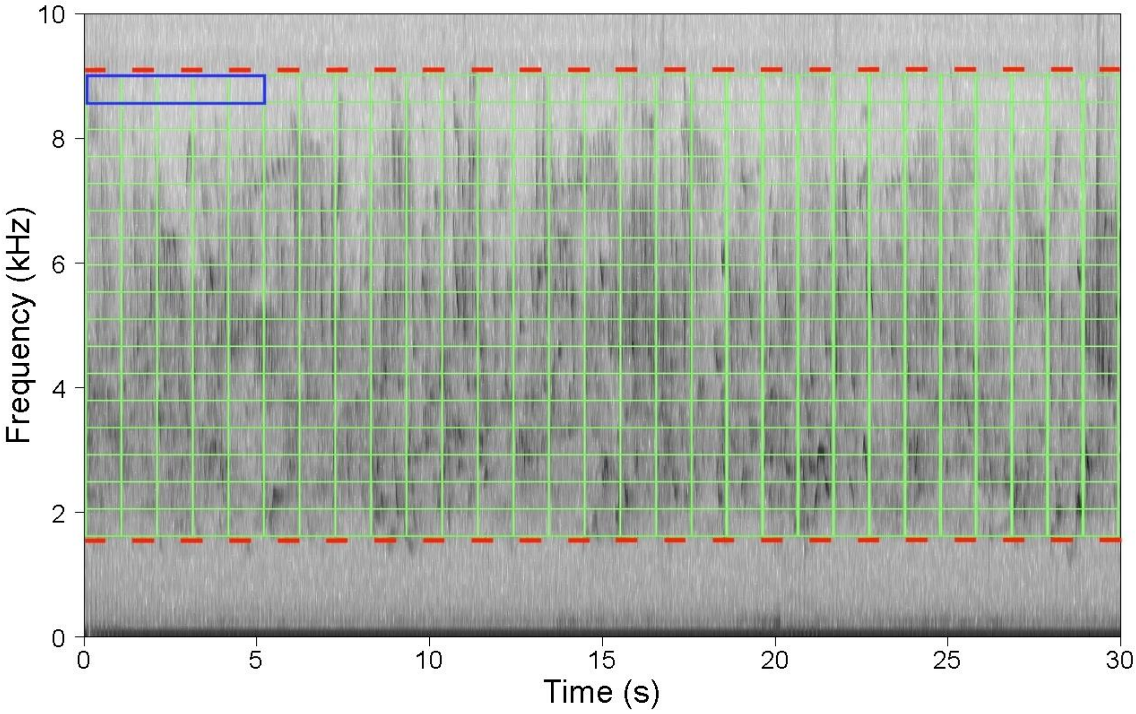


Figure 1.5. Visual representation of how the Acoustic Complexity Index (ACI; Pieretti *et al*., 2011) is calculated. Analysis occurs within the specified frequency range (red dotted lines) by partitioning spectrogram values into 'boxes' of equal size (green boxes) determined by the FFT window size specified (default is 512). For each row, the absolute difference between the FFT value for each box and its neighbour is calculated in turn, and these values are then summed together in clumps, usually 5 seconds in length (blue box). Clump values are added together for each row and the process is then repeated for each row before finally adding all row scores together to obtain a single value for the whole spectrogram. Note that boxes are typically much smaller than shown here; the actual box size using a window length of 512 samples for a 48 kHz recording would be approximately 0.011 seconds (x-axis) by ~94 Hz (y-axis).

Although the way ACI is calculated attempts to account for constant frequency signals typical of anthropogenic noise, Fairbrass *et al*. (2017) found that while ACI was positively correlated with their own biotic diversity and activity metrics derived from spectrograms, it was also positively correlated with anthropogenic noise. Eldridge *et al*. (2018) also found that the correlation between ACI and species richness was stronger for temperate sites in the UK, but weaker for sites in the neotropics. This was likely due to the presence of non-avian taxa (e.g. insects and anurans) within recordings in neotropical Ecuador, as vocalisations by these organisms would also contribute to index values, potentially skewing any comparisons with biodiversity assessments that did not account for this (Eldridge *et al*., 2018). This interpretation seems reasonable, given that acoustic indices are not designed to discriminate between the sounds produced by different vocalising taxa, and could explain why some studies performed in areas with more varied acoustic communities have found weaker or non-significant correlations between indices and measurements of avian diversity (Mammides *et al*., 2017; Buxton *et al*., 2018c; Eldridge *et al*., 2018).

1.3.3.2 Bioacoustic Index (BI)

The Bioacoustic Index (Boelman *et al*. 2007) was conceived as a means of representing avian abundance (total birds per site) by calculating the area under the curve of the averaged frequency spectrum, with frequency on the x-axis and sound level in dB on the y-axis, bounded by the minimum sound intensity within the recording (Figure 1.6). BI offers a relatively simple measure of the total acoustic energy within the frequency range over which analysis is performed and should therefore be tuned to the main frequencies of interest (2-8 kHz by default) that contain bird vocalisations (Boelman *et al*. 2007). It is suggested that this index works best when detection probabilities across species and habitats are fairly constant, as BI does not inherently account for such differences (Boelman *et al*. 2007).

Boelman *et al*. (2007) found significant correlations between BI values and direct measures of avian abundance obtained by manual surveys in Hawaii. Despite being developed as a measure of abundance, of the 26 indices that were compared against aural assessments of the same recordings by ornithologists, Eldridge *et al*. (2018) found that BI was strongly correlated with avian species richness in UK sites, and the density of vocalisations for sites in Ecuador. Fairbrass *et al*. (2017) also found that BI was significantly correlated with biotic activity and diversity; however, like ACI, it was also positively correlated with anthropogenic activity suggesting that some indices may not be well suited to urban monitoring.

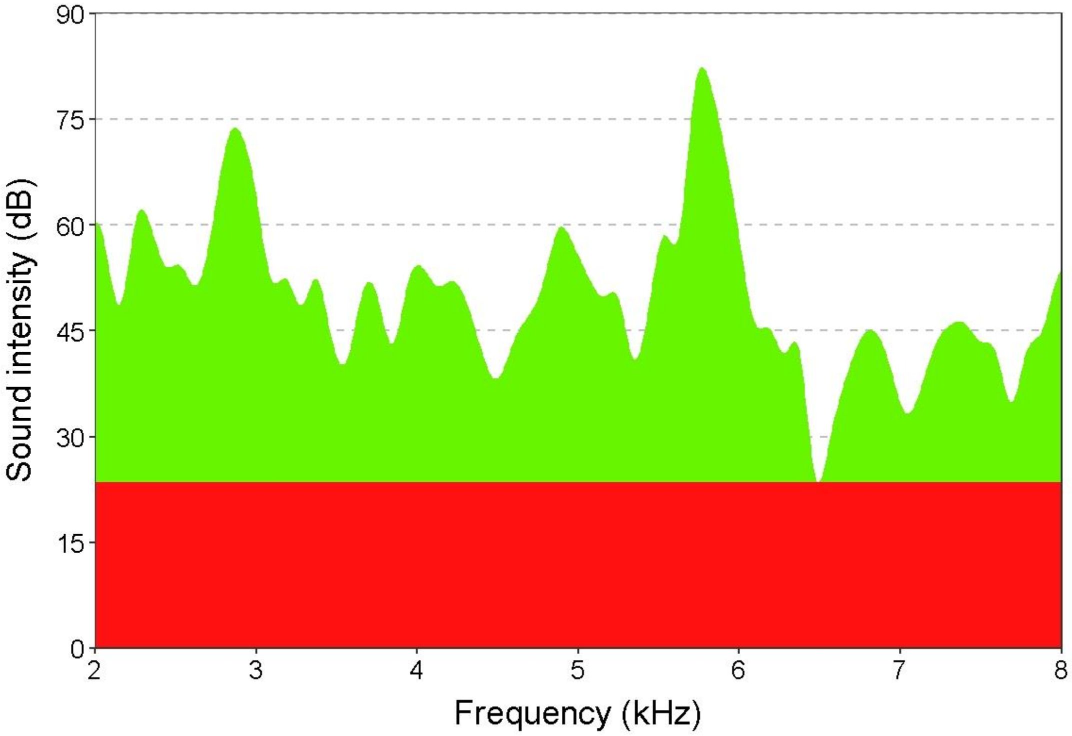


Figure 1.6. Visual representation of how the Bioacoustic Index (Boelman *et al*. 2007) is calculated. The index score is the area under the curve of the average frequency-intensity spectrum of a recording that is above (green area) the lowest level in the recording (red area). This value thus represents a function of both the frequency range and sound intensities of all calls within the recording. Note that digital recordings are normally represented as negative scores in dBFS and need to be converted to equivalent amplitudes in dB before calculation.

1.3.3.3 Acoustic Evenness Index (AEI)

The Acoustic Evenness Index (Villanueva-Rivera *et al*., 2011) divides the spectrogram of an audio file into several equally sized frequency bands, typically in steps 1 kHz wide, up to a maximum specified frequency, which is 10 kHz by default. The total amount of sound energy contained within each frequency band above a specified amplitude (default = -50 dBFS) is calculated and then normalised to the level of the frequency band with the most energy (Villanueva-Rivera *et al*., 2011). All the frequency band values are then used as input to calculate their Gini coefficient (Gini, 1971), which represents how evenly acoustic energy is distributed across the frequency spectrum (Villanueva-Rivera *et al*., 2011). As the scale represents evenness, and is normalised, values closer to one thus represent the presence of similar amounts of acoustic energy in all frequency bands, while values closer to zero occur when the majority of acoustic energy is limited to one or two bands (Villanueva-Rivera *et al*., 2011).

The concept behind AEI is that environments with higher biodiversity are likely to contain more species vocalising across the entire frequency range, thus producing more evenly balanced soundscapes; alternatively, degraded soundscapes should contain more gaps, where vocalising species are missing, across the frequency range and will thus be less even (Villanueva-Rivera *et al*., 2011). The AEI, and the Acoustic Diversity Index (ADI; Villanueva-Rivera *et al*., 2011) which is essentially an inverse function of AEI based on Shannon Entropy, have exhibited strong (Machado *et al*., 2017; Eldridge *et al*., 2018) to moderate (Mammides *et al*., 2017; Jorge *et al*., 2018) correlations with bird species richness. Acoustic Entropy (*H*; Sueur *et al*., 2008a), another index that quantifies acoustic activity as a measure of entropy, has also demonstrated positive correlations with bird species richness (Joo *et al*., 2011; Fuller *et al*., 2015). However, careful interpretation is required for indices that quantify evenness, and also entropy, as soundscapes at opposite ends of the spectrum (i.e. silence and saturation) could produce similar results (Eldridge *et al*., 2018).

1.3.3.4 Normalized Difference Soundscape Index (NDSI)

The NDSI (Kasten *et al*., 2012) was designed to estimate the amount of human-generated noise within a soundscape and includes a frequency band, from 1 to 2 kHz by default, specifically to account for this. The power spectral densities of this 'anthropogenic' band, and for 1 kHz bins across the frequency band where most biophony typically occurs (2 to 8 kHz), are calculated (Kasten *et al*., 2012). NDSI is then computed as a ratio of (biophony - anthrophony) / (biophony + anthrophony) using the value of the anthropogenic band and the largest 1 kHz bin value calculated for the biophony frequency band (Kasten *et al*., 2012). The resulting index scores are automatically scaled from 1 to -1; where 1 represents the complete absence of anthrophony and lower values indicate increasingly higher levels of anthropogenic noise intrusion (Kasten *et al*., 2012).

Despite being created with the intention of measuring anthrophony, Fuller *et al*. (2015) reported a significant correlation with bird species richness and Fairbrass *et al*. (2017) also found that NDSI was significantly correlated with biotic diversity. However, as NDSI calculations do not discriminate between the sources of sounds in each band, the presence of bird species with low frequency calls occurring within the anthropogenic noise band can result in lower NDSI values (Kasten *et al*., 2012; Eldridge *et al*., 2018).

General observations suggest that indices are best suited to assessments of birds where they are the predominant, or preferably only, vocalising taxa. Index results from urban environments and during adverse weather conditions should also be treated with caution or even avoided where possible. This is not particularly surprising when, as demonstrated by Figures 1.5 and 1.6, any sounds occurring within the frequency ranges under analysis will be included within index calculations. Some discrepancies are naturally more likely to occur when comparing counts of birds with index results based on the sounds made by birds plus any additional sounds originating from non-avian, or even non-biotic, sources. Furthermore, while there is some general evidence that acoustic indices are correlated with various aspects of avian diversity, there is also some variation regarding which indices best represent which particular aspects with no single index consistently outperforming all of the others. One possible explanation for this is that indices may not necessarily represent a single, typical measure of either richness or abundance, but rather some combination of the two (Buxton *et al.*, 2018c). For example, Buxton *et al*. (2016) and Hilje *et al*. (2017) both reported that ACI values increased with species richness and the abundance of a vocally dominant species. The presence of more individuals of a particular species and the presence of more species vocalising both potentially contribute to a fuller or more complex soundscape, which could be especially true for birds, who can adjust their song timing to reduce interspecific overlap (Brumm, 2006).

1.4 Applications of PAM for Studying Habitat Management Effects

The following discussion focuses on previous applications of PAM in terrestrial environments that have assessed the effects of habitat and conservation management practices similar to those in this study: the impact and control of invasive species, managing tree species richness for bird diversity and rewilding disused land for conservation.

1.4.1 Invasive Species

Invasive non-native species pose a significant threat to biodiversity and ecosystems across the globe with the prospect that increasing globalisation will further exacerbate this situation (Early *et al*., 2016). However, the impacts of invasive plants are not necessarily uniform or negative across native taxa and more information is needed to address current gaps in knowledge (Schirmel *et al*., 2016). Studies using PAM to investigate the possible impacts of invasive species have mostly focused on animals which vocalise, either using their vocalisations to assess their effect upon the native acoustic community (e.g. Hu *et al*., 2009; Farina *et al*., 2013; Taylor *et al*., 2017) or for pest detection (QUT, 2016). Examples of using PAM to assess the effectiveness of invasive species management strategies by monitoring the disturbed species, rather than the invasive, also exist but are less common. Buxton and Jones (2012) used PAM to investigate how the removal of an introduced predator, the Arctic fox (*Alopex lagopus*), affected the activity of nocturnal seabirds on islands from which foxes had been removed over the course of several years in the Aleutian Archipelago. The translocation of a native bird species, the hihi (*Notiomystis cincta*), from areas with invasive predators into locations from which they had been removed or excluded, has also been monitored using PAM to assess post-release dispersal behaviour and territory establishment (Metcalf *et al*., 2019).

PAM has only occasionally been used to study the indirect effects of invasive plants on native species, usually bats. The effect of clearing invasive vines and trees (*Cinnamomum verum* and *Tabebuia pallida*) that were obscuring the roosting and foraging sites of Seychelles sheath-tailed bats (*Coleura seychellensis*) was evaluated by Gerlach (2009; 2011) with a combination of PAM and closed-circuit television. Welch *et al*. (2016) assessed whether decreased resource availability due to invasive feral goats (*Capra hircus*) and lantana shrub (*Lantana camara*) affected the activity of Pacific sheath-tailed bats (*Emballonura semicaudata rotensis*). While there was no evidence of reduced activity in areas browsed by goats, these authors did find that the bats tended to avoid areas dominated by lantana and, consequently, made a strong recommendation for its management. These studies illustrate the potential for monitoring the indirect effects of exotic plants, as well as vocalising invasives, on native species. Welch *et al*. (2016) called for more studies of this kind and, in Chapter 3, an investigation is performed to assess whether *Rhododendron ponticum*, an invasive shrub in the UK, indirectly affects the activity of native bat species.

1.4.2 Tree Species Richness and Composition

While natural forest cover continues to decline globally, plantation forests have increased, accounting for around 7% of global forest cover and constitute the main type of forest in numerous countries (Irwin *et al*., 2014). Although plantations are generally considered to have lower biodiversity than natural forests, the implementation of effective management strategies can improve this situation for taxa such as birds (Castaño-Villa *et al*., 2019). For instance, forest stands composed of several tree species, and mixed conifer-deciduous forest stands in particular, typically have higher levels of avian abundance and species richness than pure conifer plantations (Peck, 1989; Donald *et al*., 1998; Poulsen, 2002; Diaz, 2006; O'Connell *et al*., 2012). Irwin *et al*. (2014), and Donald *et al*. (1998), also noted that coniferous plantations and broadleaf forests hosted different communities of bird species, and that combinations of the two could enhance bird species richness. However, only Peck (1989) recorded specific tree species preferences for the birds in their survey. Nevertheless, all these studies agreed that planting more species of trees and admixing conifer and deciduous species offered potentially important strategies for improving bird diversity and abundance in commercial forest plantations. Indeed, a recent meta-analysis of 123 case studies (Castaño-Villa *et al*., 2019) identified the use of native tree species and mixed forest stands rather than monocultures as key management strategies for improving bird diversity in forest plantations.

At present, studies utilising PAM to investigate the effect of tree species richness and composition are quite rare for birds. The effect of tree species richness was examined using acoustic indices, with the predominant focus on birds, as part of a study in olive groves by Myers *et al*. (2019) who did not find any significant relationship between index values and tree species richness. Klingbeil and Willig (2015) deployed ARUs to measure bird species richness at twenty sites in coniferous and deciduous forests in the USA; however, the main focus of their study was to compare the performance of point counts with PAM and, although they examined the effect of some site characteristics such as canopy cover and elevation, they did not consider tree species composition. In the UK, Turner *et al*. (2018) calculated five acoustic indices for dawn choruses they manually recorded on several dates at 73 sites in lowland coniferous plantation and compared the results with a range of stand characteristics. These authors found AEI (lower values) and ADI (higher values) were significantly correlated with stand age, higher tree species richness and diversity, and more canopy cover, while more open sites, closer to the forest edge and with less canopy cover, were correlated with higher ACI values (Turner *et al*., 2018). In Chapter 4, PAM and acoustic indices are used to compare how the acoustic activity of avian communities differs between monocultures and mixtures with different species of deciduous and coniferous trees.

1.4.3 Rewilding Habitats

Rewilding is becoming an increasingly prominent form of land management which generally aims to increase overall biodiversity, rather than focusing on specific species or habitats, and create more self-sustaining ecosystems (Sandom *et al*., 2019). With approaches varying from simply abandoning land to reintroducing large carnivores and/or herbivores, rewilding encompasses a range of passive and active practices employed to restore habitat, ecosystem processes and functional communities at the landscape level (Sandom *et al*., 2019). The development and adoption of appropriate methods for monitoring and assessing rewilding projects is considered to be crucial for maximising outcome benefits and improving implementations (Torres *et al*., 2018).

To assess the effectiveness of rewilding projects, PAM could be employed to monitor the reintroduced species themselves, for example wolves (Root-Gutteridge *et al*., 2014) and bison (Wyman *et al*., 2012). In addition, there is the potential for using PAM to assess the effects of rewilding by monitoring resulting changes in the habitats modified by the reintroduction of species. Other than the suggestion that PAM could be used to monitor the effects of trophic rewilding on cicadas and Orthoptera (van Klink and WallisDeVries, 2018), there do not appear to be any examples where PAM has specifically been considered for assessing the progress or performance of any rewilding projects. The rewilding of uneconomical agricultural land, an example of which is examined in Chapter 5 of this study, is likely to become an increasingly relevant and important topic with calls to implement two-tier, agri-environmental policies that rewild less-productive farmland and focus food production on more suitable land (Merckx and Pereira, 2015). Performing an evaluation of the habitats created by rewilding with PAM thus presents the opportunity to combine these emerging approaches.

1.5 Study Organisms

1.5.1 Bats

Bats are recognised as important bioindicators and can provide key ecosystem services, such as biological pest control (Jones *et al*., 2009). Although the most recent national survey by the Bat Conservation Trust suggests populations of most UK species surveyed have remained stable or demonstrated some degree of recovery since 1999, bat populations in Western Europe have declined significantly during the last century (BCT, 2018). Bats, and their roosts, are consequently protected from harm or disturbance under UK and European law (DEFRA, 2015). Agricultural intensification, which has led to reduction in favourable habitat (e.g. hedgerows, ponds and copses) and prey availability through pesticide use, is believed to be the main cause of bat decline in the UK (Wickramasinghe *et al*., 2003), while roads, pollution, degraded water quality, urbanisation, light pollution and wind farms can also have deleterious impacts on bats (Jones *et al*., 2009).

Bats are highly mobile, and some species can travel over ten kilometres per night when foraging (Altringham, 2014); landscape-scale characteristics are therefore likely to influence bat activity (Fuentes-Montemayor *et al*., 2017). However, local-scale habitat characteristics such as vegetation structure can also have a significant influence on bats (Froidevaux *et al*., 2016; Lacoeuilhe *et al*., 2018). All UK bat species are insectivores and prey on a variety of flies, moths, beetles, spiders, lacewings and other invertebrates, which can be caught in several different ways: on the wing (aerial hawking), from a perch (flycatching), taken from water surfaces (trawling) or taken from vegetation and other surfaces (gleaning) (Altringham, 2014). Over time, insectivorous bats have evolved wing morphologies and echolocation calls that favour their hunting strategies and the habitats in which they forage (Denzinger and Schnitzler, 2013). Indeed, several studies have found correlations between wing morphology and echolocation call characteristics, and between these characteristics and preferred foraging spaces (e.g. Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Siemers and Schnitzler, 2004; Figure 1.7).

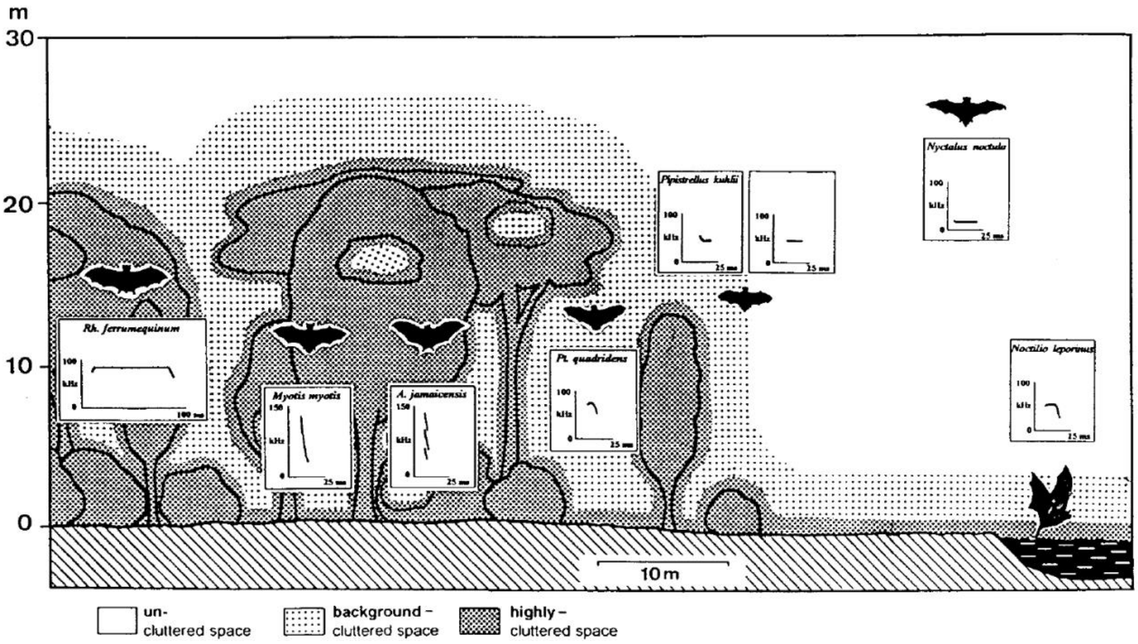


Figure 1.7. Diagram of foraging habitats classified according to clutter space, shown with representative wing morphologies and echolocation search signals of associated European bat species. Uncluttered space is open and distant from vegetation, background cluttered, or edge, space is close (within ~5 m) to the ground, water or vegetation, and highly cluttered space represents areas where prey are very close to, or on, surfaces so that echolocation return signals from prey and background clutter overlap (Schnitzler and Kalko, 2001).

Eighteen bat species are known to be resident in the UK (Table 1.2), although only a single Greater Mouse-eared bat (*Myotis myotis*) has been confirmed as resident at present (BCT, 2018). Bats in the UK typically spend November to February in hibernation or deep torpor (bats also enter a lesser torpor during active months to save energy in the daytime) and start to emerge from March onwards, depending on weather conditions and food availability (Altringham, 2014). From April to May, pregnant females will start to congregate in maternity roosts, usually giving birth in June or July (Collins, 2016). Pups grow rapidly, making their first flights within two to three weeks after birth and are weaned at six to nine weeks of age (Altringham, 2014). Females disperse to find mates in late summer/early autumn, once their current young have become independent (Collins, 2016). Swarming behaviour also occurs at this time of year, before bats return to hibernation, and may be related to the selection of hibernacula (van Schaik *et al*., 2015), mating (to ensure gene flow between colonies; Rivers *et al*., 2005) and/or for other social purposes (Burns and Broders, 2015). Temperate bat species rely completely on pre-existing roost spaces (Dietz and Kiefer, 2016). In addition to maternity roosts and hibernacula, roosts are used for resting and/or shelter, feeding, mating, swarming, and as satellite roosts, which are alternative maternity roosts that are close to the main maternity roost (Collins, 2016).

Table 1.2. Wing morphologies, echolocation call characteristics, and foraging strategies and habitats of UK bat species. Data from Altringham (2014)[1], Müller *et al*. (2012)[2], Lučan *et al*. (2009)[3], Jan *et al*. (2010)[4], Razgour *et al*. (2011) [5], Dietz *et al*. (2006)[6]

Species name	Wing loading /aspect ratio[i]	Echolocation call bandwidth/duration[ii]	Foraging space	Foraging strategy[iii]
Barbastella barbastellus[1]	M / L	N / S	Edge	H
Eptesicus serotinus[1,2]	H / M	N / L*	Open/Edge	G **H**
Myotis alcathoe[3,4]	L / L	B / S	Open/Closed	G H
Myotis bechsteinii[1,2]	M / L	B / S	Edge/Closed	F **G** H
Myotis brandtii[1,2]	L / L	B / S	Edge/Closed	G **H**
Myotis daubentonii[1,2]	M / H	B / S	Edge	**T** H
Myotis mystacinus[1,2]	L / M	B / S	Edge/Closed	G H
Myotis nattereri[1,2]	L / M	B / S	Edge/Closed	G **H**
Nyctalus leisleri[1,2]	H / H	N / L*	Open	H
Nyctalus noctula[1,2]	H / H	N / L*	Open	H
Pipistrellus nathusii[1,2]	H / H	B** / L*	Open/Edge	H
Pipistrellus pipistrellus[1,2]	M / H	B / S**	Edge	H
Pipistrellus pygmaeus[1,2]	M / H	B / S**	Edge	H
Plecotus auritus[1,2]	L / L	B / S	Closed	**G** H
Plecotus austriacus[1,5]	M / M	B / S	Open	H
Rhinolophus ferrumequinum[1,6]	H / M	N / L	Open/Edge/Closed	F G **H**
Rhinolophus hipposideros[1,6]	L / L	N / L	Edge/Closed	G H

[i] Loading values: L = Low (5.5 to 7.5 Nm^{-2}), M = Medium (7.6 to 9.5 Nm^{-2}), H = High (>9.5 Nm^{-2}). Aspect ratio values: L = Low (5.5 to 6), M = Medium (6.1 to 6.5), H = High (>6.5)

[ii] N = narrowband, B = broadband, L = long duration (>7 ms), S = short duration (<7 ms). *Broader/shorter calls in edge space **Narrower/longer calls in open

[iii] F = Flycatcher, G = Gleaner, H = Aerial hawker, T = Trawler. **Bold** = primary strategy if stated

Assessments of UK bat populations, their distribution and ecology have been complicated by the presence of several cryptic species; whiskered bats (*Myotis* *mystacinus*) and Brandt's bats (*Myotis brandtii*) were not identified as separate species until the early 1970s (Hanák, 1970) and Alcathoe bats (*Myotis alcathoe*) were only confirmed as resident in 2010, although a previously misidentified individual had been ringed in the UK seven years earlier (Jan *et al*., 2010). Even the UK's two most abundant species, the common pipistrelle (*Pipistrellus pipistrellus*) and the soprano pipistrelle (*Pipistrellus pygmaeus*) were classified as a single species until 1999 (Jones and Barratt, 1999). This situation has created gaps in our ecological knowledge of such species, particularly their habitat preferences and activity patterns (Bartonička *et al*., 2008), which this study may help to address.

1.5.2 Birds

Being widely distributed over a range of landscapes, relatively easy to detect and taxonomically well-known, birds have many intrinsic characteristics that make them attractive for monitoring environmental changes (Farina *et al*., 2011a). Indeed, many organisations (e.g. UNEP, RSPB, Birdlife International) believe birds alone can provide useful indicators of biodiversity, environmental health and changes, and have established biodiversity indices based purely on birds (e.g. the Global Wild Bird Index) (Sheehan *et al*., 2010). As birds are the vocally dominant species in many ecosystems, PAM applies itself particularly well to the study of birds with the possibility of advancing ornithological research and conservation efforts (Gasc *et al*., 2016).

PAM offers particular benefits for surveying cryptic and nocturnal birds such as owls, which are often missed by daytime surveys (Freeman *et al*., 2007); however, not all bird species are necessarily good candidates for acoustic-based surveys (Darras *et al*., 2018) and comparisons with traditional point counts have highlighted certain types of birds, which do not sing, are generally non-vocal or vocalise sporadically (e.g. waterfowl, birds of prey, woodpeckers and hummingbirds), that are repeatedly missed or underrepresented by surveys performed using ARUs (Haselmayer and Quinn, 2000; Hutto and Stutzman, 2009; Klingbeil and Willig, 2015; Kułaga and Budka, 2019). Furthermore, short and structurally simple vocalisations, such as those made by waterfowl, contain fewer distinct features that can potentially be used to train and develop automated classifiers (La and Nudds, 2016).

For the temperate habitats in England and Germany surveyed by this study, the predominant source of avian vocalisations detected by PAM is likely to be from passerines (Depraetere *et al*., 2012; Klingbeil and Willig, 2015), which generally have the most complex songs (Potamitis *et al*., 2014) and constitute approximately half of all bird species worldwide (Stowell and Plumbley, 2010). Singing activity of passerines in temperate zones is generally highest in the breeding season (March to July), peaking in spring when males are establishing territories and attracting mates (Catchpole and Slater, 2008), when it is recommended to perform surveys of resident songbirds (Buckland *et al*., 2008). Performing surveys during the dawn period offers an additional means of detecting the maximum number of species (Wimmer *et al*., 2013).

1.6 Thesis Aims

The overall aim of this thesis is to explore the potential of PAM for assessing the effects of different habitat management practices on bird and bat activity and diversity. Specific objectives of the thesis are: I) to develop and produce an affordable, autonomous recording device suitable for recording of both audible and ultrasonic frequencies; II) to assess the effects of forest understorey invasion by a non-native shrub on different bat species and the consequences of invasive species removal; III) to explore the effects of tree species diversity and tree species composition on bird species richness, and IV) to compare bat and bird communities in different habitat types within a rewilding project on former agricultural land, onto which a varied assemblage of mammalian herbivores has been introduced.

1.7 Thesis Outline

Chapter 2 discusses the process undertaken to design, create, evaluate and deploy the ARUs used in Chapters 3 and 5, and additionally examines the effects of sound attenuation when recording different frequencies and bird calls.

Chapter 3 assesses how the colonisation by, and removal of, invasive *Rhododendron ponticum* in the woodland understorey of Richmond Park, London, influences the activity levels of different bat species and introduces a novel method of analysing temporal activity patterns.

Chapter 4 investigates how tree species diversity and composition in forest plots in Hainich National Park, Germany, influence bird diversity and abundance by comparing acoustic indices in mixed- and single-species stands.

Chapter 5 examines how different habitat types created by free-roaming mammalian herbivores at the Knepp Castle Estate, West Sussex, influence bat activity and bird species diversity.

In Chapter 6, I critically review my findings and discuss their implications for the use of PAM and habitat management practices. I also provide recommendations and ideas for potential future research directions.

CHAPTER 2

2. Sound Recording Equipment

2.1 Introduction

Although purpose-built recorders (e.g. Wildlife Acoustics SM3BAT) presented the most convenient option for acoustic surveys, they were prohibitively expensive, and it was therefore necessary to design and build suitable equipment. Indeed, improving the sensors and quantification techniques used to capture and analyse sound recordings is regarded as an important area of research (Pijanowski *et al.*, 2011b). This chapter details the process and considerations involved in the production of a cheap, yet effective, piece of field equipment capable of gathering data for the purpose of this study. Playback surveys were also performed at several sites in Richmond Park on the 16th and 24th of August 2016, to assess the attenuation of bird calls and of pure tone frequencies over different distances.

2.2 Recording Equipment Design and Construction

At £216 for the basic unit without a case, the RPA2 Bat Recorder (Peersonic, 2016) was chosen as the most affordable option to record bats. The RPA2 uses SDHC cards (up to 32 GB) and can be powered externally by USB battery. Rather than constantly recording, it is triggered automatically, capturing sounds up to 192 kHz as WAV files over a pre-set duration of between 5 seconds and 4 minutes. To preserve battery life and avoid wasting data capacity during times when no bat activity occurs (i.e. daytime), the RPA2 is equipped with a sleep mode.

For non-ultrasonic audio, the original plan to use digital voice recorders to store data proved to be unfeasible. Most voice recorders evaluated were either limited to SDHC card (32 GB) capacity and/or could only record in stereo, thus doubling the size of any files generated. However, calculations showed that SDXC (64 GB capacity) cards and mono recording would be necessary to store 7 days of continuous data. Recorders with both these attributes (e.g. Tascam DR-70D) were more expensive (£200+) and consumed more power. For these reasons, a design known as the Solo (Whytock and Christie, 2016) was chosen for its low power consumption and high data capacity. The Solo software is open source and the units were built using a Raspberry Pi A+, Cirrus Logic audio card (CLAC) and PiFace clock module (used to time-stamp recordings). With a total cost of approximately £65, the Solo also presented an extremely cost-effective solution.

RPA2 units were supplied with an inbuilt ultrasonic MEMS (Micro-ElectroMechanical Systems) microphone but a separate external microphone, in conjunction with the Solo, was required for recording audible frequencies. The EM172 omni-directional, electret condenser microphone capsule (Primo, 2011) was selected based on its performance (-28 dB ± 3 dB sensitivity (ref: 1 kHz, 0dB = 1V/Pa), maximum input = 122 dB, SNR 80 dB), low cost (<£30) and small size. Although Wildlife Acoustics do not specifically state they use EM172s in their equipment, these specifications are very similar to the microphone supplied with the Song Meter SM4 (Wildlife Acoustics, 2016). Microphone capsules were ordered pre-fitted with a 30 cm cable and 3.5 mm jack. A custom, waterproof housing used to mount the microphone externally was also developed with the help of the supplier.

The RPA2 microphone is supplied fitted to the main board so that it could not be positioned at the front of any case without some modification. Fortunately, the microphone is plugged into 10 (2 x 5) 2.54 mm pin sockets and could be removed with care. This enabled 20 cm male/female jumper cables to be connected between the MEMS module and the system board, allowing the microphone to be placed as required (Figure 2.1).

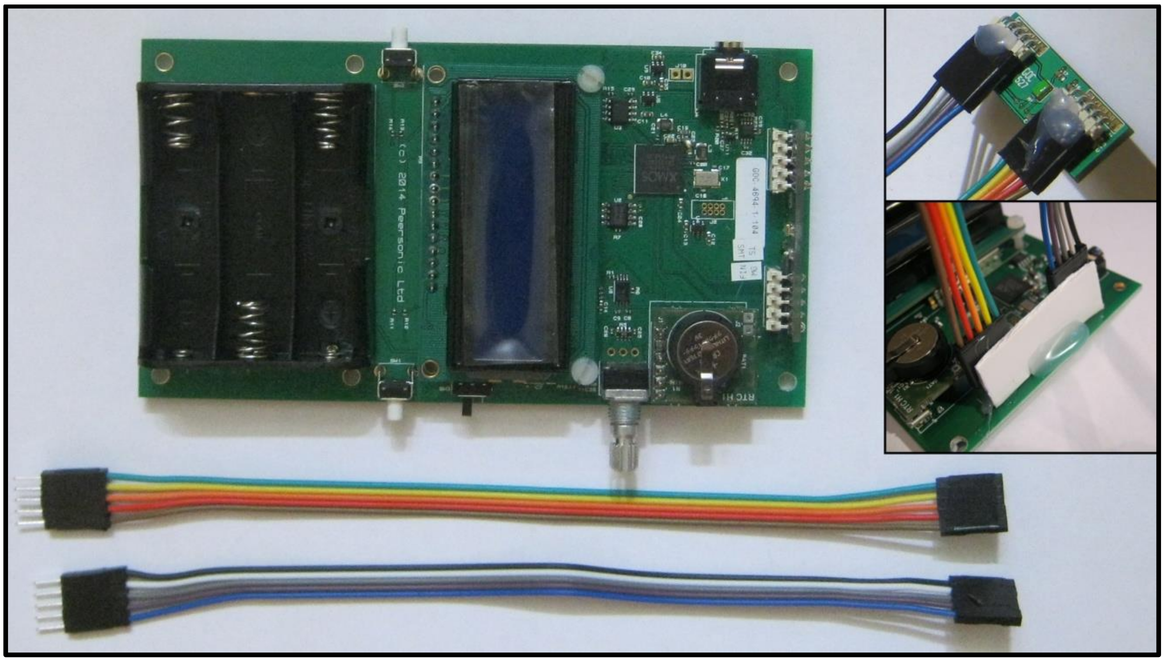


Figure 2.1. The RPA2 ultrasonic microphone was removed from the main board and re-connected via 10 jumper cables so that it could be correctly positioned within the case. Cables were secured at each end using hot glue and braced with plastic card (inset).

For convenience and to reduce costs, it was decided to fit both recorders within the same case (Figure 2.2a), rather than creating separate bird and bat units. An IP67 certified (watertight and dust proof) hard case, the MAX004 (350 x 230 x 86 mm) (Plastica Panaro S.R.L., Modena, Italy), was selected to protect the equipment inside from the elements. However, attaching the case securely to trees and enabling sound to reach the microphones necessitated making some holes in the case (see below). The case was spray-painted in camouflage colours (Figure 2.2b), to help it blend in with its surroundings and reduce heat absorption, and fitted with a combination padlock to prevent theft or tampering. It was decided to name the combined device as the AURITA (Audible and Ultrasonic Recording In TAndem).

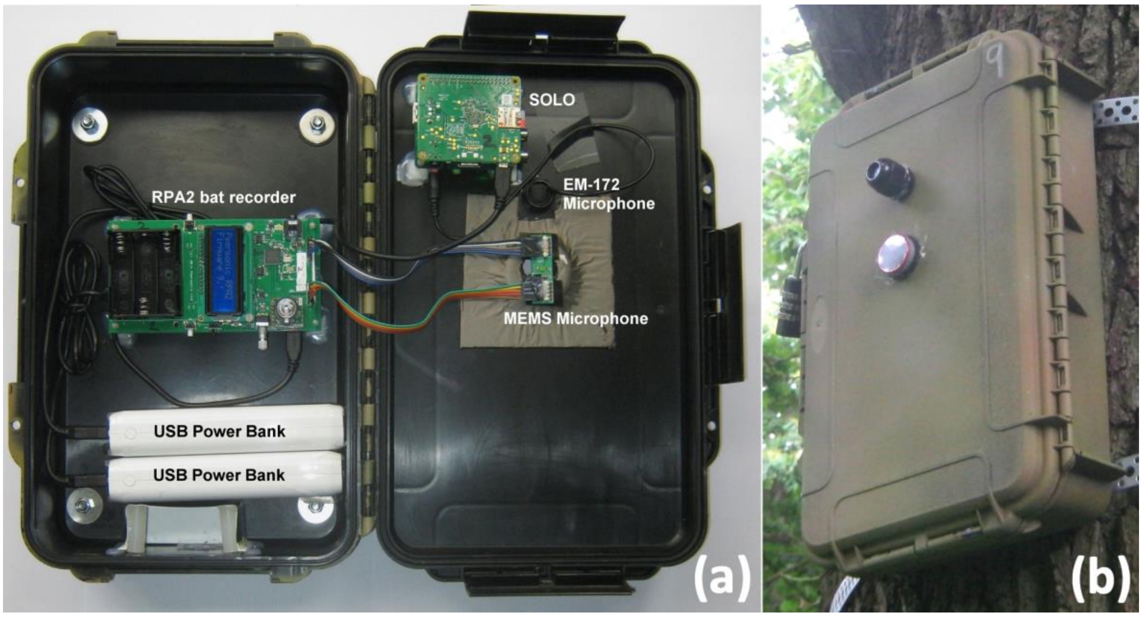


Figure 2.2. (a) Internal layout of the AURITA and (b) an AURITA attached to a tree in Richmond Park.

Each AURITA is powered by two USB power banks, one each for the RPA2 and Solo. Popular for charging mobile phones and other portable devices, the largest capacity available at the time of design was 26,800 mAh (3.7V). Most USB power banks have an energy saving feature that switches the battery off when power usage falls below a certain limit. Unfortunately, when the RPA2 goes into sleep mode, its power usage fell below this limit and the battery would turn itself off, rendering the unit inoperable. With the help of Peersonic, this issue was eventually solved by soldering an 82-ohm load resistor to a USB connector. When connected, this drew enough power (60 mA) to stop the power bank switching itself off but still used less energy than would be necessary to keep the RPA2 awake all day.

In 2017, four AURITA units were converted to use car batteries as their power source. This was achieved using 12 V to 5 V DC converters fitted with crocodile clips and dual USB outputs (Figure 2.3a) to provide a suitable voltage for the recording devices. Due to their size and mass, car batteries had to be stored on the ground in waterproof boxes and connected to the AURITA using 3 m micro-USB cables, housed within a plastic conduit to prevent animal damage and maintain a waterproof seal between the AURITA and the battery box. The use of car batteries has previously been suggested by other authors (e.g. Whytock and Christie, 2016); however, the configuration described above enabled the recording unit itself to be mounted off the ground (Figure 2.3b), thus avoiding any attenuation due to ground reflections. Although this configuration is still unsuitable for public areas, a single 45 Ah 12 V car battery is capable of powering both the Solo and RPA2 units for a period exceeding 19 days while costing less (~£25) than a single USB power bank.

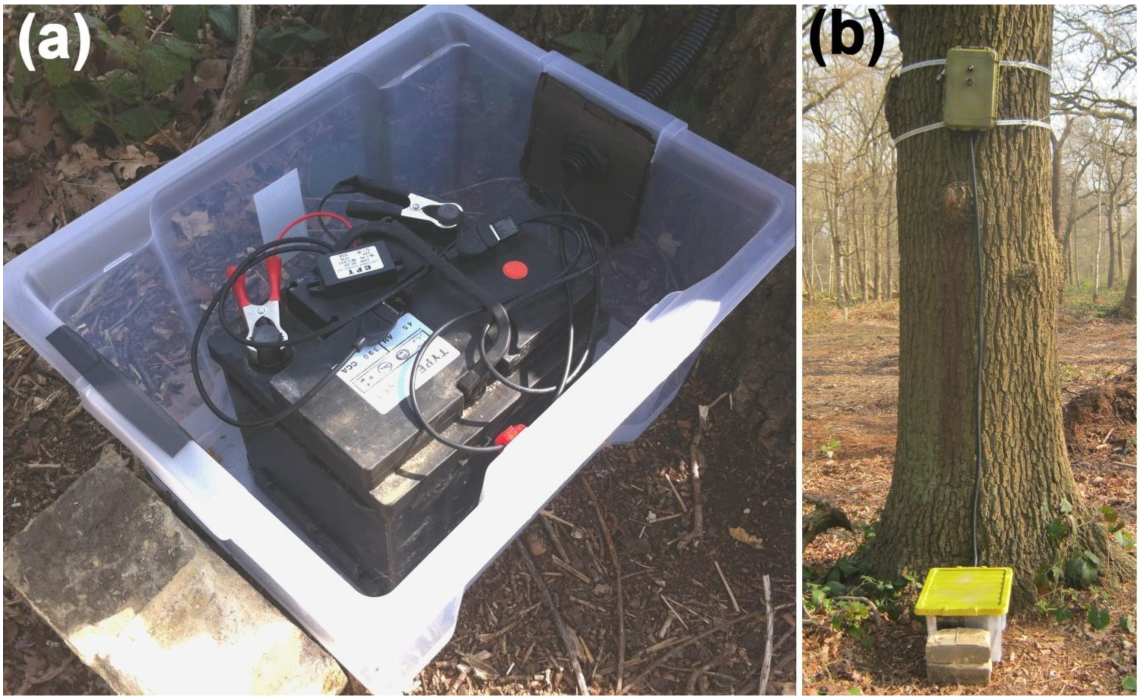


Figure 2.3. (a) Alternative power configuration using a car battery and a 12 V to 5 V DC converter fitted with USB connectors, housed within a waterproof box enabled power to be supplied to a tree mounted AURITA unit (b) via a plastic conduit tube.

To obtain recordings, microphones must either be mounted externally or provided with some form of opening to allow sound in. The EM172 was mounted externally using a custom housing, mentioned earlier. Although this prevents water from entering the case, the EM172 itself is not considered waterproof (Roast 2016, pers. comm., 7 June). As possible choices to help protect microphones from the elements, Saati HD15 acoustic fabric (Saati S.p.A., Via Milano, Italy) and cling film were evaluated as follows. Pure tones in one kHz increments, from 1 to 22 kHz, each 10 seconds in duration, were generated and recorded to CD. Two AURITA units were placed equidistant (2 m), and at the same height and facing, to the playback speaker (Technics SB-DV280) with one AURITA offset slightly left of the speaker and the other offset an equal distance to the right. Sine wave playbacks were simultaneously recorded by both units; one without any microphone covering and the other alternately covered with cling-film or acoustic fabric. As the room's shape and the surfaces within it were not perfectly symmetrical, recordings were repeated with each covering being positioned both left and right of speaker. Readings were then averaged to account for any acoustical bias due to positioning. The middle eight seconds, when recordings were most stable, of sine waves recorded at each frequency were analysed with the frequency analysis tool (Hanning window, window length = 2048) in Audacity® v2.1.2 (Audacity Team, 2016) to find their average spectral density. As analysis bins did not necessarily fall on the exact frequency of interest, results were interpolated to obtain measurements for the specific playback frequencies. The comparative performance of both materials is presented in Figure 2.4.

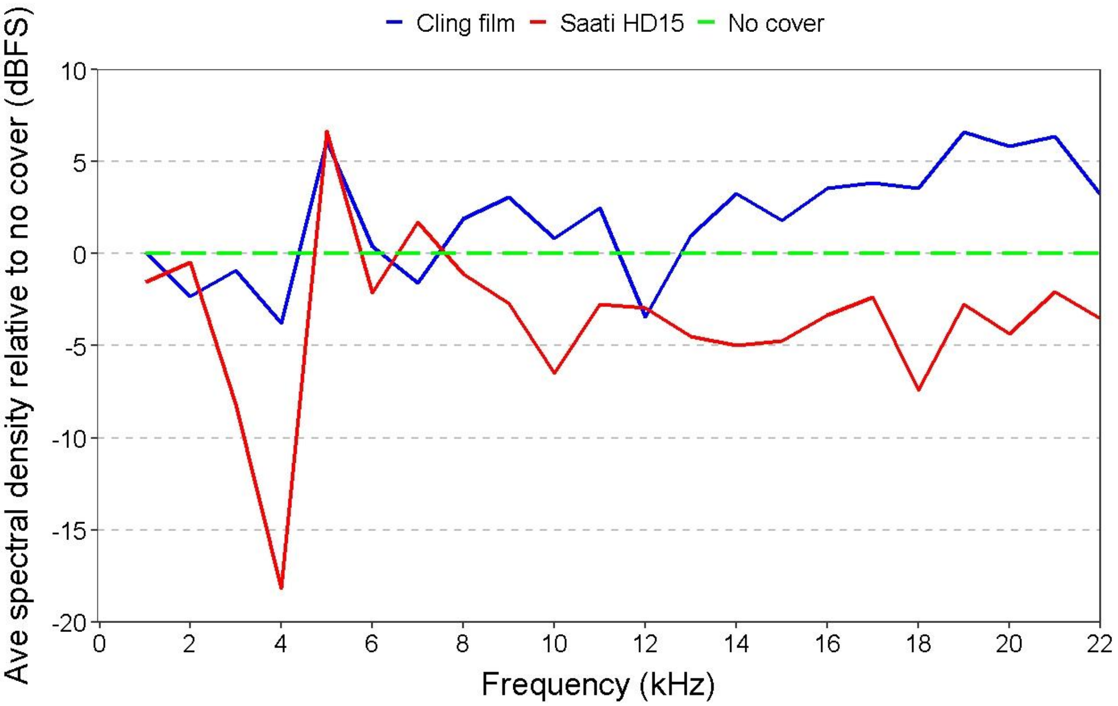


Figure 2.4. Average power spectral densities of sine waves recorded through cling film and Saati HD15 acoustic fabric, using identical AURITA devices. Levels are shown relative to a baseline of 0 dBFS, the level of recordings obtained with no microphone covering.

Results indicated that cling-film outperformed the Saati acoustic fabric and, at higher frequencies, additionally appeared to demonstrate some additional free gain in comparison to no covering. This phenomenon is potentially attributable to the acoustic properties of circular membranes, which act as good sound radiators and have multiple modes of vibration (Open University 2007). As attenuation was also less than 4 dB whenever levels recorded through cling-film were lower than using no covering, it was decided that its use would not adversely compromise recording quality.

It was not possible to perform this test for ultrasonic frequencies due to the lack of appropriate equipment and so, as there were precedents for its successful use in other studies (e.g. Pearce and Walters, 2012) and it had also been recommended by Peersonic (Flory 2016, pers. comm., 25 May), cling film was also used for bat detectors. As the RPA2 ultrasonic microphone is mounted on a small circuit board, a different mounting strategy was required. Cling film would have to be held in place so that it remained taut and secure over any opening yet could also be easily replaced in-situ if damaged. This was achieved using the design detailed in Figure 2.5.

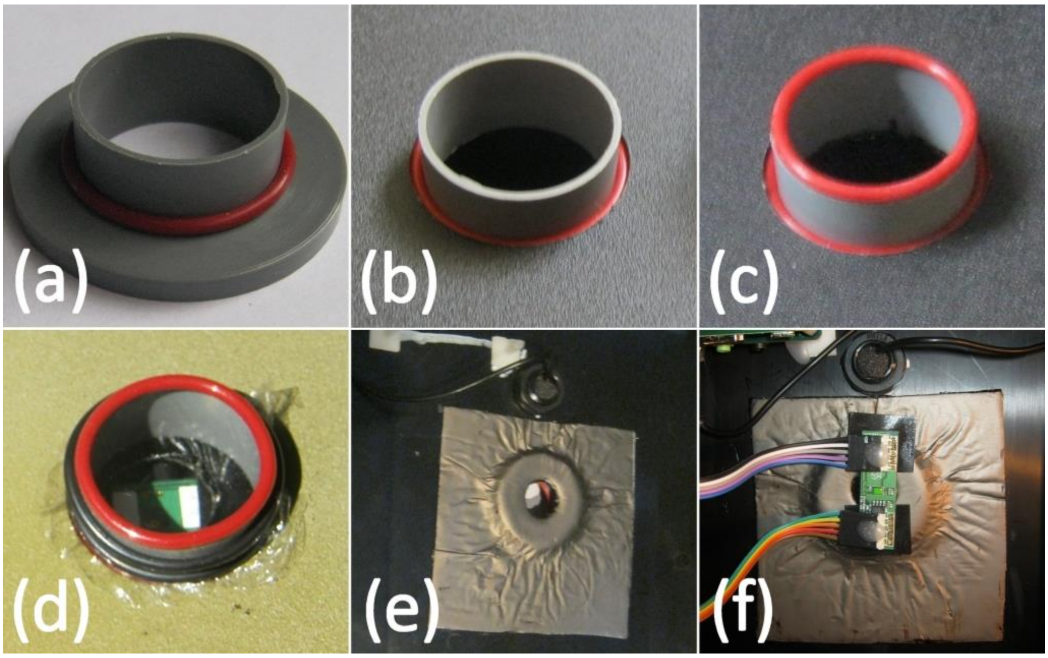


Figure 2.5. To mount cling film over the ultrasonic microphone opening, a plastic shoulder washer and O ring (a) were fitted through a hole in the case (b). As the sharp edge of the washer scarred the film during fitting, another O ring (c) was attached to provide a less abrasive seal. Cling film could then be stretched over the opening and held in place using smaller, thinner O rings (d). Inside the case, water ingress under the shoulder washer was prevented by sealing it with adhesive flash band. A hole, aligned with the centre of the opening, was cut in the band (e) where the ultrasonic microphone board was attached with double-sided foam tape (f).

AURITA units were attached to trees using galvanised steel fixing band. Four lengths of fixing band were secured to the rear of the AURITA case (one in each corner) using nuts, bolts and washers. Rubber washers were fitted inside and outside the case, underneath metal washers, to prevent water ingress. Once in position, each pair of bands (top and bottom) was then looped around the tree until the two ends met and could be joined together by passing wire, cable ties and a combination padlock (for security) through the fixing holes, in a similar fashion to putting on a belt. This method was non-destructive, cheap and offered good protection against the weather, animal damage and casual theft.

The finished design did not exhibit any leaks during preliminary testing in controlled conditions i.e. without any electronics, under the shower or in the rain. However, water could potentially enter the case if the cling film cover was compromised. To help cope with this eventuality, the RPA2 and USB power banks were sealed in Ziploc® bags and a drainage hole, covered with gauze to prevent entry by insects, was made in the bottom of the case.

2.3 Cost, Performance and Issues

The total cost of building each AURITA, including batteries, SD cards and fittings, was approximately £415. To maintain units in the field over a prolonged period of time, a second set of SD cards and batteries (~£70) was also required so that data storage and power supply could be rotated on a weekly basis with minimal interruption of recording.

Twelve AURITAs were deployed in Richmond Park from 1st July until 2nd September 2016 and from 2nd May until 3rd July 2017. Nine of these units were also deployed at the Knepp Castle Estate, West Sussex between 5th April and 12th June. 2018. All units were successfully recovered after each field season. Details of the relative number of complete and incomplete days of data recorded are provided in Table 2.1.

Table 2.1. Performance details of AURITA units deployed during this study. Days shown are for all AURITAs used in each survey. Solo values exclude days when SD card and battery swaps occurred.

Year	Location	Complete days	Partial days	No data*	File limit reached**	Total
			Solo			
2016	Richmond Park	646	10	4	N/A	660
2017	Richmond Park	618	2	4	N/A	624
2018	Knepp Estate	507	3	12	N/A	522
			RPA2			
2016	Richmond Park	591	66	57	30	744
2017	Richmond Park	569	55	50	70	744
2018	Knepp Estate	497	51	64	0	612

* Includes days when units did not record due to hardware failure, user error (incorrect configuration or SD card deleted) or ran out of battery power.

** RPA2 units have a storage limit of 3,000 files and will no longer record once this limit has been reached.

Following initial deployment in 2016, two Solo units were found to have incorrect date and time settings. In 2017, another Solo developed the same fault 6 weeks into the survey period. Setting the time and date requires an internet connection and this issue could not be rectified in the field. As the AURITA design is intentionally modular, both the Solo and RPA2 units are secured within the case using circuit board mounting feet and can be removed and replaced with relative ease while the AURITA was still attached to the tree. Faulty units were therefore retrieved and replaced with a spare Solo with the correct settings. Fortunately, the date and time were routinely spoken into the recorder whenever batteries and cards were swapped, enabling files to be renamed to represent the correct date and time at which they were actually recorded. In 2018, one EM172 microphone suffered a permanent and noticeable sensitivity drop during heavy rain. This was due to water repeatedly dripping onto the microphone, rather than water ingress, each time creating a loud sound that eventually overloaded the EM172. Once again, due to the AURITA's modular design, the microphone could be replaced in-situ. The addition of a protective shield mounted above the device (e.g. Frommolt and Tauchert, 2014) could potentially prevent this occurrence in future designs.

In 2016, one RPA2 unit developed a hardware failure and was temporarily replaced. Unfortunately, the replacement was incorrectly configured (auto record was not enabled) and 7 nights of bat data were lost due to user error. In 2017, another RPA2 developed a hardware fault which meant it failed to capture any recordings on some nights. This fault was initially intermittent and misdiagnosed as an absence of bats as it occurred on only a few nights and otherwise appeared to be performing normally. The unit's settings and automatic trigger function were additionally checked for faults and appeared to be in correct order. The unit was eventually replaced after failing to record any data over a continued period. Additionally, one RPA2 data card was accidentally erased during battery and card swaps. Several nights of bat data were potentially lost when some RPA2 units reached their maximum storage capacity of 3,000 files and ceased recording, despite still having battery power.

When preparing units for deployment in 2018, it was noticed that one of the MEMS microphones appeared to have suffered a loss in sensitivity and the associated unit was not triggering correctly. The microphone was tested by Peersonic, who confirmed this was the case, and replaced before the 2018 field season. A simple field test (clicking fingers ~30 cm in front of the MEMS microphone) was carried out each week when changing batteries to test for further microphone malfunctions after units had been deployed. During the final field season, this test revealed one more microphone that was failing to trigger correctly and had to be replaced.

Following the 2016 field season, 7 of the 48 batteries purchased became faulty with the lithium cells swelling to the point that the outer casing had split open. As the batteries were still under warranty, a full refund was received from the supplier and faulty USB power banks were replaced with car batteries in season two (2017). By 2018, a further seven USB batteries had become unusable and, being ground-based, car batteries could not be deployed in Knepp due to the presence of free-roaming livestock. Although fewer units (9) were used in 2018, this left a shortfall of two batteries that were replaced with iMuto 30,000 mAh power banks (Shenzhen Tianbaotong Technology Co., Guangdong, China). Additionally, in 2016, it was discovered that ultrasonic noise within some of the bat recordings was attributable to the USB power banks. This was initially difficult to diagnose as the frequency and level of noise encountered not only varied between power banks, but also between power ports within the same power bank. To mitigate this problem, all batteries and battery ports were subsequently tested to find the worst offenders, which were then used exclusively to power Solo units.

2.4 Data Management

In addition to changing batteries, SD data cards were also swapped over during the weekly equipment refresh. Cards with data were collected and empty cards inserted in their place. Audible data were downloaded using an SD card reader and DiskInternals Linux Reader v2.3.0.3 (Diskinternals, Seattle, USA) while bat data, being a non-standard file format (BATFAT), had to be downloaded using a spare RPA2. A random selection of files from each recording device was examined after downloading to check copying had completed successfully.

With only two cycles of SD cards, this process had to be completed within a few days so that cards were ready to be returned to the field. As each recorder generated up to 3,500 files (~60 GB of data) per week, careful management was required to ensure data were copied on time and filed correctly. File directories were created for each recorder, with weekly subdirectories containing separate daily bat and bird files. Audio files were stored using the file naming convention 'Site*xx-yyyy-mm-dd_hh-mm-ss.*wav'. Bat files were created as '*xwww_aaa*.wav', where *x* was set to A through L (signifying location 1 to 12), *www* is the peak wavelength of the file in kHz and *aaa* is an alpha-based sequential labelling system (AAA, AAB, AAC etc.).

Uncompressed WAV files are also large (~5 MB per minute) and 9 weeks of recordings at 12 locations will generate over 6 TB of data. Several Seagate® Expansion™ 5 TB USB 3.0 external drives (Seagate Technology PLC, California, USA) were used for local data storage. Two copies of all data were made; one copy was stored as uncompressed files for use in analyses and a compressed copy of every file was also stored on a separate backup drive. Audible data were compressed into FLAC (Free Lossless Audio Codec) format and zip files were used for bat data. Both methods were tested beforehand to ensure there was no degradation or loss of fidelity when restoring data and an overall compression ratio of ~50% was achieved.

To help ensure data security, it is good practice to store at least one copy of any data off-site. For this purpose, storage space was arranged on the UCL iRODS research data storage platform (UCL, London, UK) and compressed copies of all data were uploaded upon completion of each field season. Once uploaded, several files were downloaded over the internet using the iRODS graphical interface in order to test backup integrity.

2.5 Sound Attenuation Surveys

The effective range of the recorders has been a popular question during presentations of this project. The answer, however, depends on the magnitude, distance, orientation and frequency components of each individual sound source. Local weather conditions, land cover, background noise level and other factors additionally influence the range at which sounds will be captured (Taherzadeh, 2007). Nevertheless, to gain some idea of the area of interest being covered, this was an important question that required consideration.

2. Sound Recording Equipment

Differences in sensor equipment and equipment settings will also produce variations in performance across studies. Farina *et al.* (2013), for example, state a detection radius of 30 m in dense Mediterranean maqui, while Rodriguez *et al*. (2014) estimated their sensor range to be 100 m in tropical forest. It was therefore considered necessary to perform acoustic attenuation tests for the specific equipment and locations involved in this study. For this purpose, a test recording (44.1 kHz, 16-bit WAV format) was compiled, featuring 7 pure tone waves (1-7 kHz at 1 kHz intervals) and 5 bird calls (Figure 2.6). This allowed the investigation of attenuation at specific frequencies and an assessment of the distance at which bird calls could effectively be detected. Alternating between pure tones and bird calls additionally helped to avoid confusing recorded calls with actual bird calls when analysing data. Note: all spectrograms produced for this thesis are presented in greyscale as the use of colours can potentially influence the perception and interpretation of spectrogram data (Rogowitz *et al.*, 1996).

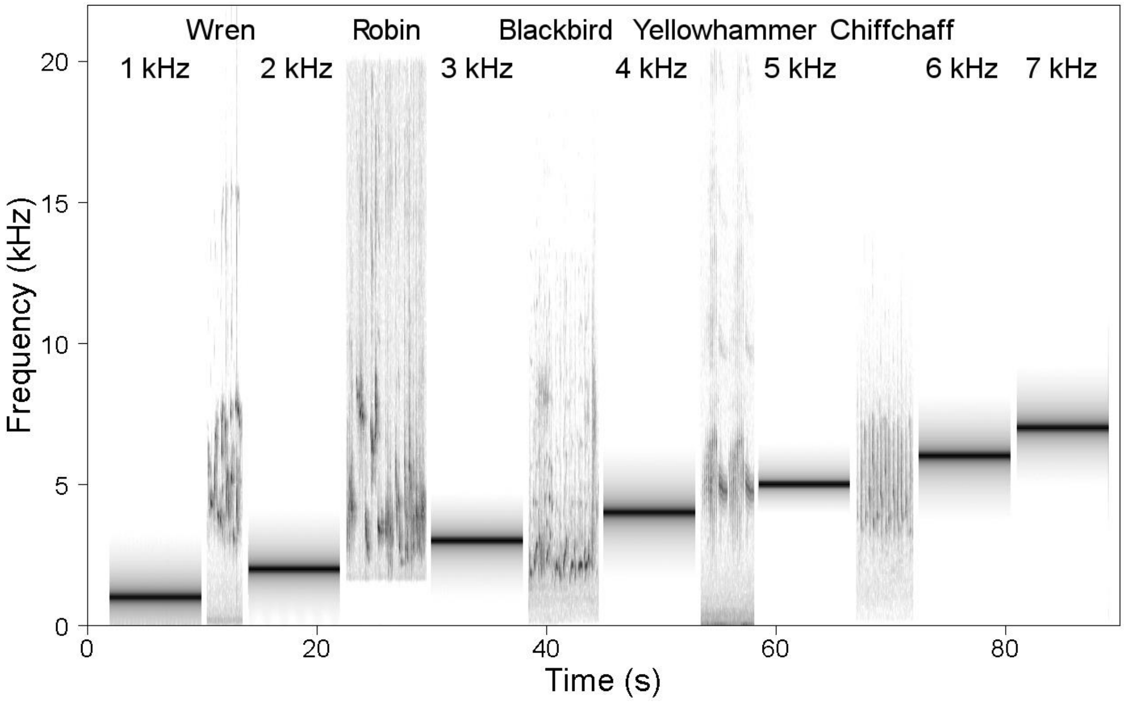
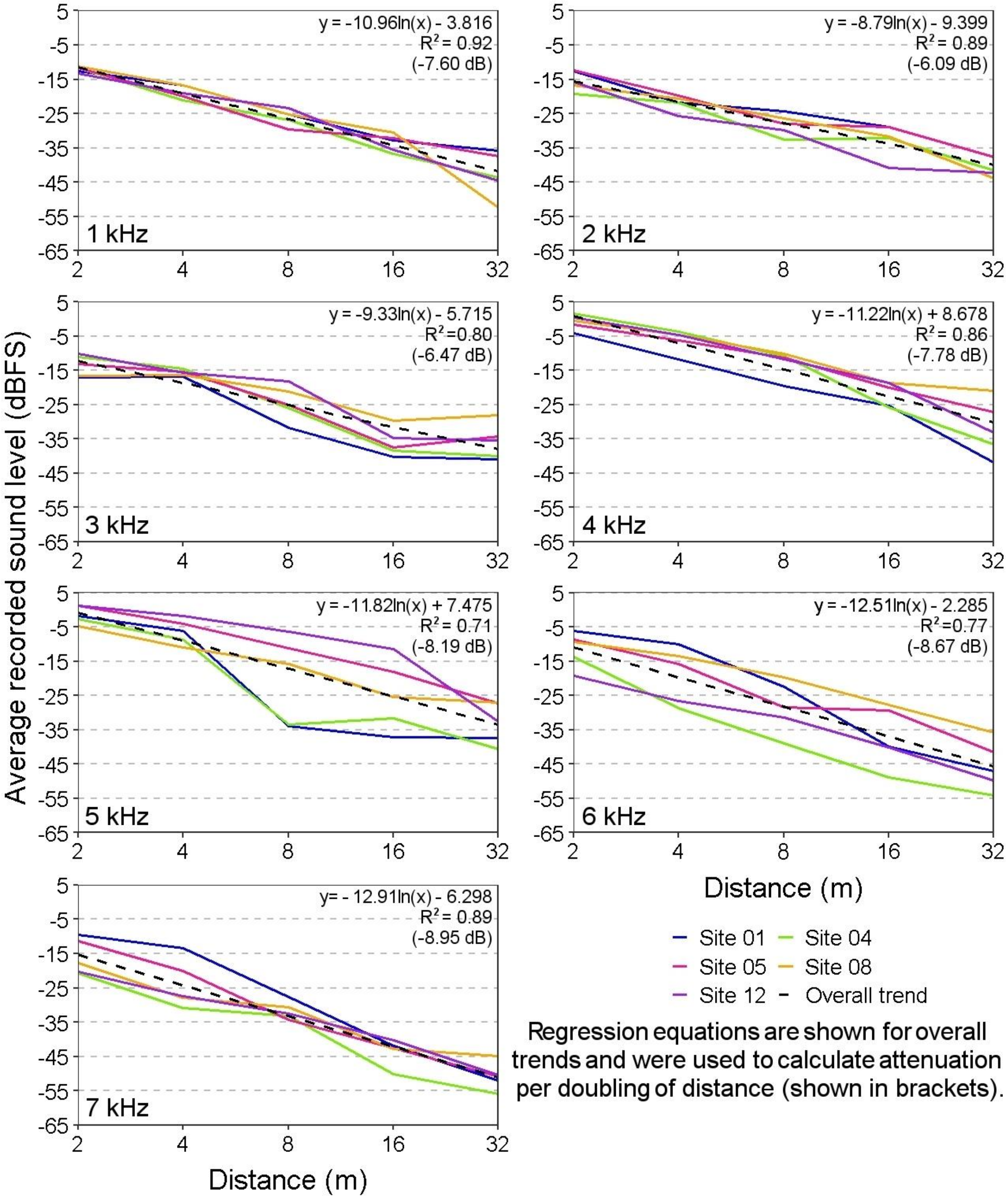


Figure 2.6. Spectrogram of the test recording file used in sound attenuation surveys. Spectrogram generated with the *Seewave* v2.1.3 *spectro* function (Window length=512, overlap=50%, dynamic range = 96 dB).

Reference SPLs for actual bird calls were obtained from Brackenbury (1979). Although the precise calls measured by Brackenbury could not be determined, and hence replicated, the peak level of each species was adjusted relatively within the recording. For example, the call of the Eurasian wren (*Troglodytes troglodytes*), listed as 90 dB at 1 m, was made 3 dB louder in recordings relative to the Common blackbird (*Turdus merula*), listed as 87 dB. A Benetech GM1356 digital sound level meter [IEC 651 TYPE2, frequency response = 31.5Hz to ~8.5KHz, Accuracy ±1.5 dB Ref: 94 dB @ 1 kHz (Shenzhen Jumaoyuan Science and Technology Co., Guangdong, China)] was then used to measure and adjust the playback level of the recorder until it was at a similar level to the actual calls i.e. ~90 dB at 1 m for the wren.

The test recording was played back using a Zoom H1 recorder (Zoom Corporation, Tokyo, Japan) connected to an iClever Portable Bluetooth Speaker; 5 W RMS power, 90 Hz - 18 kHz frequency response (iClever, California, USA). During playback, the speaker was held up at arm's length (~2 m off the ground), facing the front of the AURITA unit. This process was repeated, ground cover permitting, at 5 distances (2 m, 4 m, 8 m, 16 m and 32 m) in 6 directions (0°, 60°, 120°, 180°, 240° and 300° relative to the front of each AURITA) in each of the 5 recording locations surveyed. All recordings were made in-situ, during normal AURITA operation, and then retrieved from SD cards following the weekly data refresh. Surveys were performed for Site 1, Site 4 and Site 5 on 16/08/16, and Sites 8 and 11 on 24/08/16 (see Chapter 3 for a map of Richmond Park sites). To account for differences in atmospheric absorption due to variations in local weather conditions, temperature and humidity were measured during each survey. However, due to discrepancies (up to 18% humidity and 4.8° temperature) between local readings and weather data obtained from Richmond Park weather station, the latter were used in calculations as they were considered more likely to be accurate. Fortunately, atmospheric attenuation is relatively small at these distances and the biggest difference in values calculated for both sets of data was 0.03 dB. Sound levels were normalised to the conditions that produced the lowest amount of attenuation, the best-case scenario, for each frequency.

Figure 2.7 shows comparisons of attenuation over distance at each site, measured for pure waves of different frequencies. Average values were obtained from recordings using the frequency analysis tool (Blackman-Harris window, length=2048) in Audacity v2.1.2 (Audacity Team, 2016). As analysis bins did not always centre on the precise frequency being assessed, a spline interpolation function was subsequently applied using XlXtrFun^{TM} (http://www.xlxtrfun.com/XlXtrFun/XlXtrFun.htm) to rectify this situation. Without any other influence, it is accepted that sound pressure will decrease by 6 dB per doubling of distance between a point source and its receiver. This is due to the spherical expansion of sound energy, which enables attenuation over distance to be calculated using the inverse square law (Taherzadeh, 2007). As values were normalised to account for differences in temperature and humidity, any variation between sites should be largely due to ground cover and/or wind. Wind speed and direction data obtained from Richmond Park weather station (30-minute average) for the periods when the measurements for Figure 2.7 were performed, are listed in Table 2.2.



Regression equations are shown for overall trends and were used to calculate attenuation per doubling of distance (shown in brackets).

Figure 2.7. Attenuation over distance measured at 0° (directly in front of recorders), for pure sine waves. The *x*-axis scale is logarithmic (base 2), to represent the doubling of distances.

Table 2.2. Wind details recorded at sites used in Richmond Park attenuation surveys, 2016.

Site	Unit facing (Degrees)	Wind direction (Degrees)	Difference (Degrees)	Ave wind speed (ms^{-1})	Predominant Effect*
1	270	67.5	202.5	11.3	Headwind
4	220	67.5	152.5	9.7	Headwind
5	170	67.5	102.5	8	Side wind
8	150	22.5	127.5	3.2	Side wind
11	250	45	205	1.6	Headwind

*Signal power will be reduced at differences closer to 180° (headwind) and increased closer to 0° (tailwind).

At 2 m, ground cover is unlikely to have a large impact and diverging values at this distance are more likely due to wind. Close to ground level, differences in wind speed tend to have a more exaggerated effect at higher frequencies (Foss, 1979). This potentially explains why values for 1 kHz were more closely grouped. In terms of ground cover, sites with denser and taller vegetation such as site 1 and site 4 (rhododendron) and site 11 (bracken and saplings) generally fell below the overall trend in Figure 2.7, indicating greater than average attenuation. In contrast, site 8 (grass and bare ground) is usually above the line. While it seems logical that denser, higher vegetation should cause more attenuation, there are some inconsistencies in results and it was not possible to separate the amount of attenuation purely attributable to vegetation from wind effects without also obtaining high resolution (<3 seconds) local wind speed and direction data for the duration of each test.

Examining the attenuation values for each doubling of distance in Figure 2.7, calculated for each frequency using the overall trend-line equations, 2 kHz and 3 kHz appear to be closest (i.e. least affected by factors other than distance) to an ideal value of 6 dB. Attenuation typically increases with frequency, which is not unexpected considering higher frequencies are more susceptible to atmospheric attenuation (Taherzadeh, 2007). The notable exception is 1 kHz; in this case, excess attenuation is likely due to ground effects and absorption (Wiley and Richards, 1978). These results are consistent with the concept of a 'sound window', centred at around 2 kHz in deciduous forests, where attenuation is at a minimum (Bucur, 2007). Indeed, it is suggested that close to ground level (i.e. within a few meters), acoustic communication signals should utilise frequencies above 1 kHz and below 4 kHz to achieve maximum transmission distance, regardless of habitat type (Wiley and Richards, 1978).

In recordings captured during normal AURITA operation, the distance and SPL of any animal vocalisations will be unknown and a loud vocalisation far away could appear to be the same level as a much quieter call nearby. In order to gain some idea of the effective 'range' of the AURITA units when capturing vocalisations, it was therefore necessary to analyse recorded calls for which the reference SPL and distance were both known. As mentioned previously, the test recording playback level was calibrated using a sound level meter to confirm that calls were reasonably representative of the desired reference levels. Figure 2.8 shows SPL levels of the test recording (Figure 2.6), measured with the sound level meter, indoors, at 2 m distance.

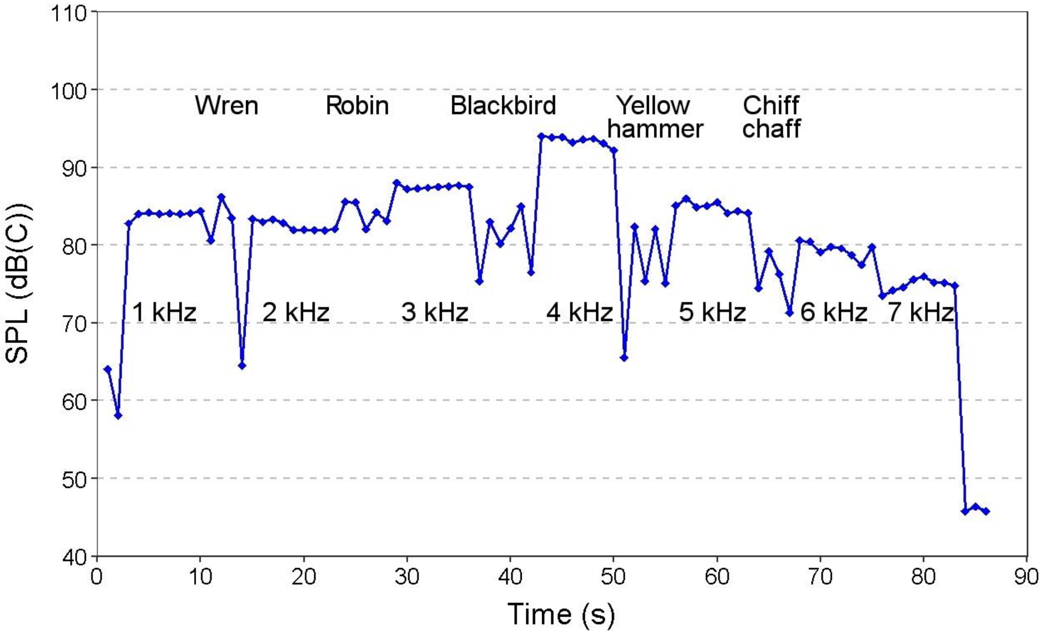


Figure 2.8. SPL measurements of the attenuation test recording (Figure 2.6) playback level, performed indoors, at 2 m distance. Each data point is a 1 second averaged reading. Note that SPL is shown using the C-weighted decibel scale, dB(C).

The drop-off at higher frequencies seen for sine waves is at least partly caused by the meter recording SPL using the C-weighed decibel scale, which negatively weights frequencies over 1.6 kHz (Taherzadeh, 2007). Higher levels recorded at 3-4 kHz are most likely caused by the sound meter being more sensitive to, and/or the playback equipment emphasising, this range of frequencies. Additionally, reference levels provided for acoustic equipment, including the sound meter used, are standardized for 1 kHz and so it is only possible to say that instruments are accurate at this frequency (Kuehn, 2009).

As bird calls were comprised of a range of different frequencies and magnitudes, the average, rather than peak, SPL for each call was calculated using the data points measured over its duration. In some cases, the appropriate data points were more obvious than others e.g. the yellowhammer (*Emberiza citrinella*), where the two-part repeated call pattern was also apparent in SPL readings. The minimum resolution of the sound meter is 1 second and, as calls varied over short (<1 second) timescales, less regular calls were harder to discern. There are also half second gaps of silence between pure tones and calls in the test recording, which could negatively skew readings whenever they occurred within the 1-second meter window. However, synchronising the test recording with meter readings enabled selection of the most likely corresponding values, and points including silent gaps to be avoided. The results (Table 2.3) confirmed that bird call playback levels used in the attenuation surveys were within 1.6 dB, or less, of the desired values.

Table 2.3. Average SPL for bird call playback levels, measured indoors at 2 m distance, compared with desired reference levels. Data from Brackenbury (1979)[1].

Bird call	Average playback SPL at 2 m (dB)	Playback SPL, adjusted to 1 m (dB)*	Desired reference SPL at 1 m (dB)[1]
Eurasian Wren	84.9	90.9	90
European Robin	84.1	90.1	90
Common Blackbird	82.6	88.6	87
Yellowhammer	78.8	84.8	85
Common Chiffchaff	75.6	81.6	80

* As calls contained a range of frequencies and were measured indoors, in the absence of wind and vegetation, it was therefore considered reasonable to increment values by the standard 6 dB to represent a halving of distance.

Test calls from audio files recorded during attenuation surveys were analysed using Audacity's frequency analysis tool (Blackman-Harris window, length = 2048). Splining was not required because, unlike sine waves, values were not required for a specific frequency. However, frequency analyses represent the amplitudes of constituent frequencies within a selected sample of audio. As sine wave recordings were of constant magnitude and frequency, their average value should thus remain relatively constant regardless of how much, or which part, of their recording was sampled. This enabled portions of recordings where noise obviously coincided with a test frequency to be omitted from analyses without adversely influencing results. This situation did not apply to bird calls, which vary in both magnitude and frequency over time, making it necessary to ensure that the duration of each call sampled remained constant so that results were comparable. This meant including parts of calls that contained noise interference or were no longer visible due to attenuation (Figure 2.9).

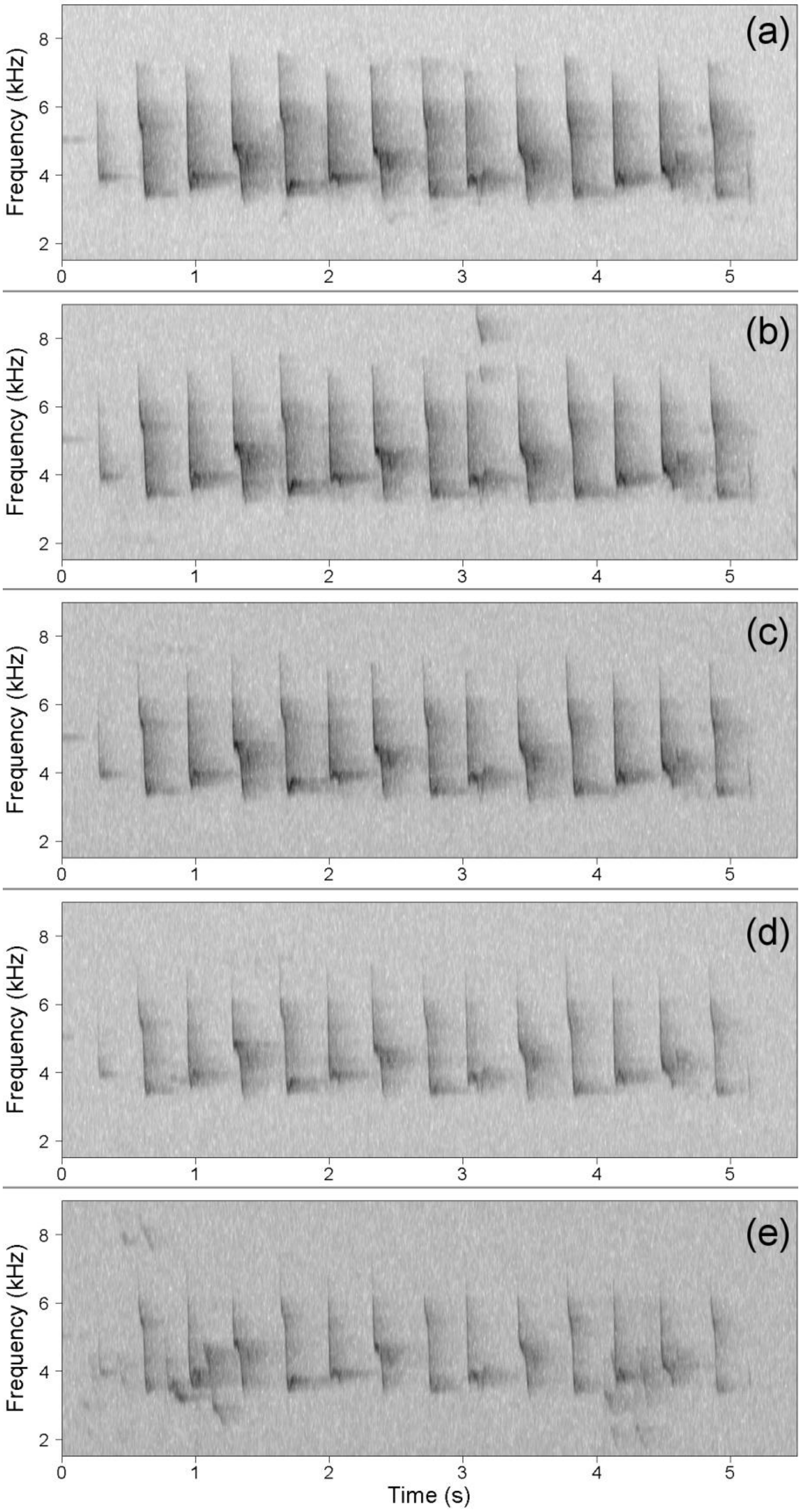


Figure 2.9. Spectrograms of chiffchaff (*Phylloscopus collybita*) playback calls recorded at 0° (facing the recorder) in site 8 for (a) 2 m, (b) 4 m, (c) 8 m, (d) 16 m and (e) 32 m distance. Spectrograms were generated with the *spectro* function in *Seewave* v2.1.3 (window length=512, overlap=50%, dynamic range = 96 dB).

Previous studies looking at the attenuation of bird calls (e.g. Aubin and Jouventin, 1998; Lengagne and Slater, 2002) have established the distance at which calls become unrecognisable using the discrimination thresholds of live specimens. Here, however, we are interested in the level at which the recording device can adequately detect incoming bird calls for a variety of species. The level at which acoustic communication can be discriminated will be significantly influenced by the type and intensity of background, or ambient, noise in that environment (Lengagne and Slater, 2002). The point at which incoming calls fell below the typical ambient noise level at that location was therefore used as reference level to determine the level at which they were no longer considered functional. Again, the best-case scenario approach was adopted and ambient levels were sampled using 10 second periods of relative silence, where there was minimum interference due to weather conditions or vocalisations, from before and after each survey. To minimize any influence from random noise events, all values were then averaged to produce the spectral profile used as an equivalent noise floor.

The spectral densities of calls recorded at each distance were then plotted together to ascertain the point at which they dropped below this reference level. In some cases, the signal had not yet fallen below this level by the maximum distance assessed (32 m) and values were also extrapolated for 64 m and 128 m. This was achieved using the attenuation values previously calculated for pure waves (Figure 2.7), with the tested frequencies at the centre of each 1 kHz band i.e. -7.6 dB attenuation at 1 kHz was applied to frequencies from 500-1500 Hz and so on up to 8.5 kHz. An alternative method considered using the average decrease over all measured distances (2 m, 4 m, 8 m etc.) for each bird at each site. This method offered higher spectral resolution (21.5 Hz frequency bins for an FFT window size of 2048) at which attenuation values could be applied. However, the uneven drop across frequencies also meant that higher frequencies had dropped below ambient levels at longer distances and positively skewed average values. Additionally, in some cases, noise or wind reinforcement produced positive attenuation at some frequencies but not others.

In Figure 2.9e, it is possible to see interference due to natural bird calls that occurred during test recordings, about 1 second from the beginning and 1 second from the end. Areas where natural calls occurred may thus appear as inconsistencies in spectral density patterns. To mitigate any influence this might have on results, the minimum values were used, regardless of distance. For example, wherever extraneous noise had increased sound levels so that parts of the call were louder at 32 m than 16 m, the value for 16 m was used instead. Figure 2.10 provides an example of the results generated by this process for the calls shown in Figure 2.9.

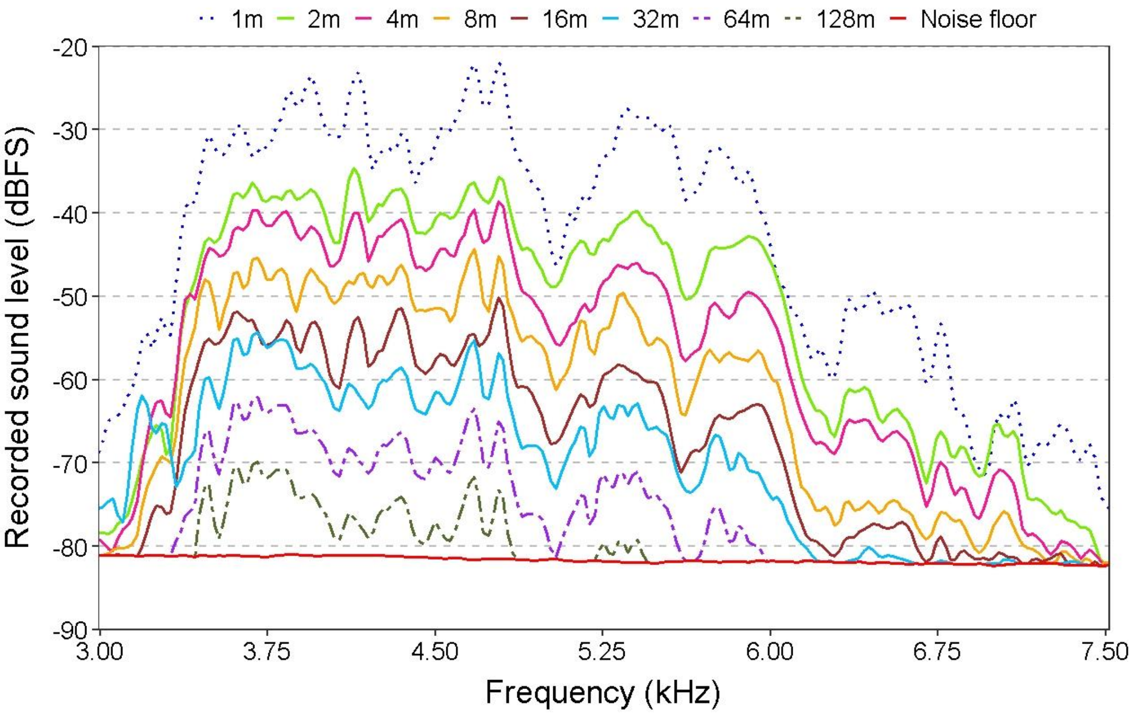


Figure 2.10. Spectral densities of chiffchaff (*Phylloscopus collybita*) playback calls recorded at site 8 (0° in front of recorder) at different distances. The 1 m reference call was recorded indoors and not subject to attenuation by wind, noise or vegetation cover. Densities at 64 m and 128 m were extrapolated using the minimum values recorded at any distance.

As mentioned previously, bird calls vary in both magnitude and frequency over time. Figure 2.10 demonstrates that even when most of a call had fallen below the reference level, a small portion of the original signal might still remain above it. This raises the question, what proportion of a call needs to be present for it to still be considered viable? The answer may become more apparent during data analysis, when the ability of various methods (e.g. Kaleidoscope Pro, ACI) to distinguish songs from background noise could provide some indication. In the meantime, the proportion of the original signal that remained above ambient noise levels at each distance was used to provide a relative measure of the overall amount of attenuation that had occurred. This was done by calculating the areas under the graphs of calls at different distances as a percentage of the area under the graph of the call recorded indoors at 1 m distance. Results for the average values of all bird calls recorded at the five sites where attenuation surveys were conducted (sites 1, 4, 5, 8 and 11), are presented in Table 2.4.

Table 2.4. Percentages of reference bird call spectral density above ambient noise levels at different angles and distances from the recording device. Values are averages of results from 5 sites surveyed. [1]Data from Table 2.3.

Bird call	Angle	Distance (m)						
	(degrees)	2	4	8	16	32	64	128
Eurasian Wren	0/360	84	68	53	37	25	12	5
(91 dB SPL @ 1 m)[1]	60	73	63	48	35	20	8	2
(2.5 - 8.5 kHz)	120	46	39	32	21	19	7	2
	180	36	33	28	21	14	4	1
	240	60	48	38	26	16	6	1
	300	72	60	45	33	20	9	3
European Robin	0/360	79	61	45	28	19	7	3
(90 dB SPL @ 1 m)[1]	60	69	57	42	28	15	6	2
(1.6 - 12 kHz)	120	36	32	27	15	14	4	2
	180	28	25	21	16	10	3	0
	240	52	38	28	19	13	4	1
	300	73	57	39	27	15	7	3
Common Blackbird	0/360	69	51	33	22	17	5	2
(89 dB SPL @ 1 m)[1]	60	57	47	31	24	12	6	2
(1.5 - 12 kHz)	120	32	29	20	13	17	4	1
	180	23	18	15	12	10	2	0
	240	40	32	20	14	12	4	1
	300	59	48	31	27	15	6	2
Yellowhammer	0/360	76	64	46	28	23	7	3
(85 dB SPL @ 1 m)[1]	60	61	51	35	22	12	3	1
(2 - 8.5 kHz)	120	33	31	21	14	14	4	1
	180	26	25	22	21	15	3	0
	240	49	38	25	16	15	4	1
	300	61	49	31	24	13	4	1
Common Chiffchaff	0/360	82	67	51	32	21	8	2
(82 dB SPL @ 1 m)[1]	60	66	53	38	27	13	3	0
(3.2 - 7.8 kHz)	120	34	31	23	15	13	4	1
	180	27	24	20	14	11	1	0
	240	52	40	30	18	14	2	0
	300	65	52	35	24	14	4	1

2.6 Discussion

In Section 2.2, this chapter demonstrated how it is possible to create an autonomous recording device that is reliable, has a reasonable field life and is capable of capturing acoustic data of a quality suitable for scientific research, at a fraction of the cost of commercially available counterparts. While requiring more effort, the process of designing and building such a piece of equipment enables the user to potentially incorporate specific design features they feel are desirable and inherently instils a higher level of familiarity and understanding of the method by which their data were captured. For example, in contrast to manufactured units, the AURITA unit (Beason *et al*., 2019) detailed in this study benefitted from an intentionally modular design that allowed individual components to be easily removed and replaced without the inconvenience and data loss due to having to remove the unit from the field, send it off for repair and then return it later. Studies such as this one, where equipment is designed at the beginning of a project and is used over the course of several years, also present the opportunity to perform an ongoing evaluation, and potential improvement, of the original design.

Although initial investigations into the possibility of using handheld digital recorders to capture and store audio data were disappointing, insomuch that this technology is currently not quite up to this task, this led to the adoption of microcontroller technology (i.e. Raspberry Pi), which turned out to be much better suited to this role. The adoption of microcontrollers by a community of developers, who freely make their designs and programs for a wide variety of applications available, additionally provides an invaluable point of access for those lacking the necessary skills and/or time to develop their own solutions. With low power consumption and high data capacity, the Solo unit selected for use in this study has proven itself to be extremely reliable and fit for purpose. The recent publication of papers on the Solo (Whytock and Christie, 2016) and AudioMoth (Hill *et al*., 2018) in *Methods in Ecology and Evolution* suggests the use of microcontroller technology is becoming more popular with the scientific community.

Arguably, the factor currently limiting the field life of such equipment is the availability of reliable, affordable, compact yet high capacity, battery power. Progress in portable USB power banks, primarily designed to recharge mobile phones and tablets, offers some hope for improving this situation. However, even the largest (26,800 mAh) of these available at the time of AURITA construction could only sustain a lower-power Raspberry Pi for a maximum of 7-8 days. The true capacity and manufacturing quality of some power banks currently available may also be questionable. Additionally, potential USB power sources for bat recorders should be tested in advance to determine whether they are likely to be a source of ultrasonic noise. The ability to power equipment such as the Solo and Peersonic RPA2 through a standard USB port is nevertheless an important feature, offering greater flexibility and choice of options than the more traditional cell-type batteries.

Section 2.3 addressed some of challenges faced when dealing with studies that generate Big Data. Although relatively small in scale, this study had generated over 18 TB of data by the time of completion. Fortunately, the storage capacity of SD cards and external hard disks, in addition to their affordability, has continually been improving and the recent development of a 1 TB SD card (SanDisk, California, USA) suggests this trend is likely to continue. The use of lossless file compression formats, such as FLAC, for acoustic data capture and analysis presents another way in which large data sets could be made more manageable. The use of cloud services (e.g. Amazon Drive, Box) to store large data sets is also becoming a realistic possibility; although confidentiality issues could preclude the use of commercial cloud storage to store research data, some universities have already started providing equivalent research data platforms of their own (e.g. UCL iRODS, RHUL Figshare).

In Section 2.4, the effective range of the recorders for birds was investigated through a series of attenuation surveys. Despite representing an important question, the literature review revealed surprisingly few details on this matter and even the studies that provided some estimate of range apparently did so without the benefit of having performed actual assessments at their recording sites. Some bioacoustics studies have used similar methodologies; however, these have focused on estimating the maximum distance at which intraspecific calls could be recognised by a particular species, using the response reactions of live specimens to gauge effective transmission ranges. Conducting attenuation surveys using both sine waves and the calls of several bird species, and subsequently finding a way to analyse their transmission effectiveness from recordings without the aid of live specimens, presented the most promising method of assessing the effective range of acoustic sensors.

In addition to helping locate and delineate playback bird calls within recorded audio files, the inclusion of sine waves in the survey helped provide a clearer picture of the level of attenuation taking place at different frequencies. Overall, results seemed to agree with the hypothesised existence of a 2 kHz 'sound window' in deciduous forests. The attenuation characteristics of different sound frequencies over distance due to air temperature and humidity are well understood, making it possible to adjust for differences in these conditions when surveys were performed. Wind effects, which can vary in direction and magnitude over short periods of time, are more difficult to account for. Without the ability to separate wind effects from results, differences in attenuation between sites could not be attributed purely to differences in vegetation cover. Continuous, high-resolution measurements of wind speed and direction for the duration of any future surveys could potentially alleviate this situation; however, without further investigation, it is not possible to say whether this would necessarily enable the derivation of a relationship between wind data and variations in attenuation.

When analysing the attenuation of regular sine waves of known frequencies, it was possible to directly compare recorded sound levels of those frequencies over different distances. As sound does not attenuate evenly across all frequencies, using a single peak value at a particular frequency to quantify and compare birds calls, which are highly variable over short time scales and contain a wide range of frequencies and sound pressure levels, seemed inappropriate. Drawing a virtual 'box' around each call used, with the length being the duration and its height being the frequency range of the call, and then analysing the total signal within this box provided a means of quantifying each call in its entirety. By keeping the box size constant, it was therefore possible to compare the relative, overall amount of signal being received. While not without its flaws, such as the inclusion of non-reference call sounds within the box and the difficulty of specifying what percentage of a call must be received for it to be considered viable, this methodology is relatively simple and easy to reproduce.

Presenting results in this way provides the interesting possibility of performing interspecies comparisons. For example, results suggest that despite being the quietest bird in the survey, the transmission efficiency of the common chiffchaff call at 0° is comparable to the loudest (Eurasian wren) and better than the 3 other, louder species tested. The chiffchaff call also has the narrowest band width (4.6 kHz) with the lowest upper frequency in the survey and, as more attenuation occurs at higher frequencies, presents the most likely reason for this occurrence. The percentage of a call that persists over distance is apparently not only determined by how loud that call is, but also the frequencies it is comprised of. There is no obvious reason why this methodology could not also be applied to evaluate the transmission efficiencies of different types of call by the same species, or for species other than birds.

Another interesting phenomenon that can be observed in the bird call attenuation results relates to directionality. As would be expected, calls recorded from directly in front of the recording device (0°) almost exclusively contained the greatest percentage of the original signal at each distance while those from directly behind (180°) contained the least. Equally, values for calls coming from 60° off-centre on either side of the recorder (i.e. 60° and 300°) were reasonably similar. There does, however, appear to be more disagreement between values for 120° and 240°, both of which are off-centre by 120°. This discrepancy is present for all species, suggesting the reason is not due to differences in the calls themselves. One possible cause is that the measured wind direction came from behind the recorder during most surveys, and in the majority of cases it came from rear, left of centre (i.e. closer to 240° than 120°). However, this bias is not also apparent in measurements for 60° off-centre and therefore difficult to attribute purely to wind effects. As mentioned in the main text, it was not possible to complete surveys in each direction at every site. It is perhaps no coincidence that the most frequently omitted, or incompletely assessed when not omitted, survey direction was 120° and the bias could be due to underrepresentation when calculating average values.

When addressing the original question, that of the effective sensor range, results indicate that at 128 m, for all calls tested from any direction, only 5% or less of the original call was likely to be recorded above ambient noise levels. Except for the loudest call (Eurasian wren) tested, directly in front of the recorder, values remained below 10% at 64 m, and 25% at 32 m. While these figures provide some general indication, apart from cases where none of the original signal was received it was not possible to specify an absolute range without the determination of a meaningful threshold value. Recent assessments of detection ranges have accounted for this by basing evaluations on the distances at which calls could be recognised by automated classifiers (Cragg *et al*., 2015; Pérez-Granados *et al*., 2019) or human observers (Yip *et al*., 2017). While these approaches provide absolute values with which to assess ARU performance, they potentially introduce an element of subjectivity into analyses through recogniser performance and observer bias, respectively. Furthermore, the performance of recognisers and observers will likely vary between species (Sauer *et al*., 1994; Wolfgang and Haines, 2016), making interspecific comparisons problematic. As the method described in the current study is based on numerical measures of spectral density it is not subject to these biases and, because results represent the percentage of the original call that is audible above the noise floor, better suited to comparing the attenuation properties of different calls and the calls of different bird species.

CHAPTER 3

3. Effects of Rhododendron Presence and Removal on Bat Activity

3.1 Introduction

Since its introduction from Iberia in the eighteenth century (Milne and Abbott, 2000), *Rhododendron ponticum* (henceforth referred to as rhododendron) has become widespread in the British Isles and was estimated to affect over 52,000 ha in 2003 (Dehnen-Schmutz *et al*., 2004). Rhododendron is currently undergoing widespread removal due to its ability to out-compete native plant species and suppress forest regeneration, and as a potential host for the fungal pathogens *Phytophthora ramorum* and *Phytophthora kernoviae* (Parrott and MacKenzie, 2013). While it is also frequently claimed that rhododendron negatively affects biodiversity (e.g. Edwards, 2006; Barron and Little, 2009; Parrott and MacKenzie, 2013), its impact may vary from negative to positive depending on the identity of the surveyed taxa (Colak *et al*., 1998; Taylor *et al*., 2003; Malo *et al*., 2013).The effects of rhododendron on bats have not been previously investigated, but could have important implications for forest management strategies as bats, and their roosts, are protected under UK law.

Rhododendron is highly shade tolerant and evergreen, which enables it to photosynthesise throughout the year and to colonise the understorey of deciduous forests (Parrott and MacKenzie, 2013). Once established, rhododendron forms a dense understorey with large leaves shading out competitors (Barron and Little, 2009), and increasing the amount of clutter found beneath the forest canopy. It is therefore likely that rhododendron's presence in the understorey would reduce activity of open space foraging bat species such as *Nyctalus noctula*, *Nyctalus leisleri* and *Eptesicus serotinus*. These species have wing morphologies better suited to faster, more efficient flight over longer distances, but their lower manoeuvrability and longer wingspans restrict them to foraging in less cluttered areas (Altringham, 2014). The longer, lower-frequency, narrowband echolocation calls they employ (Müller *et al*., 2012) are also better at detecting prey at longer range and thus more suitable for aerial hawkers hunting in open spaces where prey can be widely distributed (Schnitzler *et al*., 2003).

Alternatively, bat species able to forage in highly cluttered spaces (e.g. *Myotis nattereri*, *Myotis bechsteinii* and *Plecotus auritus*) are less likely to be negatively affected by structural changes due to rhododendron. Their shorter, broader wings provide high manoeuvrability, at the expense of speed and efficiency (Dietz and Kiefer, 2016), and are adapted for gleaning strategies, where prey are taken either directly from, or very close to, surfaces, and hawking in highly cluttered environments

(Altringham, 2014). Closed space foragers typically use broadband frequency modulated calls, which provide more detailed information about structural depth and enable precise target localization and characterization at shorter ranges (Schnitzler and Kalko, 2001). The shorter duration of these calls also enables prey to be separated from background clutter more easily by reducing signal overlap between outgoing calls and returned echoes (Schnitzler and Kalko, 2001). Nevertheless, there may be a point at which particularly dense vegetation may affect even the foraging efficiency of closed space foragers (Froidevaux *et al*., 2016). For bat species that predominantly forage in edge spaces with background clutter (e.g. *Myotis daubentonii*, *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*), the effects of rhododendron presence in the understorey may be less obvious. In previous studies that considered the effect of understorey on bats, Fuentes-Montemayor *et al*. (2013; 2017) found that activity levels of common (*P. pipistrellus*) and soprano (*P. pygmaeus)* pipistrelles were lower in areas with dense understory but higher for *Myotis* species and *P. auritus*. Müller *et al*. (2012), however, found that increased vegetation density reduced only the activity of open space foragers and did not have any significant effect on either closed or edge space foraging guilds, which included common and soprano pipistrelles and *Myotis* species. Indeed, both of these pipistrelle species display a high degree of plasticity in their echolocation calls, enabling them to forage in a variety of habitats, including dense vegetation (Kalko and Schnitzler, 1993).

When multiple rhododendron bushes grow in close proximity to each other, they can form large hedge-like structures, and rhododendron is even listed as suitable hedging material by the Royal Horticultural Society (RHS, 2018). Hedgerows are important features for some bat species as they can provide commuting routes or corridors, either for navigation purposes or to help avoid predation (Altringham, 2014), and habitat for roosting (DEFRA, 2007). Hedges may also harbour several bat prey species such as flies and moths (Maudsley, 2000), especially when they are unmanaged and/or infrequently trimmed (Froidevaux *et al*., 2019). Lacoeuilhe *et al*. (2016) found that activity of *Myotis spp*. and *P. pipistrellus* increased significantly with higher density and wood production of hedgerows. Boughey *et al*. (2011) also found that the incidence of *P. pipistrellus* and *P. pygmaeus* increased with linear features such as hedgerows, particularly when hedgerow occurred in combination with trees. The authors additionally found this relationship was not dependent on hedgerow width (up to 30 m), suggesting denser stands of rhododendron could still provide suitable edge space habitat. The presence of *P. pygmaeus* roosts is also more likely where linear vegetation features, such as hedges, are available (Jenkins *et al*., 1998) and hedgerow trees also provide roosting habitat for this species (Critchley *et al*., 2010). If rhododendron does fulfil a similar function to hedgerows for bats, we might expect higher levels of activity for pipistrelle species and *Myotis* spp., and possible evidence of roosts for *P. pygmaeus* in areas colonized by rhododendron.

In addition to altering understorey structure, rhododendron could also potentially affect the abundance of bat prey species (Welch and Leppanen, 2017). Although rhododendron has been present in the UK for over 200 years, only 31 species of herbivorous insect have been associated with it, of which only five are host-specific (Taylor *et al*., 2003). Some invertebrate species (i.e. Coleoptera and Araenae) that are negatively affected by rhododendron presence (Malo *et al*., 2013) are frequent prey items for bat species such as *M. nattereri*, *M. mystacinus*, *Myotis brandti* and *E. serotinus* (Altringham, 2014). Reduced abundance of such prey could potentially reduce foraging activity by these species in areas invaded by rhododendron. However, Stout (2007) found rhododendron's nectar-bearing flowers attracted more flies and moths, both of which are also important components in the diets of most British bat species (Altringham, 2014). Although studies on the pollination of rhododendron in the UK (e.g. Stout, 2007; Tiedeken and Stout, 2015) have focused on diurnal pollinators, Mejías *et al*. (2002) recorded two species of moth (*Noctua pronuba* and *Campaea honoraria*) visiting rhododendron at night in Spain, one of which (*N. pronuba*) is also common across the British Isles (Waring and Townsend, 2017). Although rhododendron flowers may attract potential bat prey, any positive effects on bats are likely to be limited to the period of when it is flowering.

The aim of this chapter is to investigate how the invasion of forest understorey by *R. ponticum* affects the activity of British bat species, and whether bat responses to local-scale habitat characteristics correspond with differences in species morphology and foraging preferences. Additionally, with rhododendron currently undergoing widespread clearance, the effects of removing it from invaded sites are also assessed to determine whether this potentially benefits any bat species. All activity data for the study were gathered using PAM; the ability to detect and record echolocation calls used by insectivorous bats makes them ideal candidates for this methodology. The use of autonomous recording devices, in this case the AURITA (Beason *et al*., 2019), meant that any potential influence due to human presence was completely avoided. As monitoring took place throughout the night and over prolonged periods of time, this approach additionally enabled the visualisation and assessment of nightly activity patterns in order to evaluate the likelihood that any roosts were located within, or nearby, each site.

Specific predictions tested in this chapter are that rhododendron invasion will have negative effects on activity levels of open space foragers but might have positive effects on the activity of some closed or edge space foragers such as *Myotis* spp., *Pipistrellus* spp. or *P. auritus*. In addition, this chapter investigates whether rhododendron removal has beneficial effects on bats as compared to sites were rhododendron is present or naturally absent. The effects of other habitat characteristics, such as canopy cover, density of trees, distance to water and access by deer, which could also account for differences in bat activity between sites (Bellamy *et al*., 2013; Fuentes-Montemayor *et al*., 2017), were also assessed. Rhododendron is in flower for a relatively short time each year (Snowdonia Rhododendron Partnership, 2015), typically in May and June in the UK (Cross, 1975; Dehnen-Schmutz *et al*., 2004) and was not in flower at any time during field surveys; this study therefore focuses primarily on its structural influence on bats.

3.2 Materials and Methods

3.2.1 Study Location

The study was conducted in Richmond Park, Richmond-upon-Thames, Greater London (51.4° N, 0.3° W) in July and August 2016 and May to July 2017. Covering approximately 2,500 ha, Richmond is the largest of the London parks and a designated Site of Special Scientific Interest (SSSI), National Nature Reserve (NNR) and Special Area of Conservation (SAC) (Royal Parks, 2015). Following consultation with Adam Curtis, the assistant park manager at Richmond, an initial survey was performed to select appropriate locations in May 2016. A total of twelve locations were chosen (Figure 3.1). Sites 1-4 represented woodland with a significant amount of rhododendron in the understorey (Figure 3.2), sites 5-8 were in woodland not invaded by rhododendron in the understorey, and sites 9-12 represented woodland where rhododendron had recently been removed. Mechanical and manual removal of rhododendron had taken place over successive years, with approximately one quarter of Sidmouth Wood being cleared each year, from 2011 and 2015. Sites where rhododendron had been removed were numbered chronologically, from most recent to oldest, according to the year in which they were cleared; 9 (2014/15), 10 (2013/14), 11 (2012/13) and 12 (2011/12).

Figure 3.1. Locations of recording equipment deployed in Richmond Park, 2016. White markers are sites where rhododendron was absent, red markers are sites invaded by rhododendron and yellow markers are previously invaded sites where rhododendron had been removed over successive years. Arrows indicate approximate recorder facings (created by R. Beason © Google Earth, 2018).

Figure 3.2. Rhododendron bushes can form a dense layer of understorey beneath woodland canopy, shading out competitors. Note that although rhododendron was in flower when this photo was taken (28/05/16), it was not during the survey period in July-August (Photo by the author).

3.2.2 Bat Recording, Pass Definition and Data Pre-Processing

One AURITA unit (Audible and Ultrasonic Recording In Tandem; for details see Chapter 2 and Beason *et al*., 2019) was attached to a tree at the centre of each site to record ultrasonic bat calls from 1st July until 2nd September, 2016 and from 2nd May until 5th July, 2017. Unfortunately, in 2017, the recorder at site 3 (rhododendron) developed an intermittent fault (see Section 2.3) and data were only reliable for 8 days after it was replaced. Additionally, the recorder from another rhododendron site (Site 1) suffered a drop in microphone sensitivity in 2017. Due to the loss of data from 2 out of 3 rhododendron sites in 2017, it was decided to only process data from 2016 for further analyses.

AURITA recorders were specifically designed to be mounted at height, which provides added security and increases the number of bat detections in comparison to placing recorders on the ground (Weller and Zabel, 2002). Some bats, particularly pipistrelles and Nyctaloid species, may regularly forage in or above the forest canopy (Müller *et al*., 2013); however, AURITA devices also had to be accessible enough to perform regular card and battery changes and with the limited number of devices available it was only possible to deploy one in each plot. A height of ~2 m was therefore considered a reasonable compromise as previous studies have found that pass counts at canopy level were not significantly different from those at ground level (Collins and Jones, 2009) or within 1.4 m of the ground (Froidevaux *et al*., 2014). Sites were separated by a mean distance of ~130 m, with a minimum distance of 11 m. While such small distances between recorders meant that the same bat individuals could be picked up by several nearby recorders, the aim of this study was not to assess bat population density but instead to explore differences in bat activity at a small spatial scale as the effects of rhododendron presence/absence/removal were expected to be fairly local. Potential spatial autocorrelations between sites were also tested (see Section 3.2.5).

The ultrasonic microphone attached to the RPA2 within each AURITA recorder has a cardioid polar pattern, which is only sensitive to sounds in front of it. When it was necessary to place recorders within the same area (e.g. in Sidmouth Wood for the four sites cleared from rhododendron), they were situated facing away from each other to minimise any overlap of their recording fields (Sleep and Brigham, 2003). Although it was not possible to perform ultrasonic attenuation surveys for the RPA2, Adams *et al*. (2012) found that, for synthetic bat calls of constant amplitude, three out of five commercial bat detectors failed to detect frequencies of 25 kHz beyond 30 m when the source was directly in front of the recorder, and 15-20 m when the source was at a 90° angle. At 55 kHz, the maximum detection range fell to 20 m and 15 m directly in front of the detector and at 90°, respectively; however, in both cases, only one of the five detectors tested achieved this level of performance and ranges were typically shorter (Adams *et al*., 2012). While these authors did not test response at an angle of 180°, it is reasonable to assume that detection ranges would be even shorter than those at 90° and that any overlap in detections between nearby recorders facing in opposite directions should be minimal.

Bat data were recorded as 16-bit, uncompressed mono WAV files using a 384 kHz (192 kHz Nyquist) sampling rate. Recordings were non-continuous, being automatically triggered when a sound was detected above a limit specified in the RPA2 user settings. A triggering threshold of -35 dBFS was used as a compromise between detecting too many false positives and being overly conservative. To preserve battery power and file capacity, units were programmed to record from 19:45 until 05:00 so that recording only occurred between these times and units otherwise remained in sleep mode (see Chapter 2). All recorders were configured with the same settings.

Bat activity in automated surveys is typically defined by the number of 'passes' recorded (Collins, 2016) and it is considered vital to precisely define what constitutes a 'pass' and to ensure this definition remains consistent throughout any project (Reason *et al*., 2016). In this study, a single 'pass' is defined as any activity recorded by a particular bat species within a 5.46 second time block. Using time blocks has the benefit of standardising the scale with which activity is measured for comparison between sites and directly relates the number of passes (*n*) to the length of time bats spent in each location (i.e. *n* x time interval used). Although the RPA2 can potentially record for up to 4 minutes at a time, it will only do so if the triggering threshold is continuously exceeded by bats, or other acoustic events, every 5.46 seconds (Peersonic, 2016). Consequently, even when the maximum recording time was set to longer than 5.46 seconds, there were still many recordings of this length. Splitting longer recordings into shorter ones is more practical than combining shorter ones, and shorter time blocks can also capture subtler differences in activity to avoid skewing results (Miller, 2001). The shortest, and most frequently recorded, file length (5.46 seconds) was therefore chosen as the duration of each time block, which also represented the highest time-scale resolution achievable.

As bat recordings were comprised of files of differing lengths, standardisation was necessary before performing analyses. This was accomplished using the *readWave* function in the R package *tuneR* v1.3.3 (Ligges *et al*., 2016). The minimum RPA2 file size is always 4096 KB, for a 5.46 second file, and any files longer than 5.46 seconds are always exact multiples of this amount. All files could therefore be split into equal lengths without any excess or loss. This was implemented in R, using a loop to read sections of each audio file in increments of 5.46 seconds before saving them to separate sub-files. However, as each sub-file is technically a 'new' copy, its creation and modified dates and times will reflect when the splitting process took place, rather than when the file was originally recorded. To retain this information, the R script also appended the original file creation date and time to the existing filename. To maintain consistency between split and un-split files, another version of the script was also written to rename files that did not require splitting. The R scripts used for splitting and renaming files are provided in Appendix B.

3.2.3 Bat Species Identification and Validation

Only nights on which all recorders completed a full schedule were selected so that activity at all 12 sites, for the same nights, was equally represented within analyses. This was possible for 26 nights; however, to avoid any misleading results due to adverse weather influencing bat activity, nights when it rained, when wind speed exceeded 20 km/h and/or air temperature fell below 7°C, were also excluded (Froidevaux *et al*., 2014; Berthinussen and Altringham, 2015). Weather conditions were checked using data recorded by The Royal Parks' Davis Vantage Pro2 (Davis

Instruments, California, USA) weather station based at Richmond Park. Following exclusions, a total of 22 suitable nights were available for analyses.

BatClassify v2014-07-14 (Scott, 2017) was used for automatic bat identification (see Section 1.3.2.1). Due to difficulty differentiating between calls for noctule (*Nyctalus noctula*), serotine (*Eptesicus serotinus*) and Leisler's (*Nyctalus leisleri*) bats, BatClassify combines them into a single group, NSL. It also groups *M. brandti* and *M. mystacinus* together for the same reason. As BatClassify cannot be configured or customised, interpretation of results is based entirely upon the confidence ratings produced. Scott and Altringham (2014) and Berthinussen and Altringham (2015) recommend a confidence rating threshold of >0.9 as an acceptable threshold for correct identification. However, according to guidelines in Reason *et al*. (2016), investigation into the implications of using different confidence levels is considered necessary to find a suitable balance between accuracy and the number of identifications achieved. Rather than assuming a blanket threshold of 0.91, thresholds for each species were therefore investigated by performing iterative manual validation on a random sample of recordings.

On the 22 suitable nights, 64,412 files were recorded in total. After processing in BatClassify, results were compiled for each species and sorted by their confidence ratings. Using 10% category intervals (i.e. 1 to 0.91, 0.9 to 0.81 etc. down to 0.61), ten files from each interval were chosen for each species/species group using an online random number generator (www.random.org). Whenever less than 10 files were available for a particular interval, all were selected. No occurrences of *Myotis alcathoe*, *Rhinolophus ferrumequinum* or *Rhinolophus hipposideros* were detected by BatClassify and the few files identified as *Barbastella barbastellus* were incorrect. As none of these species have recently been recorded within Richmond Borough (Richmond Biodiversity Partnership, 2010), they were excluded from further analyses. As BatClassify is not capable of identifying *Pipistrellus nathusii*, this species was also excluded from analyses.

Initial assessments of BatClassify thresholds and species identification accuracy were performed by the author and validated by Philip Briggs (Bat Conservation Trust monitoring manager). Although recordings of *M. brandti/M. mystacinus*, *M. daubentonii* and *M. nattereri* were all positively identified as belonging to the *Myotis* genus, it could not be stated with absolute certainty that identifications were correct to species (Briggs, pers. comm., 17 April 2017). Rydell *et al*. (2017) also found BatClassify frequently misidentified *M. daubentonii* as other *Myotis* species and suggested classifying to group, rather than species, could reduce error rates. For these reasons, detections of all *Myotis* species were combined into a single category. As every file in the *Myotis* categories had been identified correct to genus, an initial confidence threshold of 0.61 was considered justifiable for the *Myotis* spp. group.

Classifications of *N. noctula*, *E. serotinus* and *N. leisleri* (NSL), within the 1.0 to 0.91 confidence interval were all correct; however, this interval constituted only a small proportion of files. Misclassifications in the 0.9 to 0.81 category all had ratings below 0.85, which was chosen as an initial threshold for NSL. There was a reduction in accuracy for *P. pygmaeus* classified with ratings below 0.91 and below 0.81 for *P. pipistrellus*. An initial threshold of 0.91 was therefore used for *P. pygmaeus* while 0.86 was used for *P. pipistrellus*, as the largest incorrect value had been 0.85. *Plecotus auritus* has quiet echolocation calls making it difficult to detect and resulting in low levels of activity being recorded (Fuentes-Montemayor *et al*., 2017). Additionally, no files were classified with over 0.9 confidence and results from lower thresholds were mixed. Rather than excluding this species from analyses altogether, the small number of detections meant it was possible to manually verify files with thresholds exceeding 0.8. Further details of initial BatClassify confidence rating evaluations are provided in Appendix C. To evaluate these initial thresholds and generate accuracy statistics, one night was randomly chosen for each site for manual evaluation, which created a test pool of 2,415 files (Table 3.1).

The initial thresholds chosen for BatClassify achieved high degrees of accuracy and precision (i.e. few false positives) for all species except *P. auritus*, likely due to the small sample size (*n*=8) available (Table 3.1). Recall statistics demonstrated that initial thresholds were overly conservative (i.e. excessive false negatives) for some species and could be improved upon. For *P. pygmaeus*, it became apparent that some false positives in the initial sample were due to battery noise and lowering the threshold to 0.85 increased both accuracy and recall with only a small (0.3%) reduction in precision. Additionally, nights where battery noise was apparent in spectrograms were manually verified to correct any false positives and negatives for pipistrelles in recordings caused by battery noise.

Identification of *Myotis* bats by BatClassify proved to be quite reliable and it was possible to lower the detection threshold to 0.48, which increased recall by over 22%, without creating any additional false positives. *Plecotus auritus* was more problematic as reducing the threshold low enough to find all 8 occurrences introduced a disproportionately large number of false positives. As a compromise, the threshold was lowered to 0.75, which doubled the number of true positives without introducing further false positives. Again, because of the limited number of detections for this species, it was possible to manually check any files exceeding this threshold.

Table 3.1. Accuracy statistics based on the manual validation of 2,415 recordings comprised of one night's data per site, chosen at random. NSL represents *N. noctula*, *E. serotinus* and *N. leisleri* and *Myotis* spp. represents *M. brandti/M. mystacinus*, *M. daubentonii* and *M. nattereri*.

Species/ Species group	BatClassify threshold	Precision[1]	Accuracy[2]	Recall[3]
Initial Validation				
P. pipistrellus	0.86	98.9%	97.4%	95.6%
P. pygmaeus	0.91	99.7%	96.4%	92.2%
Myotis spp.	0.61	100%	99.5%	72.2%
NSL	0.85	96.4%	95.2%	19.4%
P. auritus	0.81	50%	99.6%	25%
Adjusted thresholds				
P. pygmaeus	0.85	99.4%	97.1%	94.1%
Myotis spp.	0.48	100%	99.9%	94.4%
P. auritus	0.75	66.7%	99.8%	50%
Including Kaleidoscope Pro true positives				
NSL	0.85	98.7%	97.4%	55.7%

[1] Precision = true positives / (true positives + false positives)

[2] Accuracy = (true positives + true negatives) / total files

[3] Recall = true positives / (true positives + false negatives)

BatClassify did not perform very well for the combined NSL group, missing over 80% of presences for these species. Furthermore, it was not possible to lower the initial 0.85 threshold without introducing a disproportionate number of false positives due to misidentification of *P. pygmaeus* social calls, which frequently occurred in recordings. To increase detections for NSL, all files were additionally processed with Kaleidoscope Pro v5.1.3 (www.wildlifeacoustics.com) using UK classifiers (Bats for Europe 5.1.0), default signal parameters and the most liberal sensitivity setting (-1), to increase the probability of detecting more bats. Positive identifications were then manually verified, to avoid introducing any further false positives. This process increased the number of detected occurrences from 19% to almost 56%. As it was not possible to further improve upon this performance without manually checking all 64,412 recordings, pass counts for NSL and *P. auritus* should thus be considered conservative estimates of activity of these species. With some calibration, BatClassify was generally more accurate than Kaleidoscope Pro (see Appendix D for Kaleidoscope statistics) for most species apart from NSL, and for *P. auritus* where performance was equal. However, relative processing times were considerably faster in Kaleidoscope Pro and enabled large numbers of files to be inspected and labelled quickly and easily. Although validation was extremely time-consuming, Table 3.1 illustrates the importance of properly checking and calibrating automated detection software (Rydell *et al*., 2017).

3.2.4 Site Characteristics

Surveys were performed for all 12 sites where recording equipment was placed and a circular area of 30 m radius, centred upon the tree to which each AURITA was attached, was used to assess the following characteristics at each location:

1. *Canopy cover.* Survey areas were divided into 16 sectors, each with a central angle of 22.5°. For each sector, angles were measured with a compass, using the facing of each AURITA as a starting point, and then delineated with survey tape. Readings were then taken along the centre of each sector, at six equally spaced intervals (2.5 m, 7.5 m, 12.5 m, 17.5 m, 22.5 m and 27.5 m), using a GRS densitometer. 'Tree' was recorded whenever canopy was observed in the crosshairs of the densitometer and 'sky' when it was not. This produced a total of 96 canopy readings for each site (Figure 3.3a) from which the percentage of canopy cover was then calculated.

2. *Ground cover.* Sites were divided and marked out similarly to canopy surveys, except using eight 45° sectors. Predominant ground coverings were visually classified as consisting of rhododendron, grass, bracken, bramble, saplings, open ground and holly, which was the only non-rhododendron shrub present in the understorey at any of the survey sites. Ground cover within each sector was mapped according to distance and angle from the centre point. Completed paper surveys were scanned and the resulting images were used to produce digital maps of ground cover distribution and tree locations (Figure 3.3b). Ground cover percentages (Appendix E) were calculated using ImageJ v1.51j8 (Rasband, 2017). Digitised surveys were converted to greyscale so that pixel colours were represented by a single number (0-255). Different ground cover types were then re-filled using colour values at intervals giving the best separation, i.e. 255/*n* where *n* = number of cover types. The histogram function in ImageJ was used to obtain pixel counts for each colour (i.e. cover type) in the image, which were then converted to percentages of the total pixels.

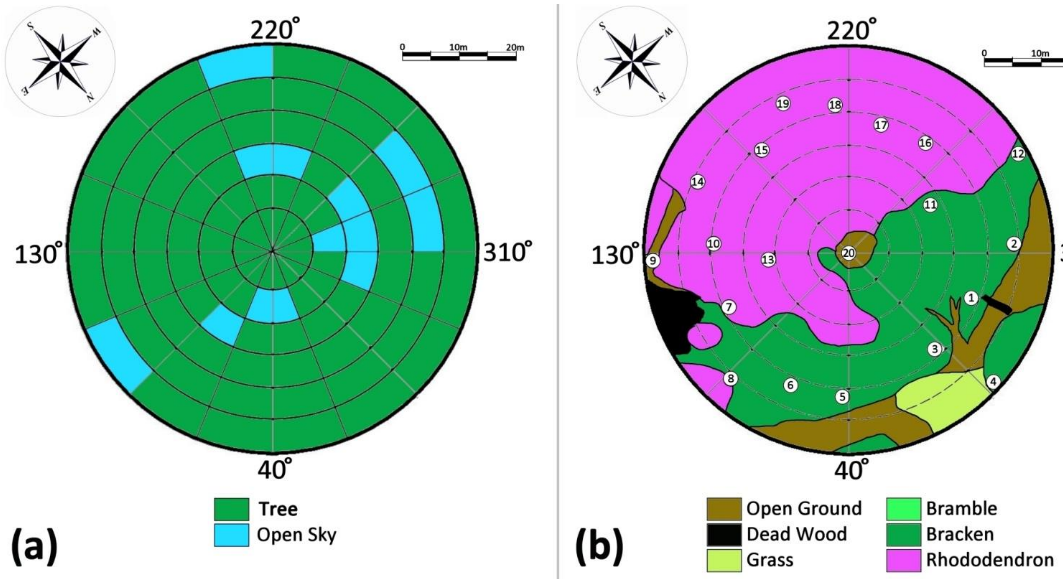


Figure 3.3. Examples of survey maps completed for (a) canopy cover and (b) ground cover and tree locations. Here, 220° is the direction in which the AURITA at this location (site 4) was facing. Numbered circles in 3.4b represent trees >7 cm DBH, each number corresponds to an entry in the tree inventory (see Appendix E) for that site.

3. *Tree inventory.* All trees within each sector were identified to species and their diameter at breast height (DBH) measured. Every tree with a DBH ≥ 7 cm was recorded (Jenkins *et al*., 2018) and numbered on the ground cover survey sheet and its details recorded separately under the corresponding number. The total number of trees recorded for each species was used to calculate the Shannon diversity Index (Shannon, 1948) for each location. The mean DBH for each site was calculated to indicate the average tree size. To represent structural heterogeneity, the standard deviation of tree DBH was also calculated for each site. The total number of living trees in each plot was included to represent tree density, as all survey areas were equal in size, and the number of dead standing trees was also recorded at each location.

4. As most UK bat species demonstrate a strong affinity for water (Bellamy *et al*., 2013), distance to the closest water body (pond or waterway) was measured for each site using the ruler tool in Google Earth Pro v7.3.2.5491 (https://earth.google.com). Richmond Park also has substantial populations of red deer (*Cervus elaphus*) and fallow deer (*Dama dama*), and deer are known to modify forest structure and reduce density of understorey foliage (Eichhorn *et al*., 2017). Fuentes-Montemayor *et al*. (2013) recorded higher activity levels for *Myotis* spp. and *P. pipistrellus* in areas where grazing stock were present although

> Barbaro *et al*. (2019) found that smaller bats were less prevalent in areas grazed by wild ungulates. Additionally, the increased numbers of flies associated with deer (Palmer *et al*., 2019) and their dung (McCracken *et al*., 1995) can provide additional food for bats. As half of the sites (6, 7 and 9-12) were not accessible to deer, access to sites by deer was also included as an explanatory variable in analyses.

Summaries of site characteristics, canopy cover and ground survey maps, and tree species inventories are all presented in Appendix E.

3.2.5 Statistical Analyses

Statistical analyses were performed using R v3.4.4 (R Core Team, 2018) within RStudio v1.0.153 (RStudio Team, 2016). Generalised Linear Mixed Models (GLMMs) were produced using the *glmmTMB* v0.2.3 package (Brooks *et al*., 2017) with the total number of bat passes per night as the dependent variable. First, to test for the influence of rhododendron on bat activity, a statistical model including rhododendron status of the site was employed for each bat species/species group:

Full model = *total passes/night* ~ *treatment* + (1|*site*) + (1|*day*)

Null model = *total passes/night* ~ 1 + (1|*site*) + (1|*day*)

The fixed factor *treatment* indicates rhododendron status (3 levels: present, absent or removed) within the site. Survey sites (*site*) were specified as a random effect to account for repeated sampling at the same locations (Bolker, 2015) and Julian date (*day*) was also included to account for possible temporal autocorrelation (Crawley, 2007). Comparison of AIC values (Appendix F) confirmed that using both *site* and *day* as random effects improved the fit of all models except that for *P. auritus*, for which *day* was not included as a random effect. As every combination of the date and site groups were included (i.e. every site was present for every day and vice versa), the model was structured using a crossed design (Quinn and Keough, 2002).

For measures of bat activity using number of passes per time interval, a Poisson distribution, which is typical for count data, was initially used (Müller *et al*., 2013). Poisson models were tested for overdispersion using the function *overdisp_fun* (Bolker *et al*., 2009) and negative binomial distributions were applied if data were overdispersed (Crawley, 2007). As presence/absence was more appropriate than number of passes for the low activity counts of *P. auritus*, this species was modelled using a binomial distribution (Quinn and Keough, 2002). Selected models were then used to assess the overall effect of treatment for each species/species group by performing likelihood-ratio tests with equivalent null models with *treatment* excluded.

QQ residual plots with one-sample Kolmogorov-Smirnov (KS) and significant outlier tests were produced for the final models using the *DHARMa* v0.2.4 package, which is specifically designed for GLMMs (Hartig, 2019), to assess 'goodness of fit' (Appendix F). As sites were randomly distributed, and some were closer together than others, *DHARMa* was also used to check for spatial autocorrelation in model residuals using Moran's I (Moran, 1950).

A second set of statistical analyses was performed to assess the relative impact other site characteristics had on bat activity. Ground cover percentages (Tables E2 and E3) were grouped into three understorey categories representing differences in vegetation structure and composition: woody understorey >1.5 m height (rhododendron, tree saplings and holly), dense vegetation ~0.5-1 m high (bracken and bramble) and open space (grass, dead wood and bare soil). All site variables were checked for collinearity (correlation coefficients >0.7; Dormann *et al*., 2013) with the *chart.Correlation* function in the *PerformanceAnalytics* v1.5.2 package (Peterson and Carl, 2018). Mean DBH was highly correlated with both Shannon Index (-0.8) and total number of trees (-0.79) and was removed from analysis. The ground cover category 'dense vegetation' was also strongly correlated with canopy cover (-0.74) and understorey (-0.7). To resolve this issue, ground cover percentages were converted to Domin Scale (Rodwell, 2006), which has been used to represent understorey cover in previous studies, e.g. Fuentes-Montemayor *et al*. (2017). The correlation table for the 9 remaining site variables is presented in Appendix G.

For reasons detailed in Section 3.2.4, deer access to the site (yes/no) was also included as a fixed effect. With random effects, this made a total of 12 explanatory variables (tree Shannon Index, standard deviation DBH, total living trees, total dead trees, canopy cover, woody understorey cover, dense vegetation understorey, amount of open ground, distance to water, deer access, site and date) for consideration in analyses. Principal components analysis (PCA) was therefore applied for factor reduction (Quinn and Keough, 2002). PCA was carried out using the *prcomp* function from the *stats* package in R (http://www.r-project.org). The option to use a common scale in *prcomp* was selected to account for differences in the units of measurement used for input variables (Crawley, 2007). Orthogonal rotation was also performed using the *varimax* function in the R *stats* package (R Core Team, 2018) in order to more evenly distribute variance between the retained principal components (Jolliffe, 2002).

Four principal components (PCs), which explained over 88% of the total variance, were retained. Higher PC1 scores represented more coverage by dense ground vegetation, less open ground and longer distances from water. Higher scores for PC2 were associated with more homogeneous tree sizes (lower std. dev. DBH) and fewer dead trees. Higher scores for PC3 primarily related to lower woody understorey cover and, to a lesser degree, lower canopy cover, while PC4 scores were positively related to higher Shannon Index scores and more living trees. Biplots, component loadings and site scores are presented in Appendix H. Combining these variables with deer access produced the following full model:

$$\textit{total passes/night} \sim PC1 + PC2 + PC3 + PC4 + deer + (1|site) + (1|day)$$

As this model contained both numeric and binary predictors, numeric input variables (PC1 to PC4) were divided by 2 standard deviations to enable direct comparison with untransformed binary predictors (deer access) (Gelman, 2008). Candidate models were constructed for every combination of variables and model selection was then performed using an information-theoretic approach with small sample AIC (AIC_C) scores, as the highest-dimensioned model (7 variables) exceeded the recommended minimum of 40 observations per variable (Burnham and Anderson, 2002). Various thresholds have been recommended for selecting the best set of candidate models (Harrison *et al*., 2018); in this case, $\Delta AIC_C < 2$ was used as higher thresholds would have meant including excessive numbers of candidate models (Grueber *et al*., 2011). Model averaging was then performed on the best candidate models with *MuMIn* v1.42.1 (Barton, 2018). Full average results were reported (Bolker *et al*., 2009) with unconditional standard errors to account for model selection uncertainty (Grueber *et al*., 2011). Details of model selection and averaging performed for site characteristics models are presented in Appendix H.

3.2.6 Temporal Pass Plots (TPP)

In order to explore temporal patterns of bat activity between sites and over the season, and to identify potential roosting sites, the following method (the Temporal Pass Plot) of visualising temporal bat activity was developed. Assessments of variations in temporal activity are infrequently presented (Newson *et al*., 2015) and previous studies analysing temporal analysis have typically presented results as line graphs or bar charts depicting single nights or average activity over several nights (e.g. Börk, 2006; Fullard *et al*., 2008). Newson *et al*. (2015) visualised temporal activity variations over several half-monthly time periods with frequency distribution boxplots of activity relative to sunset while Temporal Pass Plots are intended to examine activity using individual passes for each night in each site.

File metadata, such as creation and modified times, can easily be extracted from recordings and incorporated into filenames (see Section 3.2.2) using R scripts to split and rename, or just rename, files with the date and time appended. Following identification, date and time information could be extracted from filenames enabling each pass to be plotted as a single point according to when it was recorded using separate axes for time (x) and date (y). As all recordings were standardised to a file length of 5.46 seconds, plots automatically shared a common scale, enabling direct comparisons of different dates, species and locations. Plots produced are also inherently extremely high resolution, with up to 659 (3600/5.46 seconds) data points every hour. Additional temporal information, such as sunset and sunrise times, recording schedules, etc. can easily be plotted alongside activity. This process was implemented using Microsoft Excel (Office 365 ProPlus). Due to the low number of detections, *P. auritus* was excluded from this analysis.

The most suitable means of evaluating activity patterns observed in this study appeared to be through comparison with previous studies that also presented activity patterns for individual nights at single locations. These would additionally need to have been performed on species included in this study and, at least in part, at the same time of year (July-August). Fortunately, three studies that fulfilled these criteria were found for *P. pipistrellus* (Swift, 1980; Maier, 1992) and *E. serotinus* (Catto *et al*., 1995); however, as all of these studies related specifically to activity observed outside roosting sites, TPP assessments were therefore limited to searching for similar patterns reported in these previous studies that could potentially indicate roosting activity.

3.3 Results

Out of a total of 64,412 recordings on the 22 nights when suitable weather prevailed and all 12 recorders completed their schedule, 57,251 containing passes were detected. *Pipistrellus pygmaeus* was recorded most frequently (55.3%), followed by *P. pipistrellus* (38.6%), NSL (4.3%), *Myotis* spp. (1.7%) and *P. auritus* (0.1%). Total pass counts recorded at each site over the 22 compatible nights are presented in Appendix I. Results of Moran's I tests revealed no significant spatial autocorrelations between survey plots (Table 3.2). Likelihood-ratio tests revealed that rhododendron status of the site had a significant ($P<0.001$) overall effect on NSL but did not significantly affect any other species (Table 3.3).

Rhododendron presence had a significant negative effect on NSL bats, which were less active in sites with rhododendron compared to sites where it was absent or had been removed (Table 3.4). NSL was the only bat species/species group for which GLMM estimates in rhododendron sites were lower than both other treatments and, except for site 4, locations with rhododendron were notable for an almost complete absence of NSL species (Figure 3.4a). Activity of NSL bats at sites where rhododendron was absent was also significantly lower than in sites where it had been removed. The lower recall rate for this group (~56%) suggests numbers are probably somewhat underestimated; however, as equipment and analyses were duplicated across all sites and a fairly large number of passes were detected, the results are likely to represent a fair estimate of this group's relative distribution.

Table 3.2. Spatial autocorrelation test results for rhododendron status GLMMs obtained using *DHARMa* with 10,000 simulations.

Species model	Observed	Expected	Std. dev.	*P* value
P. pipistrellus	-0.368	-0.091	0.206	0.177
P. pygmaeus	-0.117	-0.091	0.202	0.896
Myotis spp.	-0.345	-0.091	0.207	0.221
NSL	-0.280	-0.091	0.202	0.349
P. auritus	-0.407	-0.091	0.206	0.126

Table 3.3. Likelihood-ratio tests for overall effect of rhododendron status of the site (absent/present/removed) on bat activity. Significant results are shown in bold.

Species/species group	Deviance	Chisq	Chi Df	*Pr(*>Chisq*)*
NSL	**1229.4**	**22.46**	**2**	**<0.001**
Pipistrellus pipistrellus	2593.5	0.578	2	0.749
Pipistrellus pygmaeus	2901.8	2.826	2	0.243
Myotis spp.	1069.7	3.643	2	0.162
Plecotus auritus	167.72	0.327	2	0.849

Table 3.4. Post-hoc pairwise comparisons of NSL activity between sites where rhododendron was present, absent, or had been removed. Significant results are shown in bold.

Treatments compared	Estimate	Std err	*Z* Value	*Pr(*>|*z*|*)*
Nyctalus noctula, *Eptesicus serotinus* & *Nyctalus leisleri* (NSL)				
Absent - Removed	**-1.004**	**0.476**	**-2.107**	**0.035**
Present - Removed	**-4.071**	**0.527**	**-7.727**	**<0.001**
Present - Absent	**-3.067**	**0.529**	**-5.793**	**<0.001**

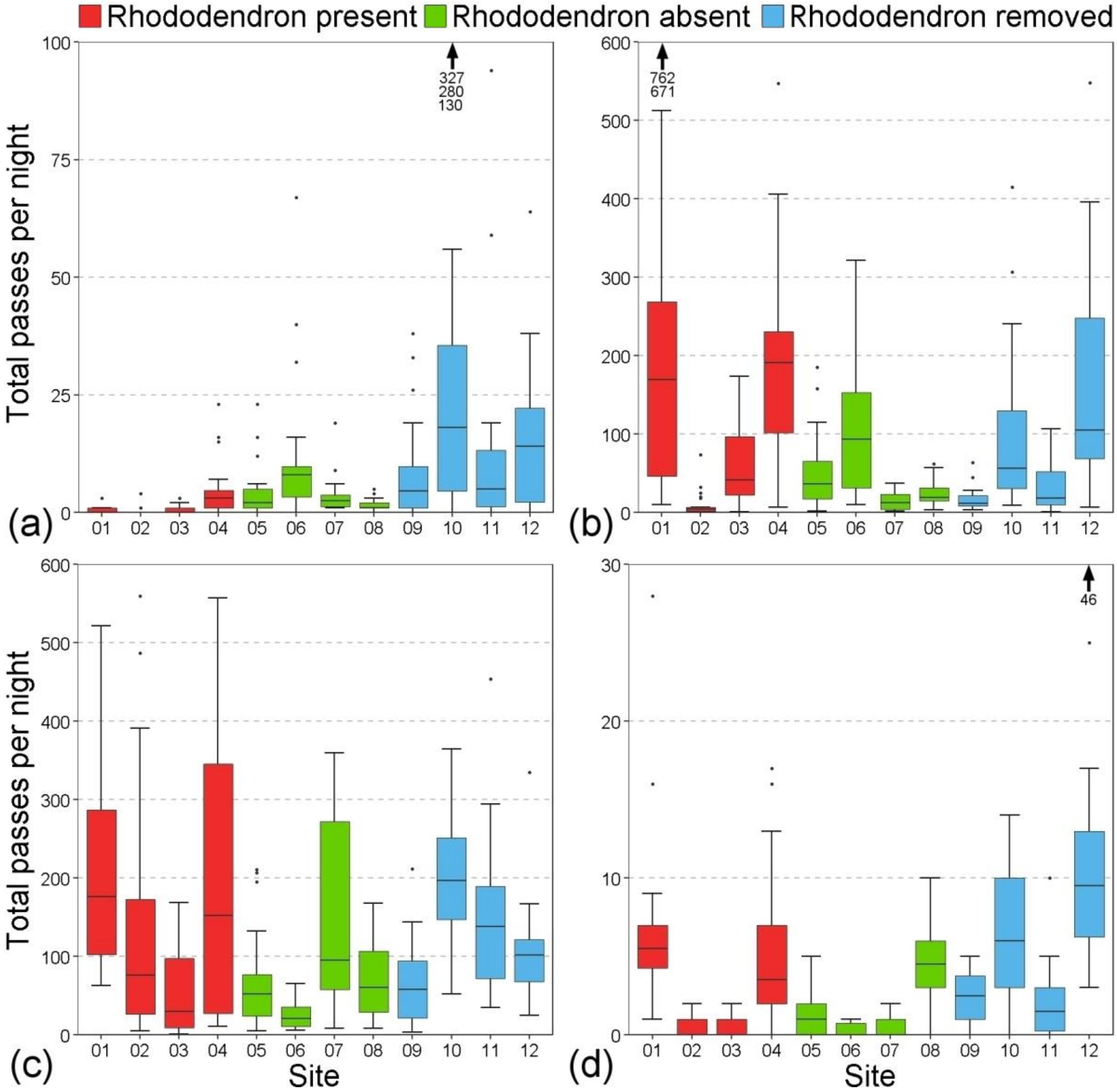


Figure 3.4. Daily pass counts recorded per site over 22 nights in Richmond Park in 2016 for (a) *N. noctula*, *E. serotinus* and *N. leisleri*, (b) *P. pipistrellus*, (c) *P. pygmaeus* and (d) *Myotis* spp. with medians (lines) and interquartile ranges shown. To improve scale resolution, some outliers are denoted with an arrow and outlier values.

Activities of *P. pipistrellus* and *P. pygmaeus* did not differ significantly between treatments (Table 3.3), but for both species activity was slightly lower at sites where rhododendron was absent in comparison to those where it had been present or removed (Figures 3.4b and 3.4c). Activity of *Myotis* bats did not differ significantly between the sites with different rhododendron status but tended to be higher at sites where rhododendron has been removed (Figure 3.4d). Activity of *P. auritus* was recorded at 8 out of 12 sites (Figure 3.5) and did not differ between treatments, although the low detection rate for this species, in combination with the low recall rate for the automated identification software, meant there were very few detections on which to base observations.

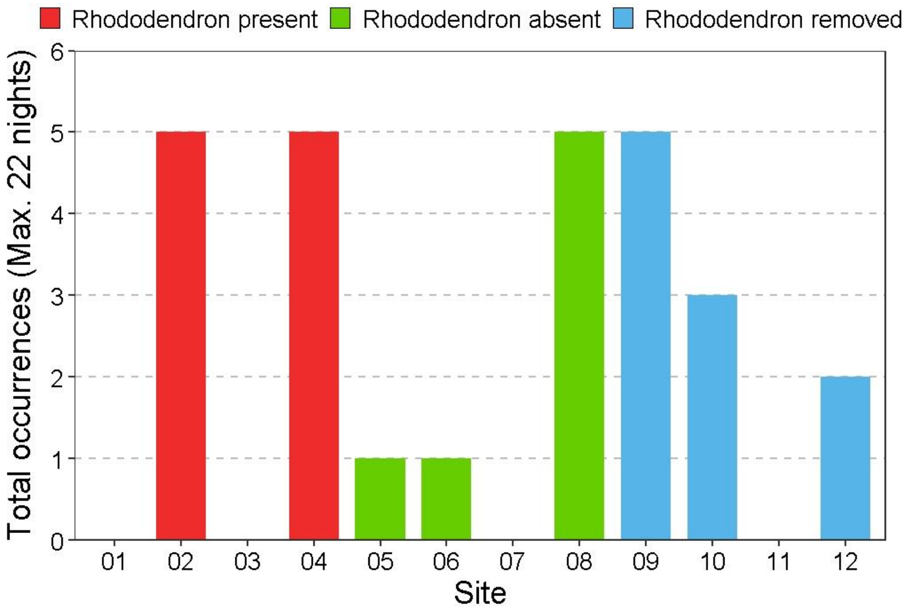


Figure 3.5. Total number of occurrences recorded for *P. auritus* over 22 nights in Richmond Park in 2016.

Effect size plots for site characteristic GLMMs demonstrated that activity of NSL was higher in sites with less canopy cover and woody understorey (PC3); however, the most important predictor of higher NSL activity was the exclusion of deer (access = no), which had a significant positive effect (Figure 3.6a). *Pipistrellus pipistrellus* displayed higher activity in sites with fewer trees (PC4) and greater woody understorey cover and preferred areas with more homogeneous tree sizes and fewer dead trees (PC2) (Figure 3.6b). Activity of *P. pipistrellus* was also higher at sites with denser ground vegetation and less open ground (PC1), and those accessible by deer. *Pipistrellus pygmaeus* demonstrated similar preferences to *P. pipistrellus* for PC3 and PC4, except that the effect of increased woody understorey cover (PC3) was significantly positive in this case (Figure 3.6c). Contrary to *P. pipistrellus*, activity of *P. pygmaeus* was lower in sites that were accessible by deer, had denser ground vegetation or were further away from water. Activity of *Myotis* spp. and *P. auritus* (Figures 3.6d and 3.6e, respectively) was not significantly affected by any of the measured site characteristics. Activity of *Myotis* spp. tended to be higher in sites containing denser woody understorey, more diverse tree sizes and fewer trees. Full results of GLMMs for site-specific characteristics are provided in Appendix I.

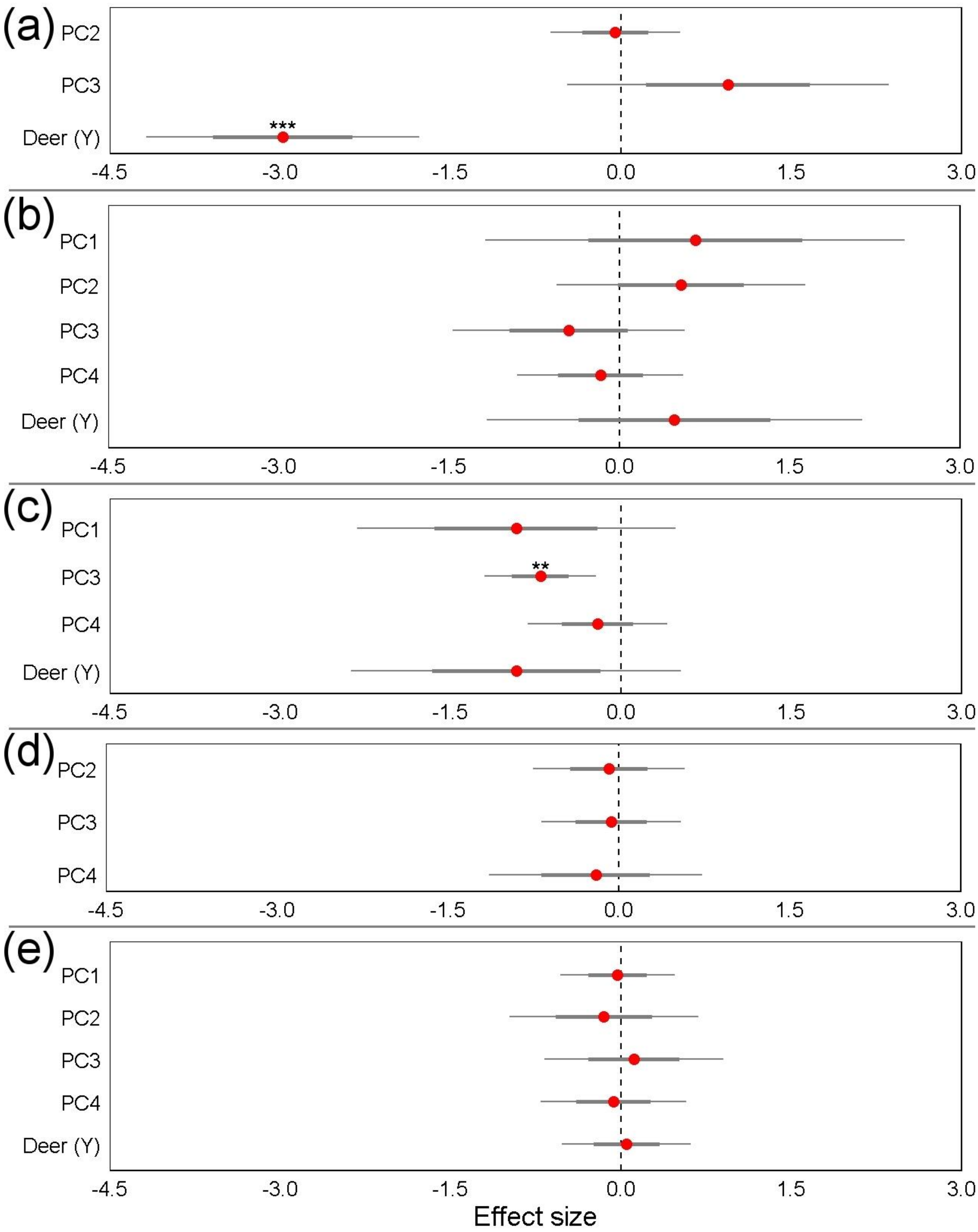


Figure 3.6. GLMM results of site-specific characteristics for (a) NSL, (b) *P. pipistrellus*, (c) *P. pygmaeus*, (d) *Myotis* spp., and (e) *P. auritus*. Numeric input variables (PC1 to PC4) were divided by 2 standard deviations to enable direct comparison with untransformed binary predictors i.e. deer access. Effect sizes are represented by red circles; thick grey lines indicate standard errors and thin grey lines show 95% confidence intervals. Significance codes: <0.001 '***', <0.01 '**', <0.05 '*', <0.1 '.'

Temporal Pass Plots (TPPs) were produced for each species/species group at each site for the 22 days when all recorders completed their schedule. As 48 TPPs (4 species x 12 sites) were produced in total, these are presented together in Appendix J. Example TPP results for *P. pygmaeus* at two sites (2 and 11) are provided in Figure 3.7. These sites had similar totals over the 22 days analysed (3045 and 3216, respectively) and were intentionally chosen to illustrate that similar activity levels did not necessarily represent similar temporal activity patterns.

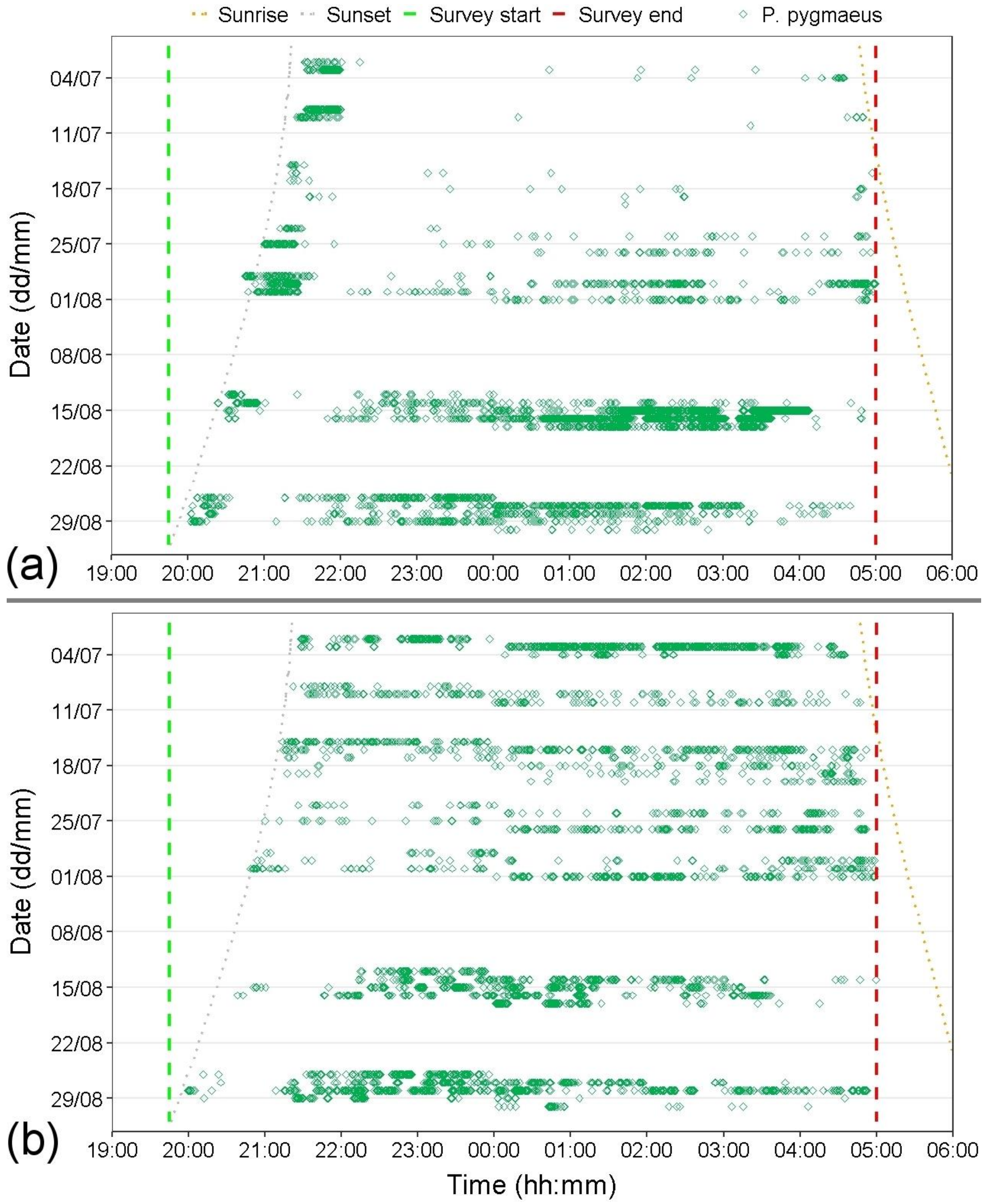


Figure 3.7. Temporal Pass Plots for *P. pygmaeus* in Richmond Park, 2016 in (a) site 2 and (b) site 11 for the same 22 nights. Each point represents bat activity with a 5.46-second time period; sunset and sunrise times were obtained from HM Nautical Almanac Office (2017).

In site 2, there are distinct peaks in activity lasting roughly 30 minutes at, or shortly after sunset (Figure 3.7a). In early July, these are followed by an almost complete absence of activity for the rest of the night before gradually increasing from late July through August. In contrast, activity at site 11 (Figure 3.7b) was more evenly distributed throughout the night while lacking the intense activity spikes around sunset seen in site 2. Patterns of temporal activity observed for site 2 are likely to indicate the presence of a roost close by, from which the bats emerge in the evening and to which they return in the morning. Table 3.5 therefore offers a tentative suggestion as to which sites may have either contained roosts, or had a roost nearby, at some point during the survey period based on the presence of observable peaks in activity at, or shortly after, dusk in TPPs.

Table 3.5. List of sites in Richmond Park, 2016, where visual inspection of Temporal Pass Plots suggested the possible presence of a roost or a roost nearby (X).

Site	NSL	*P. pipistrellus*	*P. pygmaeus*	*Myotis* spp.
Rhododendron present				
1		X	X	X
2			X	
3				
4		X	X	
Rhododendron absent				
5	X			X
6	X	X	X	
7			X	
8			X	X
Rhododendron removed				
9	X			X
10	X		X	X
11	X			X
12	X	X	X	X

3.4 Discussion

This study represents the first assessment of rhododendron effects on the activity of British bat species. The results of the current study support the hypothesis that rhododendron effects on bat activity are dependent on the foraging strategy employed by the particular bat species/species group, and thus, range from negative to neutral.

3.4.1 Effects of Rhododendron and Other Site-Specific Characteristics on Bats

3.4.1.1. NSL

As predicted, activity of the larger, less manoeuvrable, aerial hawkers *N. noctula*, *E. serotinus* and *N. leisleri*, which prefer foraging in open spaces, was significantly lower at sites with rhododendron present in the understorey. However, NSL activity was also significantly higher in sites where rhododendron had been removed in comparison to those where it was absent, suggesting that rhododendron may not have been the only influencing factor at play. Indeed, the most significant overall predictor of NSL activity was the accessibility of sites to deer. The presence of deer can potentially have positive and negative effects on bats. The deer themselves may attract increased numbers of biting flies, which are then preyed upon by bats (Palmer *et al*., 2019), and a number of fly and beetle species potentially associated with deer dung are also eaten by some bats (McCracken *et al*., 1995; Stewart, 2001). Alternatively, the presence of grazing stock in woodland has been shown to significantly reduce the abundance of moths (Fuentes-Montemayor *et al*., 2012), which are also potential prey for all three NSL species (Altringham, 2014). It has also been suggested that grazing stock could potentially benefit aerial hawking species by reducing clutter and creating more open spaces (Fuentes-Montemayor *et al*., 2013). Indeed, there is evidence that deer had a similar effect on clutter in Richmond park as the two non-rhododendron sites where deer were present (5 and 8) were also the only sites without any woody understorey (Eichhorn *et al*., 2017). However, despite the total lack of woody understorey, NSL activity in these two sites was more similar to that of rhododendron sites where woody understorey was present. This suggests that, of these two possible effects, prey reduction would appear to be more influential. This may help explain the large differences in NSL activity between treatments as all four sites with rhododendron present were accessible to deer, compared to two sites with rhododendron absent and none in sites where it had been removed. Therefore, the negative influence of rhododendron observed for NSL species may have been more pronounced due to a combination of two negative influences, access by deer and greater woody understorey coverage.

There is some evidence that NSL species may be more frequently detected above the canopy layer in closed canopy stands (Collins and Jones, 2009; Müller *et al*., 2013), which could potentially have influenced pass counts for these species as recorders were only located beneath the canopy. However, most sites in Richmond had similar levels of canopy cover (~78%) with three sites (2, 3 and 12) having exactly the same level of canopy cover (81%). In sites two and three (rhododendron present) total NSL activity was consistently low (5 and 11 passes, respectively) while in site twelve (rhododendron removed) 347 NSL passes were recorded, the second highest number for any site. Furthermore, the fifth highest total of NSL passes (188) was recorded at the site with the lowest amount of canopy cover (56%) and the highest number of passes (1080) for NSL was recorded at a site with 78% canopy cover (Appendices E; I). Differences in canopy cover would not therefore appear to be responsible for differences in the number of NSL passes recorded between the sites in this survey.

Although NSL bats were grouped together out of necessity, *N. noctula* and *N. leisleri* are generally considered to be relatively similar in terms of morphology, diet, foraging strategy and seasonal activity patterns (Müller *et al*., 2012; Altringham, 2014; Ruczyński *et al*., 2017). *Eptesicus serotinus* is also typically classified as a less manoeuvrable, aerial-hawking bat with similar foraging habitats and seasonal activity patterns to *N. noctula* and *N. leisleri* (Ciechanowski *et al*., 2010; Obrist *et al*., 2011; Müller *et al*., 2012; Müller *et al*., 2013; Lacoeuilhe *et al*., 2018) and has frequently been included within the same group or foraging guild as *N. noctula* and *N. leisleri* by previous studies (e.g. Vaughan *et al*., 1997; Collins and Jones, 2009; Müller *et al*., 2012; Lacoeuilhe *et al*., 2018). Nevertheless, there are some differences in the preferred prey and roosting locations of these three species (Entwistle *et al*., 2001; Altringham, 2014), which could potentially complicate the interpretation of results. Furthermore, grouping NSL together meant it was not possible to assess the relative influence of any effects on each of these species individually.

3.4.1.2. Pipistrelle Species

Previous studies have recorded negative (Fuentes-Montemayor *et al*., 2013; 2017) and neutral (Müller *et al*., 2012) responses to dense understorey for *P. pipistrellus* and *P. pygmaeus* activity and it was therefore uncertain how these adaptable, edge space foragers would be affected by the increased clutter due to rhododendron. In this study, neither *P. pipistrellus* nor *P. pygmaeus* demonstrated any significant reduction in activity at rhododendron sites and pass count totals of both species, by treatment, were actually higher for rhododendron sites as a whole (Appendix I). Increased activity levels of *P. pipistrellus* and *P. pygmaeus* have previously been associated with hedgerows and hedgerow trees (Boughey *et al*., 2011; Lacoeuilhe *et al*., 2016) and the hypothesised use of rhododendron edges as proxies for hedgerows offers one potential explanation. However, as specifics on the height, composition or structure of understorey cover were not available for the previous studies, it was not possible to say whether differences in understorey structure could potentially explain differences from previous findings.

Pipistrellus pipistrellus activity showed weak positive associations with deer presence and lower tree density, which have also been suggested by previous studies (Fuentes-Montemayor *et al*., 2013; 2017). Overall though, there was no single significant predictor for *P. pipistrellus* activity. This is perhaps not surprising, because, as an edge space forager, *P. pipistrellus* can adjust its echolocation calls in order to forage in a wide range of habitats (Kalko and Schnitzler, 1993). Müller *et al*. (2012) also found that higher density of vegetation did not negatively influence activity by edge space foragers, including *P. pipistrellus*.

Interestingly, large differences in *P. pipistrellus* activity were recorded between sites which were very close to each other. For instance, the highest total number of *P. pipistrellus* passes (4,785) across all 12 sites was recorded at site 1 and the lowest total (224) was recorded at site 2; both of these sites had rhododendron present and were within 30 m of one another. This difference in bat activity could be explained by the large amount (53%) of open, unvegetated ground at site 2, which was higher than at any other site and one of the factors that had the largest negative effect on *P. pipistrellus*. A similar situation occurred in site 9, which also had comparatively lower counts of *P. pipistrellus* compared to other nearby sites (10 and 12) in Sidmouth Wood. In this case, the lower amount of canopy cover and the higher variation in DBH were recorded in site 9, both of which had negative effects on *P. pipistrellus* activity (Figure 3.6b). Alternatively, high levels of variation between nearby sites could be due to some of the recorders being situated along commuting routes used by bats emerging from a nearby roost while others were not.

The significant positive relationships between activity of *P. pygmaeus* and woody understorey and canopy cover could explain the lack of negative effect of rhododendron on this species. In line with previous studies, *P. pygmaeus* demonstrated higher activity in sites with lower tree densities (Fuentes-Montemayor *et al*., 2017) and proximity to water also appeared to be more influential for *P. pygmaeus* than *P. pipistrellus* (Davidson-Watts *et al*., 2006; Bellamy *et al*., 2013). Unlike *P.*

pipistrellus, *P. pygmaeus* demonstrated a negative, but non-significant, association with sites that were accessible by deer. Although the abundance of moths may be reduced by the presence of grazers (Fuentes-Montemayor *et al*., 2012), it is suggested that pipistrelles generally avoid moths as prey items and primarily feed on flies (Altringham, 2014). An increase in the abundance of flies due to the presence of deer (Palmer *et al*., 2019) could thus account for the positive relationship observed for *P. pipistrellus*. Despite having similar prey preferences, *P. pygmaeus* typically spends a larger proportion of time foraging over water (Vaughan *et al*., 1997) and is more reliant on species associated with aquatic environments (Altringham, 2014). It is therefore unlikely to gain as much benefit as *P. pipistrellus* from any increases in prey abundance associated with deer or their dung. Additionally, the ability of high numbers of deer to significantly reduce the density of understorey (Eichhorn *et al*., 2017) could also contribute to different responses of the two pipistrelle species. As *P. pygmaeus* activity was significantly influenced by the presence of woody understorey, it is logical that this species would be more negatively affected by any reduction in understorey due to deer grazing than *P. pipistrellus*. Somewhat surprisingly, sites with rhododendron, where the highest levels and overall totals for *P. pygmaeus* activity were recorded, were the only treatment where all four sites were accessible to deer. At these sites, however, woody understorey was comprised entirely of rhododendron, which appeared to be unaffected by grazing.

3.4.1.3 *Myotis* Species and *P. auritus*

Activity of *Myotis* species (*M. brandti, M. mystacinus, M. daubentonii* and *M. nattereri*) and *P. auritus* was not significantly affected by the presence of rhododendron. As these bats are predominantly gleaning species capable of foraging in cluttered spaces (Altringham, 2014), one might expect to see higher activity levels in rhododendron sites where more understorey was present. Instead, it was found that sites where rhododendron had been removed tended to have higher activity levels for *Myotis* species. It is feasible that reduced biomass of arthropod prey species such as spiders (Malo *et al*., 2013) and the low number of insect herbivores (Taylor *et al*., 2003) that are found on rhododendron would negatively affect gleaning species, which take prey directly from vegetation, more than species which take prey from the air. If so, any potential benefit due to increased vegetation surface area from which to capture prey could effectively be cancelled out by the associated reduction in prey species.

Generally, effects of site characteristics on *Myotis* spp. agreed with the foraging strategies of this species group although the preference for lower tree densities was somewhat contrary to expectations for gleaning bats (Fuentes-Montemayor *et al*., 2013). The likely explanation for this stems from the necessity of combining the *Myotis* species into one group. Although there are similarities in their echolocation calls and wing morphologies, there is nevertheless some variation in foraging strategies and habitats between species within this guild; Siemers and Swift (2006) reported differences in the diets of *M. nattereri* and *M. bechsteinii* that were respectively typical of edge space aerial hawkers and narrow space passive gleaners, while *M. daubentonii* is a trawler that habitually forages over water (Altringham, 2014). Assessing the specific habitat preferences of these species as a single group is therefore potentially problematic. If the *Myotis* spp. group happened to consist primarily of one particular species, results would naturally be biased towards its preferences. Alternatively, if the group contained a fairly even mix of different species, the preferences of individual species could be lost amidst the 'noise' of the other species' preferences. Fuentes-Montemayor *et al*. (2013) found a positive, significant relationship between higher tree densities and activity of *Myotis* spp. In this particular study, they trapped and manually identified bats in addition to using acoustic monitoring and found over 90% of the species were *M. nattereri*. In a later study, again combining *Myotis* species but this time using only acoustic surveys (Fuentes-Montemayor *et al*., 2017), they did not detect any significant relationships between *Myotis* spp. and local habitat variables (including tree density). It would thus appear that interpretation of habitat preferences for *Myotis* species as a group should be treated with some caution.

Detectability of bat species may also be influenced by differences in environmental characteristics such as dense vegetation. Patriquin *et al*. (2003) found that sounds at 40 kHz were unaffected by increased vegetation density and although sounds at 25 kHz were affected, detection range was only reduced by three metres. In the current study, any such effect would most likely influence the number of passes detected for NSL, which vocalise around this frequency. However, the lowest number of NSL passes was recorded in site 2, where understorey was similar in coverage (~30%), if not in constitution, to that of sites 10, 11 and 12, where the highest numbers of NSL passes were recorded. For these reasons, it was assumed that any detectability issues due to vegetation density were unlikely to have significantly influenced results.

Problems detecting *P. auritus* currently make it difficult to go far beyond confirming its presence and even then, as is the case for any bat species, a lack of detection should not be assumed to confirm its absence (Collins and Jones, 2009). Analyses did not reveal any significant predictors for *P. auritus* activity. Positive effects observed for lower understorey cover and fewer trees were contrary to expectations for a gleaning species; however, both effects were weak. Other acoustic studies have also reported small numbers of detections for this species (e.g. Collins and Jones, 2009;

Bellamy *et al*., 2013; Fuentes-Montemayor *et al*., 2013). At least for now, detection of quieter bat species such as *P. auritus* remains problematic for acoustic bat surveys.

3.4.2 Temporal Pass Plots

Plotting bat activity over time potentially reveals behavioural patterns indicating the presence of nearby roosts, navigation routes etc. (Kerbiriou *et al*., 2019), yet this type of analysis is rarely employed in bat studies (Newson *et al*., 2015). Previous assessments of variation in bat temporal activity have typically been presented as line graphs or bar charts depicting single nights or average activity over several nights (e.g. Börk, 2006; Fullard *et al*., 2008; Ruczyński *et al*., 2017). More recently, Newson *et al*. (2015) visualised temporal activity variations over several half-monthly time periods with frequency distribution boxplots of activity relative to sunset. The increasing use of autonomous recording devices that produce digitally time stamped audio files now provides the means of plotting individual passes over periods of days, weeks or even months.

Temporal Pass Plots developed in this study revealed some distinctive patterns of temporal activity across sites. Some activity patterns for *P. pygmaeus*, such as those in Figure 3.7a, most closely resembled observations made outside *P. pipistrellus* roosts by Swift (1980), who noted roughly bimodal activity peaks around dusk and dawn during July, with shorter emergence times in August followed by more evenly distributed activity through the night, tailing off before dawn. Although the study by Swift (1980) supposedly relates to *P. pipistrellus*, it was performed almost 20 years before *P. pygmaeus* was classified as a separate species (Jones and Barratt, 1999). Indeed, the study by Maier (1992) also stated to be on *P. pipistrellus*, recorded quite different activity patterns (more tabletop in nature for late July and August) and, unlike Swift (1980), reported that bats would frequently remain outside roosts for majority of the night. The activity patterns Maier (1992) describes are actually more consistent with those observed for *P. pipistrellus* at some sites in this study, e.g. Figure J6a. Based on the differences in activity patterns between pipistrelle species observed in this study, the species studied by Swift (1980) would appear more likely to have been *P. pygmaeus*, whereas Maier (1992) does appear to have studied *P. pipistrellus*. If so, this would help reconcile the differences in activity observed by these two studies and assessments of roosting activity were therefore based upon this assumption. Indeed, Bartonička *et al*. (2008) found that during lactation, *P. pygmaeus* females in the Czech Republic demonstrated the highest levels of foraging activity in the first third of the night; while suckling, females are less active overnight as they must balance foraging activity with feeding their young and keeping them warm (Ruczyński *et al*., 2017). In

August, when juvenile bats start to become independent, females will spend more time foraging, swarming and searching for mates outside the roost (Collins, 2016). In several sites, this shift in behaviour, at least for *P. pygmaeus*, was also apparent in activity patterns and further supported assessments of roosting activity for this species. More generally, it is worth noting that variations in activity levels present in box plots can also be attributed to changes in activity patterns due to the annual breeding cycle, which are more apparent when examining activity as TPPs.

Peaks in activity at, or shortly after, sunset with secondary peaks before dawn were also discernible to varying degrees for NSL and *Myotis* spp. (Appendix J). Data from Catto *et al*. (1995) suggest such patterns may also signify roosting activity for *E. serotinus*, and Ruczyński *et al*. (2017) also observed similarly bimodal patterns for *N. noctula* and *N. leisleri* in Poland and Belarus, suggesting that roosting activity is fairly consistent for all three NSL species. In the absence of any comparable data for *Myotis* species, roosting activity was also assumed to be roughly bimodal.

Based on the analysis of the Temporal Pass Plots, none of the sites invaded by rhododendron demonstrated any apparent roosting activity for NSL species. While this may seem logical, given the low activity of this species in sites with rhododendron, other sites where similarly low numbers of passes by NSL were recorded did appear to exhibit activity patterns indicative of roosting. In contrast, potential roosting activity of *P. pipistrellus* and *P. pygmaeus* appeared to be unaffected by the rhododendron status of the site and fairly equally distributed across the three treatments (Table 3.5). *Myotis* spp. also demonstrated less evidence of roosting activity in sites where rhododendron was present in comparison to both other treatments, particularly sites from which it had been removed. This would appear to indicate that, contrary to our hypothesis, rhododendron did not encourage roosting by *Myotis* species through the provision of hedge-like habitat.

Here, I have suggested how assessments of temporal activity patterns could facilitate the incorporation of roosting information within future automated surveys. However, as a fairly new concept, this is not without its challenges. While activity patterns for *P. pygmaeus* were reasonably apparent, this is likely due to a combination of the higher number of passes recorded for this species and the tendency of their roosts to contain more individuals (Barlow and Jones, 1999). Interpretations of Temporal Pass Plots for *P. pipistrellus* are potentially more problematic as sustained activity throughout the night near roosts could also be indicative of continuous foraging by one, or several, bats or the consecutive flights of many bats commuting through the area, or even both as *P. pipistrellus* uses linear features for commuting and foraging (Boughey *et al*., 2011; Lacoeuilhe *et al*., 2016). Additionally, most of the studies that were suitable for assessing activity (Swift, 1980; Maier, 1992; Catto *et al*., 1995) were over 23 years old and performed before several UK species had been identified. The authors of these studies also specifically focused on bats that belonged to a particular colony. This study, however, recorded all bats within each area, including those that did not necessarily belong to a nearby roost, which could thus possibly obscure some roosting activity patterns. These issues could potentially be addressed through evaluation of Temporal Pass Plots by experts in bat behaviour or by performing manual site inspections for roosts in tandem with acoustic surveys to validate suggested roost locations. The recent suggestion that acoustic surveys be paired with camera traps (Buxton *et al*., 2018a), either infrared or thermal in this case, could also potentially help close this knowledge gap. The ability to initiate electronic recording equipment when triggered by an external sound source is already employed by modern bat detectors and there is no obvious reason this capability could not be extended to visual equipment. Such a device could produce paired image and audio files for each pass, thus providing data that could be respectively used for assessing numbers and activity and performing species identification.

3.4.3 Implications for Park and Forestry Management

No negative impacts of rhododendron removal on activity for any bat species were found and significantly higher activities of NSL species occurred in areas where rhododendron had been removed. Out of the four sites where rhododendron had been removed, activity levels were generally lower for most species in site 9, where removal had taken place most recently in 2014/15. This could be indicative of a recovery period following rhododendron removal and, indeed, site 9 was notable for an almost total absence (1%) of woody understorey in comparison to the other removal sites where regrowth by tree saplings all exceeded 30% coverage. Alternatively, this could be related to other distinguishing characteristics, for example, site 9 also had the lowest percentage of canopy cover for any site and at least 19% less canopy cover than any of the other sites where rhododendron had been removed. Without the benefit of any baseline data, it is not possible to state with any certainty that the removal of rhododendron led to any increase in bat activity at these sites.

Pipistrellus pygmaeus, and to lesser degree *P. pipistrellus* and *Myotis* species, all displayed positive associations with woody understorey and even NSL bats were higher in numbers at sites where some was present in the form of tree saplings. It is therefore recommended that some degree of woody understorey should be restored following the removal of rhododendron, either naturally by excluding grazers and/or by planting suitable alternatives. In the sites studied here, excluding deer allowed tree saplings to reach around 30% coverage in sites where rhododendron had been removed less than 3 years previously. Apart from tree saplings, the only other woody understorey recorded exceeding 1.5 m in height was holly (*Ilex aquifolium*), which occurred in one of the sites where deer were excluded, under beech (*Fagus sylvatica*). Indeed, holly may be a suitable replacement for rhododendron as it can establish itself as evergreen thickets under oak and beech in the absence of sustained grazing (Peterken, 2001). Ironically, rhododendron seems ideal for creating understorey in oak woodland; it is evergreen, shade tolerant, prefers acidic soils and avoided by most grazers (Dehnen-Schmutz and Williamson, 2006). Finding a native equivalent with all these characteristics may not be easy and recommended rhododendron alternatives are generally also non-natives such as *Lonicera japonica* and *Prunus laurocerasus* (Robertson, 1992). However, as this study illustrates, it is unlikely there will be one particular habitat type that benefits all bat species equally and a mosaic of varying ground cover densities, which accounts for their varied foraging strategies, should be considered (Rainho *et al*., 2010).

Excluding deer from sites, in addition to regenerating understorey, potentially has other benefits for some bat species, notably NSL. Although this group demonstrated the predicted negative association with increasing woody understorey, allowing deer to access sites had a significantly larger negative effect overall. This contradicts the logical assumption that increased grazing activity could benefit larger bat species by creating open areas for foraging (Fuentes-Montemayor *et al*., 2013). The most likely explanation would therefore be the reduction of moth species found within grazed areas by Fuentes-Montemayor *et al*. (2012). Deer in the UK are increasing in both population and spread, and there is mounting evidence that the associated reduction in understorey is having negative impacts on some bird species (Dolman *et al*., 2010; Newson *et al*., 2012). The research presented here provides some initial evidence that the presence of deer may also negatively impact some bat species and potentially warrants further investigation.

CHAPTER 4

4. Effects of Tree Species Diversity and Composition on Bird Diversity

4.1 Introduction

While it is generally accepted that animal diversity increases with plant species diversity, the strength of this relationship may vary considerably between different groups of animals (Tews *et al.*, 2004; Castagneyrol and Jactel, 2012). Studying the effects of tree species diversity on animal diversity is currently of particular importance due to the rapid expansion of plantation forests, which has been incentivised through national policies and international agreements (Castaño-Villa *et al*., 2019). Indeed, despite an overall decrease in global forest cover of 130 million ha between 1990 and 2015, coverage of plantation forests has increased by over 110 million ha during this time (Payn *et al*., 2015). Although a large proportion (~76%) of planted forest is focused on the production of wood and other commodities, afforestation and reforestation are also performed for other reasons such as carbon sequestration, restoring forests damaged by natural disasters, preventing desertification and as protection against floods and soil erosion (FAO, 2010). While the majority of forest plantations are comprised of native tree species, with some exceptions in Europe and North America (FAO, 2010), they are predominantly planted as monocultures (Kelty, 2006; Verheyen *et al*., 2016). As tree species compositions in many forests planted for production and conservation are now determined by humans (Wesołowski *et al*., 2018), evaluating which tree species, individually and as part of a mixture, are better for biodiversity could potentially influence forest management in order to maximise benefits for different animal species, including birds (Poulsen, 2002; Castaño-Villa *et al*., 2019).

Birds represent a diverse group of species that have adapted to occupy a wide variety of ecological niches with interspecific dietary and habitat preferences (Storchová and Hořák, 2018). Planting mixtures of tree species thus offers the possibility of providing suitable habitat for a greater number of bird species (Wesołowski *et al*., 2018) and increasing the number of habitat niches available (Peck, 1989). In some cases, different habitats may be used for different purposes by the same species; for example, common firecrests (*Regulus ignicapilla*) prefer to nest in conifers and forage amongst broadleaved trees while willow tits (*Poecile montanus*) exhibit the opposite behaviour (Wesołowski *et al*., 2018). Planting mixtures of different tree species in close proximity can thus result in higher population densities of bird species with different foraging and habitat requirements (Wesołowski *et al*., 2018).

Mixing coniferous and broadleaf tree species additionally creates a more diversified forest structure, which benefits birds by providing a wider range of opportunities for nesting and foraging (O'Connell *et al*., 2012), and can potentially host a broader range of prey species, such as spiders and beetles (Irwin *et al*., 2014).

In addition to tree species richness, tree species composition is also likely to influence bird species richness and abundance. Many temperate bird species demonstrate preferences for woodlands dominated by particular tree species or types of trees (Holmes and Robinson, 1981; Petty and Avery, 1990; Irwin *et al*., 2014; Roberge *et al*., 2018) as well as preference and avoidance patterns for specific tree species within woodlands (Peck, 1989; Korňan and Adamík, 2017). European beech (*Fagus sylvatica*), for example, appears to be avoided by many bird species, while sycamore *(Acer pseudoplatanus*) is often preferred (Peck, 1989; Korňan and Adamík, 2017). Planting forests with mixtures of different types and species of trees thus offers a promising management strategy for improving bird diversity, particularly in temperate regions where over 55% of global plantation forests are located (Castaño-Villa *et al*., 2019). Although some studies (e.g. Charbonnier *et al.*, 2016; Barbaro *et al*., 2019) have previously assessed the effects of tree species diversity on birds, these studies have focused on the overall effect of tree species composition across plots in different countries and were based on single 15-minute bird surveys performed at each plot. In contrast, studies which have assessed the effects of specific tree species and their mixtures on bird species richness and abundance have generally been limited to monocultures and mixtures of only two tree species (e.g. Peck, 1989; Donald *et al*., 1998; Diaz, 2006; Felton *et al*., 2010; O'Connell *et al*., 2012). Hence, there is a need to explore the relationship between tree species richness and composition across a broader diversity gradient and over a longer time period.

The use of PAM enables the collection of data at more frequent, regular intervals over longer timescales than have previously been used. However, identifying bird species within each recording is challenging, especially when recordings are captured continuously throughout the day, over multiple dates and plots. Acoustic indices offer an alternative, and more feasible, approach by assessing bird species richness and abundance at the community level (see Section 1.3.3) and are being increasingly used as proxies for bird diversity (e.g. Turner *et al*., 2018; Myers *et al*., 2019). Acoustic indices, in combination with PAM, could offer a fast and cost-effective means of monitoring and surveying various habitat management practices, which is particularly attractive for projects where budget, time and/or available expertise is limited (Turner *et al*., 2018).

This chapter will therefore investigate whether acoustic indices can detect differences in the vocal activity of bird communities in forest stands with different tree species richness and species compositions (from monoculture to mixed-species, broadleaved and coniferous). Specific predictions to be tested in this chapter (in line with those discussed in Section 1.4.2) are as follows:

a) Acoustic indices will reflect higher levels of bird species richness and abundance for plots with higher tree species richness
b) Acoustic indices are also likely to indicate higher levels of bird species richness and abundance in plots containing mixtures of both broadleaves and conifers than plots which contain only one of these types of trees.

The effect of individual tree species on bird diversity will also be assessed as this information could be important for informing plantation managers which tree species are beneficial for bird communities. It is also expected that other plot characteristics (e.g. canopy cover, distance to forest edge, understorey cover) may affect bird activity and community composition. Assessing indices in relation to these factors potentially offers an additional means of checking whether they appear to demonstrate similarities with traditional assessments of bird diversity in the published literature, e.g. higher activity levels at the forest edge.

4.2 Materials and Methods

4.2.1 Study Location

The study was conducted in the Hainich National Park, Thuringia, Germany (51.1° N, 10.5° E). Hainich National Park covers approximately 75 km^2 and is situated within Hainich forest, which is the largest contiguous area (160 km^2) of deciduous forest in Germany (Nationalpark-Verwaltung, 2018). From the mid-1800s, Hainich was managed for the production of large-dimensioned timber and presently contains many large, old trees as a result (Mölder *et al*., 2006). Forest management ceased around 1964 when the park became a military training ground, enabling the development of large areas of near-natural forest (Batáry *et al*., 2014). In 1997, Hainich National Park was designated as a UNESCO World Heritage site and almost all (~90%) of the park remains unmanaged (Batáry *et al*., 2014).

Acoustic surveys were performed at plots previously used for the FunDivEurope EU project (Figure 4.1, Table 4.1, Baeten *et al.,* 2013). These plots were established in mature, existing forest to investigate the functional significance of forest biodiversity and specifically selected to minimize differences in characteristics other than tree species diversity between plots, such as topography, altitude and soil characteristics (Baeten *et al*., 2013). The plots were also assessed against the German National Forest Inventory to ensure they were representative of regional landscapes (van Der Plas *et al*., 2016). Each plot represents a monoculture or a mixture of the following target tree species: European oak (*Quercus robur*), sessile oak (*Quercus petraea*), European beech (*Fagus sylvatica*), European ash (*Fraxinus excelsior*), sycamore *(Acer pseudoplatanus*) and Norway spruce (*Picea abies*). Target tree species richness varied from 1 to 4 species per plot, thus offering a broader tree species richness gradient than typical forest mixture trials (Baeten *et al*., 2013). While admixture of non-target tree species was unavoidable in natural forests where stands tend to be dominated by one or a few tree species, care was taken to select plots containing <10% of non-target species and a minimum evenness of 60% for the target species, both of these measurements were assessed using basal area (Baeten *et al*., 2013). European beech is the dominant tree species in Hainich forest, and a plot size of 900 m^2 (30 m x 30 m) was chosen as the largest size possible to avoid a complete dilution design with beech appearing in every plot (Baeten *et al*., 2013). Plots were surrounded by a 10 m buffer zone of similar species composition and structure to account for edge effects (Baeten *et al*., 2013). Due to the remote locations of some plots, only 35 of the 38 original FunDivEurope plots were used for acoustic surveys (Figure 4.1).

Bird surveys have been performed in Hainich since 1993 by the Thüringen State Institute for Environment and Geology species detection program (Thüringer Arten-Erfassungsprogramm der TLUG) and have detected the presence of 157 bird species (TLUG, 2017). Of these species, 77 are typically associated with deciduous or coniferous forest, or both, including 51 species of Passeriformes (Storchová and Hořák, 2018), the order most likely to be detected by PAM due to singing activity (Depraetere *et al*., 2012; Klingbeil and Willig, 2015).

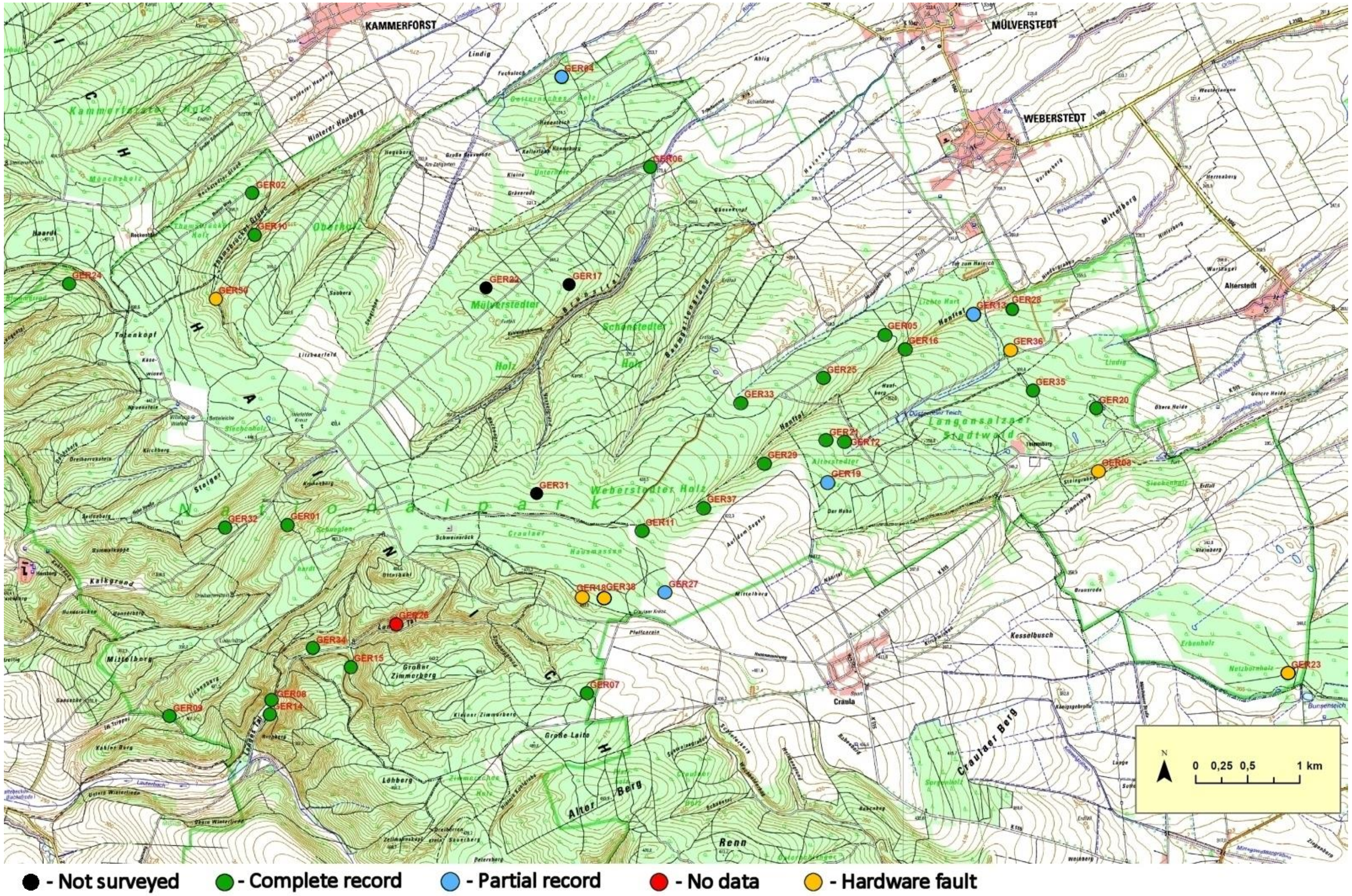


Figure 4.1. Map of the Hainich National Park (Thuringia, Germany) with locations of the FunDivEurope plots used for acoustic recording and acoustic recorder performance at each location (Base map provided by FunDivEurope, 2017).

Table 4.1. Characteristics of plots in the Hainich National Park used for acoustic surveys in 2017. Plots where recorders were not deployed or failed are excluded.

Plot ID	Species Mix*	Total basal area** (m^2 ha^{-1})	Tree density** (trees ha^{-1})	Canopy cover (%)	Understorey >1.5 m (%)	Dist. to forest edge (m)
GER01	B	30.5	356	95	0	1509
GER02	B	25.5	300	94	52	403
GER04	A	50.9	556	84	16	150
GER05	O	38.2	567	80	7	340
GER06	BO	58.1	678	80	4	76
GER07	N	29.5	1011	78	6	80
GER08	N	41.8	1078	69	6	30
GER09	ABS	34.1	1811	93	13	303
GER10	ABS	23.9	678	92	8	740
GER11	AB	39.0	378	94	4	276
GER12	BO	30.6	244	91	94	491
GER13	AOS	41.4	344	91	3	443
GER14	BN	31.1	533	81	5	29
GER15	AN	42.0	522	56	1	862
GER16	BNO	46.3	389	72	36	550
GER20	ABO	28.2	689	85	9	289
GER21	ABOS	27.5	222	92	79	312
GER24	ABS	18.1	233	94	66	1379
GER25	BOS	28.6	444	86	3	489
GER28	AS	20.8	356	85	2	211
GER29	ABO	41.5	478	87	43	139
GER32	ABS	47.4	556	86	1	950
GER33	ABNS	39.0	511	85	5	733
GER34	ABN	34.6	756	88	31	635
GER35	BNOS	54.0	322	70	46	550
GER37	ABOS	31.2	344	88	13	120

* Species key: A = Ash, B = Beech, O = Oak, N = Norway spruce and S = Sycamore

** Data obtained from FunDivEUROPE plot surveys

4.2.2 Passive Acoustic Monitoring

As the number of available AURITA devices was not sufficient to cover the large number of plots in Germany, it was arranged with Prof. Dr. Michael Scherer-Lorenzen and Dr. Sandra Müller from the BeSound project (Biodiversity Exploratories, 2017) to borrow 45 Lunilettronik Soundscape Explorer (Lunilettronik, Fivizzano, Italy) recording devices for the duration of the project. The Lunilettronik Soundscape Explorer is time-programmable, has two microphones (one 48 kHz for audible, one 192 kHz for ultrasonic), a data capacity of up to 64 GB (2 x 32 GB SDHC), can automatically calculate Acoustic Complexity Index values of recordings and also records ambient light level, air pressure, temperature and humidity (IInstEco, 2018). The unit is powered by up to two 4 x D cell battery packs, each of which provides 4 weeks recording time when sampling for one minute out of every ten (IInstEco, 2018). Adopting a sampling regime of one minute in every ten and using two battery packs (8 x D cell batteries) was therefore necessary to achieve the intended recording period of approximately 8 weeks. One-minute recording segments are frequently used to calculate acoustic indices (Pieretti *et al*., 2015) and are considered appropriate for capturing the character of a soundscape (Phillips *et al*., 2018). Although sampling more frequently typically provides the best representation of the soundscape and one minute out of every five is ideally recommended, sampling one minute every ten represents a reasonable compromise between the amount of detail that is retained in comparison to continuous recordings and the power and storage requirements of recording devices (Pieretti *et al*., 2015). Automatic calculation of ACI values was not used as it consumes extra battery power (Müller 2017, pers. comm., 10 February). To further preserve power and storage capacity, ultrasonic recording was also disabled.

To avoid potential damage by resident wild boar (*Sus scrofa*) and attenuation due to ground interference, Lunilettronik recorders were mounted on trees at ~2 m height and secured using 3 mm wire rope. An additional length of 2 mm wire rope was secured across the cover to prevent access to internal components (Figure 4.2).

Figure 4.2. A Lunilettronik Soundscape Explorer device attached to a tree in Hainich National Park, Germany.

Installation of Lunilettronik recorders was carried out between 2nd and 6th of May 2017. GPS locations and maps for all plots were available and used to locate survey locations with a Garmin eTrex Legend HCx GPS tracker. Arrival at each plot was confirmed by locating wooden stakes that marked the centre and corners of each plot and/or trees with numbers on them, which matched numbers in the plot maps. Once the centre of the plot had been established, a recorder was placed ~7 m from the centre of each plot with the audible frequency microphone facing the centre to account for the higher sensitivity to sounds directly in front of the microphone. As a limited number of monoculture plots were available, capturing data from these plots was particularly important for the analysis of tree species richness effects, and two recorders were therefore placed opposite each other at equal distances (~7 m) from the centre of the plot, with microphones facing inwards, in each of the single species plots to provide some redundancy in case of equipment failure.

Retrieval of the recording devices was carried out between 2nd and 7th of July 2017 and all recorders were successfully collected without loss or damage. As the last recorders were installed and activated on May 6th, the maximum consecutive period over which simultaneous recording took place at all plots was 56 days (7th May to 1st July). Soundscape Explorer SD cards were checked to confirm whether they contained any data and, if so, that the first and last file recorded could be read by the computer and contained actual sounds. Of the 41 recorders deployed, i.e. 1 in each of the 29 mixed species plots and 2 in the 6 single species plots, it was found that two recorders (GER01 and GER26) had completely failed to record and two (GER04 and GER36) had an obvious microphone fault. As GER01 and GER04 were situated in single species plots, data could be taken from the second recorder installed at each location. However, the second recorder at GER04 inexplicably stopped recording for a period of 6 days in the middle of the survey (07/06/17 to 12/06/17) before resuming again. As this was the only plot with ash monoculture and the alternate unit was faulty, it was decided to omit these 6 days from the survey rather than omitting this plot. The recorder at GER13 also exhibited the same behaviour on the same dates and was also otherwise okay. Omitting these dates, rather than recorders, therefore meant that GER13 could also be retained for analyses. Two more recorders were incorrectly configured; GER38 recorded for one minute every two, rather than ten, minutes and ran out of space after 2 weeks and GER23 only recorded for a period of 5 days in each month. Another four recorders (GER03, GER18, GER19 and GER27) either ran out of power or only recorded to one SD card and did not complete the entire survey period.

In 2018, all of the recorders used in the Hainich survey were evaluated using playback tests by Dr. Sandra Müller at Freiburg University who reported faults or loss of microphone sensitivity for four additional units; GER02, GER03, GER18 and GER30 (Müller 2018, pers. comm., 20 March). Of these, GER02 was a monoculture plot and data from the backup recorder could be used instead. Duplicates were not available for the other three devices and these locations therefore had to be omitted from analyses, although two of these devices (GER03 and GER18) had failed to complete the full survey period anyway. Playback testing of all devices at Freiburg additionally provided the benefit of retrospective quality control for all the devices used for the survey. For the three monoculture plots in which both recorders completed the whole schedule without fault, only one of these was selected for analyses based on which appeared to have the clearest (i.e. lowest equipment noise) recordings. After eliminating faulty recorders and plot duplicates, a total of 26 recorders (~1.7 TB of data) were suitable for use in analyses (Table 4.1).

4.2.3 Site Characteristics

In July 2017, the following surveys were performed within each 900 m^2 plot:

1. *Canopy cover.* Using the centre of each plot as a starting point, 100 point readings were taken at roughly equal intervals (3 steps) by walking out towards the plot edge in a spiral pattern. At each point a reading was taken with a GRS densitometer and 'tree' or 'sky' was recorded whenever canopy did, or did not, appear in the densitometer crosshairs, respectively. This produced a total of 100 canopy readings for each plot, which could be directly converted to percentage canopy cover.

2. *Understorey cover.* Understorey cover can be an important determinant of forest bird species richness and abundance (Diaz, 2006). At each plot, the amount of woody understorey (shrubs, saplings etc.) cover higher than 1.5 m with a DBH < 7 cm was mapped relative to its distance and angle from the wooden stakes marking the corners, edges and centre. The amount of cover was drawn onto paper maps of each plot and then scanned to produce digital images. These were used to calculate the percentage of understorey cover by converting each image to black (understorey) and white (no understorey). Using ImageJ ver.1.51j8 (Rasband, 2017), the number of black pixels in each image were counted using the histogram function and then converted to percentages of the total pixels in the image.

3. *Tree diversity.* The Shannon diversity index (Shannon, 1948) for each plot was calculated using basal area as a measure of abundance for each tree species (Baeten *et al*., 2013). Non-target species that were present in low abundances were also included in calculations as the presence of rarer tree species within forest stands may be preferred by foraging birds (Korňan and Adamík, 2017). Shannon index values were then converted to 'true Shannon diversity' values (i.e. *exponent*(Shannon index)) to better reflect the number of tree species (Jost, 2006). Within each plot, the basal area of individual tree species was used to represent composition and the percentage of conifer trees was calculated to examine the effect of mixing conifer and broadleaf species. Basal areas of the tree species within each plot were obtained from previous surveys performed by FunDivEurope in 2011. Although these data were collected six years before the current study, the relative differences between plots are unlikely to have changed. Additionally, trees within each plot had previously been (non-destructively) numbered and were checked against the corresponding maps to confirm their validity.

4. *Other variables.* Distance from the forest edge has previously been found to influence the composition of bird communities, including the shrub and tree nesting birds in Hainich (Batáry *et al*., 2014). The distance from the centre of each plot to the closest forest edge was therefore measured using the ruler tool in Google Earth Pro v7.3.2.5491 (https://earth.google.com).

Species mixtures and site characteristics for each of the survey plots are presented in Table 4.1.

4.2.4 Data Selection

The maximum continuous recording period of 56 days was achieved at 26 plots: beech (x2), oak, ash and spruce (x2) monocultures, 6 plots with two species mixes, 10 of three species mixtures and 4 plots with a mix of four species. However, as discussed above, 6 days in the middle of the survey could not be used due to gaps in recording. Files were recorded as uncompressed 1 minute 48 kHz WAV files, with 144 files being produced by each recorder per day. This represented a possible total of 187,200 audio files requiring analysis for the 50 days on which recordings were completed at 26 plots.

Rain can profoundly affect ecoacoustics analyses as well as affecting biophony directly when heavy enough (Gage and Farina, 2017). The presence of rain in recordings can additionally cause over-estimation issues with acoustic indices such as ACI, Acoustic Richness and Spectral Entropy (Depraetere *et al*., 2012). In order to identify rainy days, weather data were obtained through Nationalparkverwaltung Hainich for the closest available weather stations, which were based in the nearby towns of Weberstedt and Craula, both approximately 1 km from Hainich (see Figure 4.1). Hourly and daily totals of rainfall were assessed and whenever either exceeded 0.5 mm in either plot, that day was excluded. Any dates where rain was indicated in weather station data were also verified manually before exclusion by listening to recordings. This process identified 14 days when rainfall was more than slight and/or sustained, which were excluded from analyses.

As an additional quality check, after acoustic indices had been processed, results for each plot were converted into heatmaps for the 36 days that had been retained for initial analysis. Inspection of these heatmaps revealed several dates displaying apparent gaps (Appendix K), which typically appeared on the same dates across several plots: 20/05/17 (9 plots), 31/05/17 (7 plots), 05/06/17 (2 plots), 16/06/17 (11 plots), 23/06/17 (11 plots) and 30/06/17 (10 plots). Such gaps were more likely to be caused by adverse weather than equipment faults, which was confirmed by examining the corresponding audio files. The 6 dates listed above were therefore omitted from analyses.

4.2.5 Configuration and Validation of Acoustic Indices

Following the removal of dates with adverse weather conditions, a total of 30 days was considered suitable for analyses, which constituted a total of over 112,000 files. Although a large number of acoustic indices have been developed, in line with the aim of the current project, those indices that have previously been shown to demonstrate a relationship with bird species richness and/or abundance (Section 1.3.3) were calculated: Acoustic Complexity Index (ACI; Pieretti *et al*., 2011), Bioacoustic Index (BI; Boelman *et al*., 2007), Acoustic Evenness Index (AEI; Villanueva-Rivera *et al*., 2011), Normalised Difference Soundscape Index (NDSI; Kasten *et al*., 2012) and temporal entropy (H_t; Sueur *et al*., 2008a). Analyses were performed using RStudio v1.0.153 (RStudio Team, 2016) and R v3.4.4 (R Core Team, 2018). The *Soundecology* v1.3.3 package (Villanueva-Rivera, 2015) was used to calculate ACI, AEI, BI and NDSI, and *Seewave* v2.1.3 package (Sueur *et al*., 2008b) to calculate H_t. An R script was written to automate the processing of large numbers of audio files with results for all indices being summarized in a single spreadsheet. On some occasions, a brief

(~0.5s) noise was noted at the beginning of recordings when the device switched itself on. To avoid possible interference with index values when the recorder switched itself on and off, the first and last second of each recording were omitted from each file so that only the middle 58 seconds were analysed. This had the additional benefit of ensuring all audio files were of equal length and was achieved using the *readwave* function in *tuneR* (Ligges *et al*., 2016), which allows specified time intervals to be selected for processing so that no editing of files was required.

Some of the acoustic indices used have configurable settings enabling them to be 'tuned' to the frequency bands of interest (i.e. those used by the species being studied) in order to improve results (Eldridge *et al*., 2018). Acoustic indices typically use a default range of 2 to 8 kHz for the frequencies where biophony is considered to be most prevalent (Kasten *et al*., 2012). However, the calls of some birds that prefer coniferous trees, such as the goldcrest (*Regulus regulus*) and coal tit (*Periparus ater*), can reach frequencies of up to almost 10 kHz (Thomas, 2019). Indeed, Turner *et al*. (2018) reported that higher frequency ranges (7 to 10 kHz) for birds were more pronounced in older, coniferous forest. To assess the most appropriate band settings for the current study, dawn choruses were examined across plots to confirm the frequencies where most bird vocalisation occurred. This represented the most suitable period as it should contain the highest number of concurrent vocalisations by the species present. The frequency band where the majority of dawn chorus activity occurred was from ~1.5 kHz up to ~9 kHz. It was also noted, however, that recording devices at some plots contained equipment noise just above 9 kHz, visible as horizontal lines. Although some indices (e.g. ACI) have been designed to account for constant, anthropogenic noise sources (Pieretti *et al*., 2011), the cumulative effects of including this noise in index calculations over the days being analysed could introduce bias for plots where it was present. It was therefore decided to limit the upper biophony band to 9 kHz, which represented the best compromise between capturing the maximum amount of bird activity while also excluding equipment noise.

For the lower frequency limit, machine self-noise (background hiss) was evident in the bottom 50 Hz for all recorders but was too low to have any impact on biophony. Anthropogenic noise, typically due to commercial jets passing overhead, generally tended to be loudest below 100Hz but rising to ~1 kHz when jets were closer (i.e. louder). The lower limit of dawn chorus activity (1.5 kHz) was therefore selected as it should exclude the worst effects of planes and wind, while also retaining the majority of bird biophony. For ACI, BI and NDSI, a frequency band of 1.5 to 9 kHz was therefore specified as the biophony band, and 500 Hz to 1.5 kHz (default = 1 to 2 kHz) was additionally specified as the anthrophony band for NDSI to avoid overlap with the biophony band. For AEI, only the maximum frequency could be specified, which was set to 9 kHz, and it was not possible to specify any frequency bands of interest for H_t. Where possible, an FFT window size of 1024 was also specified, which increased frequency resolution from 94 Hz to 47 Hz with a temporal resolution of 20 ms.

In addition to rain, wind (Gage and Farina, 2017) and anthropogenic noise (Fairbrass *et al*., 2017) can also influence the results of different indices. Fortunately, Hainich National Park lies within a rural landscape and all of the survey plots were at least 1 km from the nearest town or village (Figure 4.1). Although there are some roads within the park, access is controlled by gates that only park staff and special permit holders can open. A blanket speed limit of 30 km/h (19 mph) also applies to anyone using these roads. Any influence due to traffic noise, at least from within the park, should be minimal and the most pervasive source of anthropogenic noise was therefore likely to be the sound of aircraft flying over the park. For any plots that happen to be particularly windy or on a low flight path, the use of indices susceptible to such events could produce over-estimates and should obviously be avoided. It was therefore not only necessary to determine which indices offered the best representations of bird activity, but also those that were less likely to be overly influenced by unwanted sounds.

As a preliminary assessment of the suitability of the indices listed above, a set of recordings with examples of typical sounds encountered in Hainich was compiled to evaluate and compare index performance for desirable (biophony) and undesirable (anthrophony and geophony) soundscape elements. All files were recorded in Hainich and, where possible, examples of each sound element were obtained from different plots. This set was comprised of 10 recordings each containing only, or predominantly, wind, aeroplane noise, silence, dawn chorus, dusk chorus or the calls of one or two individual birds. While not technically undesirable, silent recordings were included as a quality control, to ensure indices were ranking biophony higher than quiet soundscapes. Ideally, indices should rank the 30 files with biophony (dawn and dusk choruses, and individual birds) higher than the 30 files without. This process also provided some indication of which sources of interference each index is most susceptible to (Appendix L).

In terms of separating biophony from undesirable soundscape elements, NDSI, ACI and BI performed best, with higher values for 30, 29 and 27 out of the maximum of 30 files containing biophony, respectively. In addition to detecting biophony, the NDSI ranked 9 of the 10 aeroplane recordings within the bottom 11 values suggesting this index is indeed useful for detecting anthrophony. However, incidental aeroplane noise present in the background of some of the biophony recordings did not appear to produce an overly negative bias in NDSI results either. Although the ACI's top 30 included one recording of wind, this was ranked below all of the choruses with the only individual bird outside the top 30 being ranked 31st.

Although AEI performed well for choruses, it was less representative of individual birds and particularly susceptible to wind. AEI assesses evenness across frequency bands and test files with only one or two birds were less likely to disturb the evenness of the soundscape than wind, for which the highest SPLs occur at lower frequencies and gradually dissipate with rising frequency so that sound is unevenly spread across frequency bands. As some of the individual bird recordings were fairly quiet, AEI's default detection threshold of -50 dBFS may not have been low enough to account for this; however, decreasing this setting to -70 dBFS did not improve this situation (Appendix L). This would appear to confirm that AEI's susceptibility to wind is due to its acoustic unevenness rather than any issue with the recording level. In agreement with Eldridge *et al*. (2018), it was also found that lower AEI values were associated with files containing higher levels of bird activity. The performance observed for H_t also supports the assessment of these authors that higher values for entropy indices can represent soundscape elements that are diametric opposites (Eldridge *et al*., 2018). Additionally, H_t was the only index that could not be restricted to the frequencies of interest (1.5 to 9 kHz), which is unlikely to have improved its performance. For these reasons both AEI and H_t were omitted from further analyses.

The above test demonstrated the indices' ability to differentiate biophony from other soundscape elements but did not provide any assessment of how effective they were at quantifying biophony within recordings. In order to test the extent to which acoustic indices reflect bird species richness, the number of bird species in each chorus was counted for the 30 audio clips described above by the author and cross-validated with Lara Nouri (BTO qualified 'C' permit bird ringer and host of the #WarbleWednesday bird call identification quiz on Twitter), see Appendix M for details. Acoustic index values for each of the test files were then evaluated against bird species richness assessments with linear regression models. NDSI demonstrated a clearly non-linear relationship with bird species richness and was therefore excluded from further analyses (see Section 4.3.1).

For spatial separation, the minimum distance between plots that fully completed their recording schedule was ~124 m, measured using the ruler tool in GoogleEarth Pro v7.3.2.5491 (https://earth.google.com). Bibby *et al*. (2000) recommend a minimum distance of 200 m between traditional point counts in dense forest to reduce the possibility of birds flying from one survey location to the next and being double counted; however, in the current study, recordings were performed simultaneously at all stations. Furthermore, this study is concerned with the presence of birds in and around each forest plot, rather than establishing overall population levels within the forest, and some of the same individuals may well be recorded at different plots during the two-month survey period. Attenuation surveys performed in Section 2.5 demonstrated that even under ideal circumstances (i.e. low wind speed and directly facing the recorder) the songs of louder passerines, such as the European robin (*Erithacus rubecula*) and Eurasian wren (*Troglodytes troglodytes*) with SPLs of 90 and 91 dB, respectively, can fall to ~10% of their original power spectral density at 64 m distance and 5% or less by 128 m (Table 2.4). The distance between the recording device and any vocalising species will thus have some effect on index results, with species closer to the microphone exerting more influence (Lellouch *et al*., 2014). A simple test confirmed this was also the case in the current study and at a distance of 60 m the ACI value was almost half of what it would be 2 m from the recorder, while BI had dropped by over 60% (Appendix N). This inherent, positive weighting of species closer to the recorder is potentially beneficial for the current study, where the objective is to compare bird activity between distinct locations surrounding each recorder and it was not desirable to include, or equally weight, the calls of distant birds outside of each plot, especially as survey plots were relatively small in Hainich.

4.2.6 Sampling Periods for Acoustic Indices

For birds, the dawn chorus is generally considered the most important time of day when the majority of species will be vocalising, often as a means of defending their territories (Catchpole and Slater, 2008). For the current study, the dawn chorus is particularly important as it represents the best time of day to capture the largest number of species (Wimmer *et al*., 2013), particularly songbirds (Buxton *et al*., 2016), with the additional possibility that many of the species recorded at this time of day will be at locations (i.e. our study plots) within their territory. Indeed, many studies investigating bird activity and diversity in relation to acoustic indices have focused either entirely, or predominantly, on the dawn chorus (e.g. Wimmer *et al*., 2013; Farina *et al*., 2015; Mammides *et al*., 2017; Turner *et al*., 2018). However, the dusk chorus represents another important peak in bird singing activity, albeit usually to a lesser degree than the dawn chorus (Catchpole and Slater, 2008), and has therefore also been accounted for in a number of studies using acoustic indices (e.g. Sueur *et al*., 2008a; Farina *et al*., 2011b; Pekin *et al*., 2012). Additionally, as limiting analyses to dawn chorus activity excludes the possibility of assessing how acoustic indices respond to variations in the density of vocalisations (Eldridge *et al*., 2018), it was therefore decided to include a measure of daytime activity, which would include all activity from the end of the dawn chorus period up to the beginning of the dusk chorus period. Each day was thus divided into 3 time periods representing dawn chorus, dusk chorus and daytime activity. While it would equally be possible to assess night-time activity using acoustic indices, this was not considered appropriate because (i) night-time activity was generally very low (Appendix K) and thus unlikely to offer a useful representation of bird diversity, (ii) most vocalising bird species were owls, many of which have calls below the 1.5 kHz minimum frequency specified for indices (e.g. male tawny owl (*Strix aluco*) ~870 Hz and long-eared owl (*Asio otus*) ~400 Hz), and (iii) the vocalisations of non-bird species, such as the red fox (*Vulpes vulpes*), were present in many night-time recordings and could produce misleading results.

Sunrise and sunset times were obtained from www.sunrise-and-sunset.com for Mihla (~3km east of Hainich) and Bad Langensalza (~6 km west of Hainich) and then averaged, as details were not available for Hainich itself. Sunrise occurred at 05:25 ±15 minutes with sunset at 21:04 ±17 minutes in May and 05:06 ±3 minutes and 21:28 ±7 minutes in June. Sampling periods used to represent dawn and dusk choruses are usually defined relative to sunrise or sunset times to account for temporal and spatial differences in daily light cycles. While there is some variation in the definitions used by different studies, sampling from 1 hour before sunrise to 2 to 2.5 hours after sunrise has been used regularly (Depraetere *et al*., 2012; Eldridge *et al*., 2018; Myers *et al*., 2019). Examination of indices heatmaps revealed that 1 hour before sunrise was sufficient to capture the majority of pre-sunrise activity while excluding the majority of night-time 'silences' before activity began. For dusk chorus, a sampling period from 1.5 hours before sunset up to 1.5 hours after has previously been used (Depraetere *et al*., 2012); however, heatmaps (see examples in Appendix K) indicated the majority of acoustic activity had ceased some time before 90 minutes after sunset. It was therefore decided that the dawn sampling period would begin 1 hour before sunrise and end 2 hours afterwards, while the dusk sampling period would mirror this by beginning 2 hours before sunset and ending 1 hour after so that both survey periods covered were of equal length.

When comparing the results of acoustic indices, the use of median values is considered appropriate (Machado *et al*., 2017; Myers *et al*., 2019) and, being less susceptible to outliers due to microphone noise or extreme weather, may offer better performance than mean averages (Eldridge *et al*., 2018). Median values of index results during the three periods described above were therefore extracted for analyses.

4.2.7 Statistical Analyses

All statistical analyses were performed using RStudio v1.0.153 (RStudio Team, 2016) with R v3.6.0 (R Core Team, 2018). Acoustic index values were treated as continuous variables and modelled using normal probability distributions (Quinn and Keough, 2002). As ACI values were positively skewed and non-normally distributed for dawn, daytime and dusk, as were the dusk values for BI, a logarithmic link function was therefore also applied to all models, so that methods were consistent, to account for this (Quinn and Keough, 2002). Generalised Linear Mixed Models were built using *glmmTMB* v0.2.3 (Brooks *et al*., 2017) and examined using the *DHARMa* v0.2.4 package, set for 10,000 simulations (Hartig, 2019). QQ plots of scaled residuals and one-sample Kolmogorov-Smirnov tests obtained from *DHARMa* for ACI models demonstrated significant deviations from uniformity were still present. All ACI input data were therefore transformed to a more normal distribution using a Lambert-W transformation (Goerg, 2011); this method has previously been applied to normalize ACI data distributions by Fairbrass *et al*. (2017).

Explanatory variables (canopy cover, understorey cover >1.5 m, distance to forest edge, tree species richness, true Shannon diversity, percentage of conifer and the basal areas of each tree species within the plots) were checked using the *chart.Correlation* function in *PerformanceAnalytics* v1.5.2 package (Peterson and Carl, 2018) to ensure that correlation coefficients between variables did not exceed ±0.7 (Dormann *et al.*, 2013). Results, presented in Appendix O, indicated tree species richness and true Shannon diversity were highly correlated (0.93) and true Shannon diversity was therefore used in preference as it accounted for tree community evenness as well as species richness. Additionally, the total basal areas of beech and spruce trees and the percentage of conifers within each plot were strongly correlated with canopy cover with values of 0.63, -0.74 and -0.68, respectively. Canopy cover was therefore omitted from models. Norway spruce was the only conifer species present; spruce basal area and the percentage of conifers were therefore also significantly correlated (0.98) so that both could not be used in the same model.

The relationship between acoustic index values and the percentage of conifer trees in each plot was expected to be non-linear as high and low values of conifer cover represented plots comprised entirely, or almost entirely, of either conifer or broadleaf, respectively. Higher acoustic index values should therefore be observed in plots with fairly even mixtures of the two tree types, creating a bell-shaped response curve. This hypothesis was assessed using linear models of median index values, for each plot during each time period, and a polynomial of the percentage of conifer cover:

Index median value ~ % conifer + I (%conifer^2)

Although models revealed some evidence of the expected response curve with some minor trends, none of these relationships were significant. It was also apparent that out of the 26 plots included in analyses, only 3 fell within the range of 20% to 90% conifer cover with most plots being dominated by broadleaves. With the low number of plots representing a reasonable mixture of conifer/broadleaf mixed, analyses therefore focused on the composition effects of individual tree species, rather than tree types.

To test the hypothesis that higher tree species richness would have a positive effect on acoustic index values, and to investigate whether tree species composition also had any effect, the following model was used to analyse dawn, daytime and dusk time periods for both ACI and BI:

Index median value ~ *true Shannon diversity* + *distance to edge* + *understorey* + *ash* + *beech* + *oak* + *spruce* + *sycamore* + (1|*plot*) + (1|*day*)

Survey plot and Julian date were included in all models as random effects to account for repeated sampling at the same locations (Bolker, 2015) and temporal autocorrelation (Crawley, 2007), respectively. As every combination of dates and plots were included in models, a crossed design structure was used (Quinn and Keough, 2002). To make estimate effect sizes directly comparable, all independent variables were centred and standardised by one standard deviation (z-transformation), which is considered suitable when no binary predictors are included (Schielzeth, 2010). Models were also run using non-standardised values in order to create predictor effect displays for significant relationships scaled in original units, which was performed using the *effects* package in R (Fox and Weisberg, 2018). It was originally planned to perform model averaging using an information-theoretic selection process to account for model uncertainty (Burnham and Anderson, 2002) with the *MuMIn* package (Barton, 2018); however, model output from this package is in a non-standard format that was not compatible with *effects* or other predictor effect display packages available e.g. *visreg* (Breheny and Burchett, 2017). Full models were therefore used to maintain compatibility between predictor effect plots and model results although averaged models were also run for comparison and results were fundamentally the same. All models were assessed for outliers and goodness-of-fit with one-sample Kolmogorov-Smirnov tests created with the *DHARMa* package (Hartig, 2019), set for 10,000 simulations (Appendix P).

4.3 Results

4.3.1 Acoustic Indices as a Proxy for Bird Species Richness

All acoustic indices showed a significant, positive relationship with bird species richness counts (Figure 4.3). The relationship between ACI and bird species richness counts accounted for more variation (67%) than any of the other indices tested ($F_{1,28}$=55.56, P<0.001; Figure 4.3a). Values for BI and bird species richness (Figure 4.3b) were also significantly correlated ($F_{1,28}$=16.71, P<0.001) but BI only accounted for just over half of the variation shown by ACI. NDSI (Figure 4.3c) appeared to be the second-best predictor of bird species richness ($F_{1,28}$=51.61, P<0.001) although the relationship between bird species richness and NDSI values was clearly non-linear. The relationship between values for the NDSI biophony band and bird species richness (Figure 4.3d) was similar to that of BI ($F_{1,28}$=17.47, P<0.001).

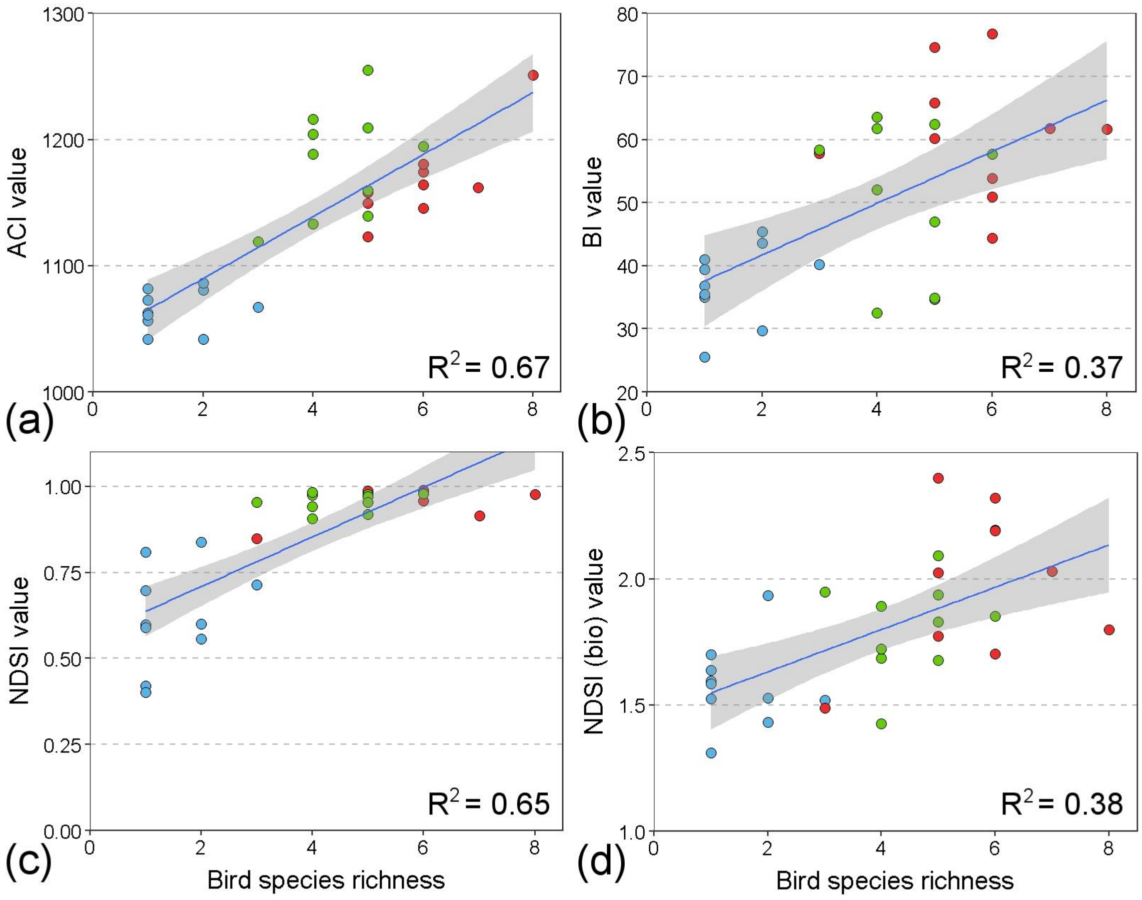


Figure 4.3. Linear regression models of acoustic index results (a) ACI, (b) BI, (c) NDSI, and (d) NDSI (biophony band) and bird species richness assessed for 30 1-minute test files containing different levels of bird activity (10 each containing relatively few species, dawn chorus and dusk chorus). Blue dots represent recordings with one to three species, green dots are dusk choruses and red dots represent dawn choruses. Linear trendlines are shown with 95% confidence intervals (grey shaded areas).

4.3.2 Effects of the True Shannon Diversity of Trees, Tree Species Composition and Conifer-Broadleaf Mix

True Shannon diversity of trees had a highly significant positive effect on ACI and BI values during all three time periods (Table 4.2; Figure 4.4).

Table 4.2. Estimates for GLMMs examining the effects of true Shannon diversity and tree species composition on acoustic index scores during dawn, daytime and dusk periods. Effect sizes are directly comparable as input variables were centred and standardised to one standard deviation. For convenience, only significant results and trends are presented below, full results are available in Appendix P. Significance codes: <0.001 '***', <0.01 '**', <0.05 '*', <0.1 '.'

Characteristic	Estimate	Std err	Z Value	*Pr(>|z|)*	Sig.
ACI (Dawn)					
True Shannon diversity	0.010	0.003	3.1	0.002	**
Sycamore	-0.012	0.004	-3.0	0.002	**
ACI (Daytime)					
True Shannon diversity	0.009	0.002	3.9	<0.001	***
Sycamore	-0.008	0.003	-3.2	0.002	**
ACI (Dusk)					
True Shannon diversity	0.007	0.002	3.7	<0.001	***
Beech	-0.007	0.002	-2.9	0.004	**
Sycamore	-0.007	0.002	-2.9	0.004	**
BI (Dawn)					
True Shannon diversity	0.088	0.022	4.0	<0.001	***
Sycamore	-0.081	0.026	-3.1	0.002	**
BI (Daytime)					
True Shannon diversity	0.093	0.024	3.9	<0.001	***
Sycamore	-0.083	0.003	-3.0	0.003	**
BI (Dusk)					
True Shannon diversity	0.100	0.025	4.0	<0.001	***
Distance to forest edge	-0.038	0.023	-1.7	0.098	.
Sycamore	-0.077	0.029	-2.6	0.009	**

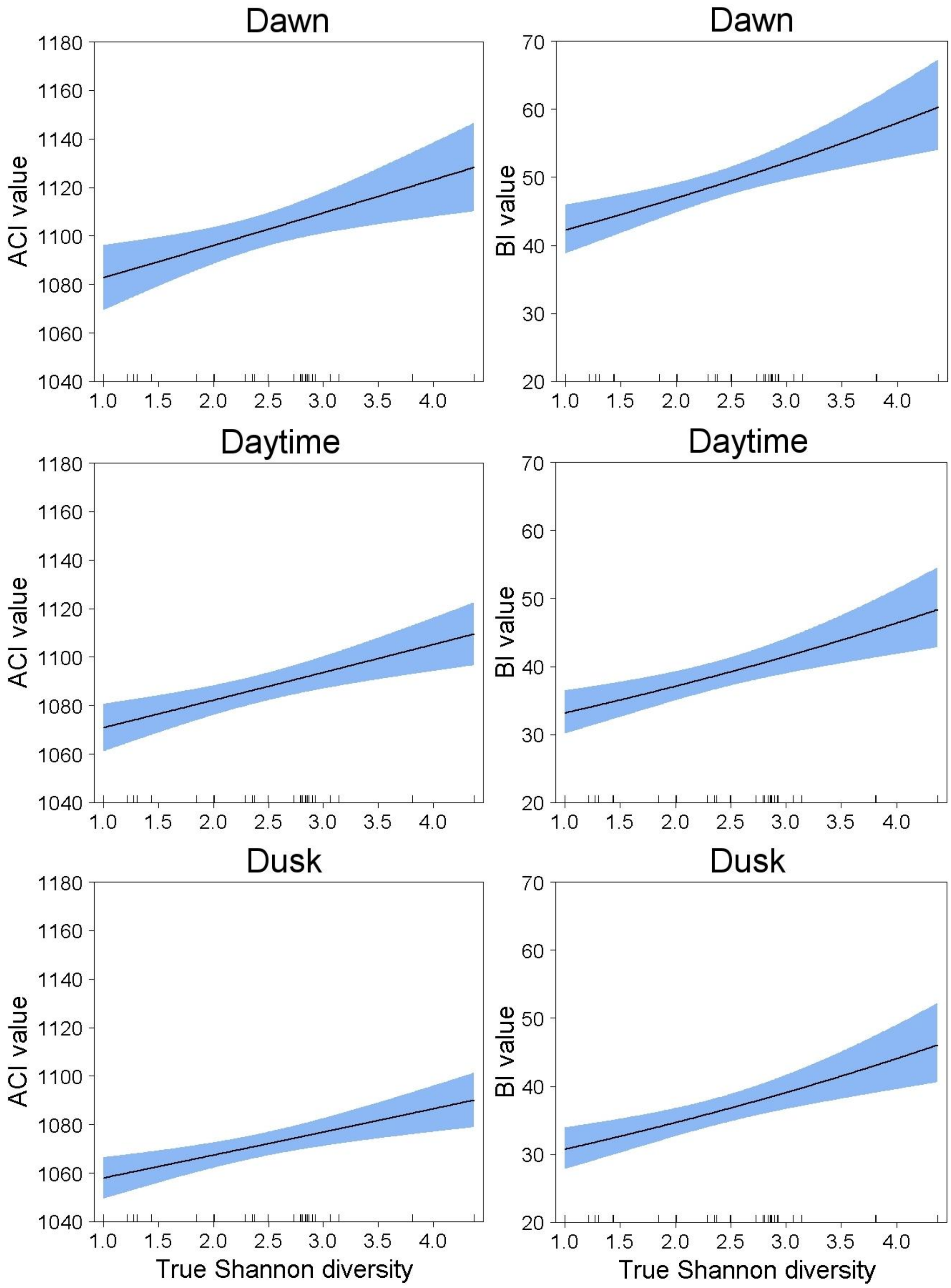


Figure 4.4. Predictor effect displays of true Shannon diversity for ACI (left) and BI (right) during dawn, daytime and dusk periods. Plots are scaled in original units; inner tick marks represent observations and shaded areas show 95% confidence intervals.

Increase in the basal area of sycamore per plot had a significant negative effect on ACI and BI values during all three time periods (Figure 4.5; Table 4.2) while an increase in the basal area of beech had a significant negative effect on ACI values during the dusk period (Figure 4.6). Basal area of oak, ash and spruce had no significant effect on bird acoustic indices (Appendix P). Box plots of ACI and BI values for each survey location are presented for the 30 days used in analyses in Appendix Q. Out of the other plot characteristics, only distance to edge demonstrated a negative trend during dusk for BI values.

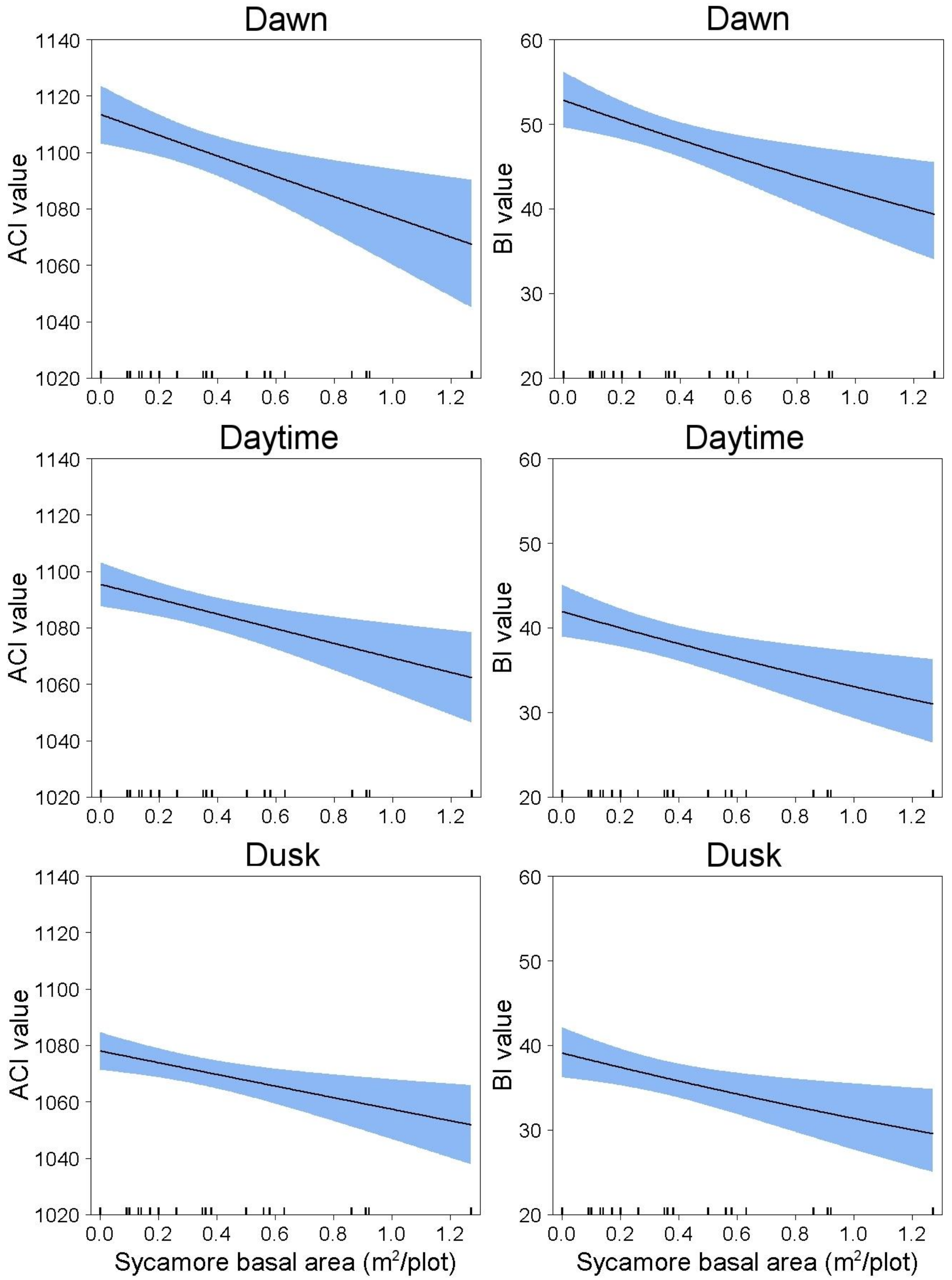


Figure 4.5. Predictor effect displays of sycamore basal area for ACI (left) and BI (right) during dawn, daytime and dusk periods. Plots scales shown in original units, inner tick marks represent observations and shaded areas are 95% confidence intervals.

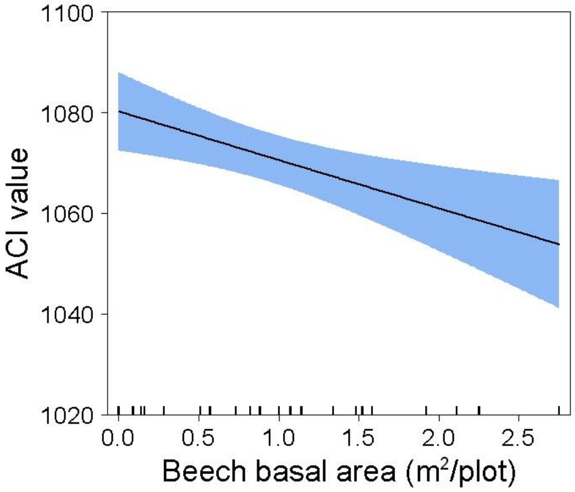


Figure 4.6. Predictor effect display for ACI values during the dusk period for beech basal area per plot. Plots are scaled in original units. Inner black tick marks represent observations with the 95% confidence interval shown by the shaded area.

Linear models assessing the relationships between acoustic index values and the percentage of conifer cover in each plot generally demonstrated response curve shapes that might be expected if mixing broadleaves and conifers were to increase bird species richness and abundance (Figure 4.7). None of these relationships were significant although there were minor trends for ACI during the daytime (Estimate = -105.5, std. error = 55.9, *P*=0.07) and for BI at dawn (Estimate = -44.4, std. error = 24.0, *P*=0.08). The low number of sites with reasonably equal proportions of conifer and broadleaves likely reduced the power for this analysis.

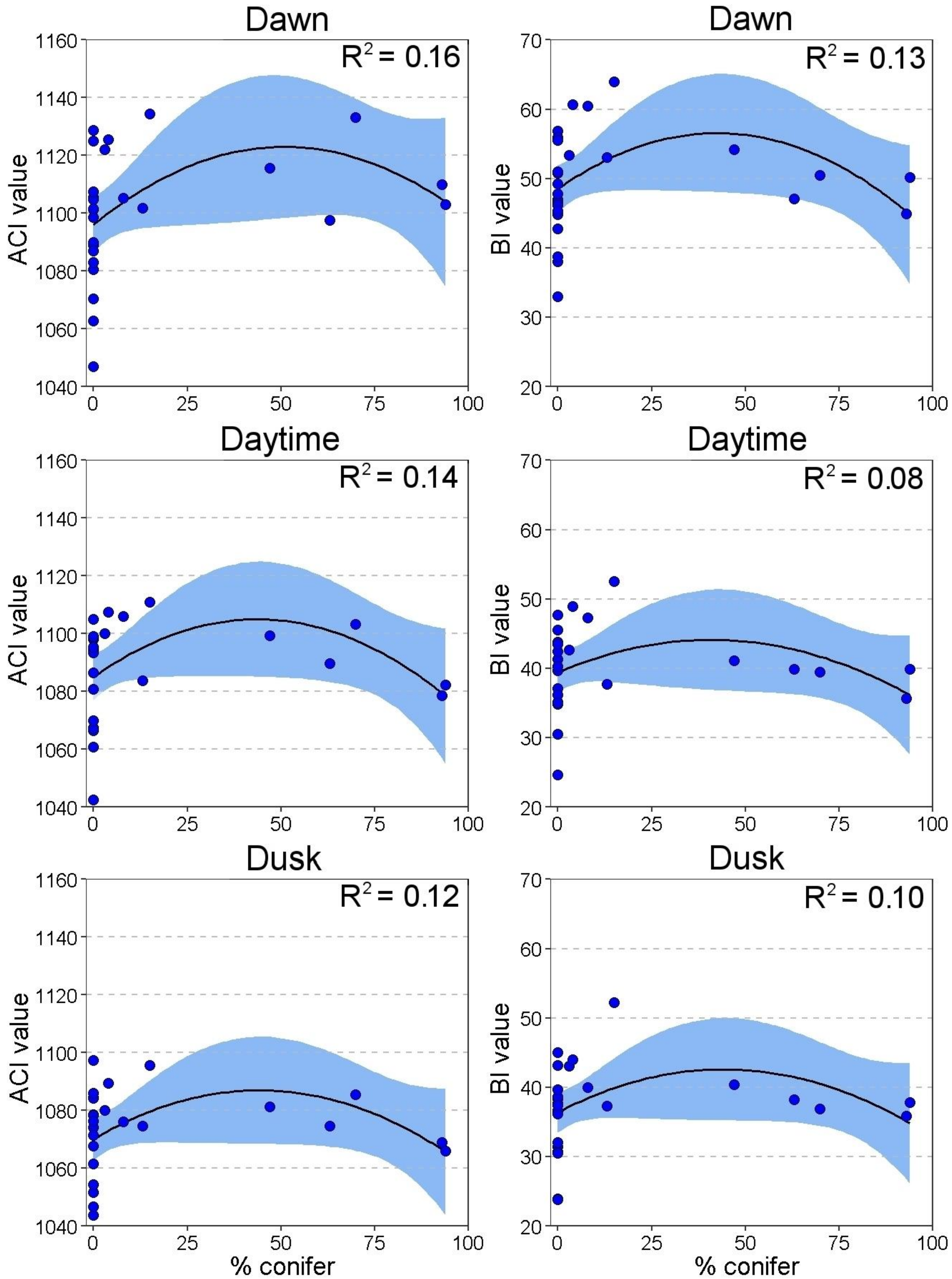


Figure 4.7. Linear model results examining the effect that mixing conifer and broadleaf tree species has on ACI (left) and BI (right) values during dawn, daytime and dusk periods. Points represent median values for individual plots, trendlines are shown in black and shaded areas represent 95% confidence intervals.

4.4 Discussion

This study assessed the feasibility of using acoustic indices as a proxy for bird species richness and revealed significant effects of tree species richness and composition on bird diversity. As predicted, tree species diversity (true Shannon diversity) of the plot had a positive effect on bird acoustic diversity whereas conifer admixture had no significant effect. Instead, basal area of some broadleaf species, especially sycamore, had a negative effect on bird acoustic diversity.

4.4.1 Acoustic Indices as a Proxy for Bird Species Richness

All the indices tested demonstrated significant positive relationships with bird species richness, but the strength of the relationship varied between indices. Overall, ACI appeared to offer the best proxy for bird species richness, which is in agreement with previous findings (e.g. Towsey *et al*., 2014b; Buxton *et al.,* 2016; Hilje *et al*., 2017) that higher ACI values are correlated with higher bird species richness. ACI values corresponded to bird species richness best at lower (1-3) and higher (6-8) species richness whereas more variation was observed at intermediate levels of species richness (4-5 species; Figure 4.3a). Discerning every single species present within a dawn chorus is not simple (Pieretti and Farina, 2013) and calls beyond a certain distance can be masked enough by other species to make them difficult to distinguish, yet they will still make some contribution to the soundscape, and hence the ACI value. If any counts were incorrect, it is therefore more likely that species richness would have been underestimated, rather than overestimated, and undercounting by only one or two species could potentially account for some of the higher ACI values seen for 4 and 5 species.

BI was originally devised as a measure of overall abundance (Boelman *et al*., 2007) and accounted for a lower percentage of variation in bird species richness than ACI suggesting that BI may be less well-suited as a measure of species richness. BI values were generally higher for dawn chorus recordings than for dusk choruses (Figure 4.3b) which is likely to be due to a higher number of individuals vocalising at dawn than at dusk, and this was apparent in spectrograms of the recordings where 'fuller' soundscapes (i.e. greater acoustic activity in both the time and frequency domains) were typically observed for dawn recordings in comparison to those made at dusk. In a couple of cases, recordings with one or two particularly vocal species produced similar BI values to recordings that contained more species. As BI values reflect the total level of sound intensity within a specified waveband, this could potentially be due to multiple individuals of the same species and/or birds being closer to the microphone (see Appendix N).

The relationship between NDSI and bird species richness was clearly non-linear with NDSI values starting to plateau around 4 or 5 species and then remaining relatively similar all the way up to 8 species (Figure 4.3c). This result is most likely explained by the fact that, as a measure of anthropogenic intrusion (Kasten *et al*., 2012), NDSI is calculated as a ratio of sound energy in the biophony band (0.5-1.5 kHz) to sound energy in the anthrophony band (1.5-9 kHz). NDSI is thus limited in range from 1 to -1 and values already start to approach their maximum when only 3 or 4 species are present. As all the test recordings contained biophony, with little to no anthrophony, NDSI values would appear to be accurate in this respect. The use of NDSI as an indicator of bird species richness would nevertheless seem inappropriate as it fails to represent any difference in the number of bird species present beyond a certain point. Additionally, recordings in which anthrophony and biophony were both present could result in lower NDSI values than recordings which contained an equal amount of biophony but no anthrophony. This situation could potentially introduce a negative bias for plots that were closer to flight paths or roads by including frequency ranges that were intentionally excluded from ACI and BI for this very reason.

As mentioned above, NDSI is calculated using separate frequency bands for biophony and anthrophony and it was therefore possible to assess the biophony band in isolation to see whether this offered any improvement (Figure 4.3d). Indeed, the relationship between the NDSI biophony band and bird species richness did appear to be linear and did not peak prematurely as NDSI did. Results were generally similar to that of BI, which is not surprising given that both indices represent measures of power spectral density. However, NDSI partitions the biophony band into 1 kHz bandwidths and only reports the single highest value within any of these (Kasten *et al*., 2012). In contrast, BI includes all the frequencies specified for analysis and represents a measure of their total power spectral density. This situation was reflected in results for the NDSI biophony band where a recording containing only two birds had a higher value than several other recordings which contained 5 or 6. It therefore appears that calculating the index value based on a single 1 kHz band can produce results where a particularly loud or frequent singer will score higher than a dawn chorus. As such, the NDSI biophony band did not appear to be as reliable as ACI as an indicator of species richness, or as BI as a potential measure of abundance.

4.4.2 Effects of Tree True Shannon Diversity and Species Composition

As hypothesised, models indicated that higher tree species diversity, as measured by the true Shannon diversity, had significant positive effects on both ACI and BI values for all three time periods analysed. These results agree with several previous studies which also recorded higher bird species richness and abundance in temperate forests with a higher number of tree species (e.g. Peck, 1989; Donald *et al*., 1998; Fuller, 2000; Poulsen, 2002). A higher number of tree species provides greater habitat heterogeneity and supports more bird species by offering a wider variety of ecological niches (Peck, 1989; Tews *et al.*, 2004; O'Connell *et al*., 2012) with a wider range of food resources (e.g. seeds; Broome *et al*., 2016 or invertebrate prey; Poulsen, 2002). While a previous study in Hainich by Batáry *et al*. (2014) did not find a significant relationship between tree species richness and bird species richness and abundance, it used only 12 plots which were either 'beech-dominated' or 'species rich', where each category had a mean tree species richness of 3.1 and 6.4, respectively. In this case, beech-dominated sites may still have contained a sufficient number of tree species, or been structurally similar enough, to support similar, or at least not significantly different, bird communities to the species rich transects (Batáry *et al*., 2014).

As the structural properties, phenologies and invertebrate communities will vary between different tree species, the specific associations formed with trees by different bird species will also vary in accordance with their specific resource requirements (Hewson *et al*., 2011; Korňan and Adamík, 2017). These species-specific requirements tend to exhibit themselves as preference and avoidance patterns for different tree species, or combinations of tree species (Holmes and Robinson, 1981; Peck, 1989; Böhm and Kalko, 2009; Korňan and Adamík, 2017). Trees that are generally avoided by most, or many, bird species will thus be exemplified by lower bird species richness and/or abundance; increasing the number of tree species, especially by adding those that are more frequently visited by a larger number of bird species, can therefore potentially dilute the negative influence of tree species that are typically avoided by birds.

While sycamore has been shown to be preferred by birds in some previous studies (Peck 1989; Korňan and Adamík 2017), in the current study, acoustic indices were consistently negatively affected by the increase in basal area of sycamore. Sycamore (and the genus *Acer* in general) are associated with fewer species of insects compared to oak, beech and spruce (Kennedy and Southwood 1984; Brändle and Brandl, 2001), and hence might provide less prey for birds. In addition, the negative effect of sycamore observed in the current study could be explained by differences in tree phenology and the associated seasonal peaks in prey abundance. Many birds time their breeding cycles to coincide with annual peaks in prey abundance (Visser *et al*., 2006) and changes in foraging preferences can be attributed to changes in the availability of popular prey species such as caterpillars, which occur in higher numbers in the first few weeks after buds start to open (Murakami and Nakano, 2000). In a study conducted by Böhm and Kalko (2009) in Germany, within ~150 km of Hainich, sycamore was visited by birds more frequently than oak for much of April, when the leaves of oak trees had not yet emerged, but sycamore was in-leaf. In early May, however, when oak leaves were fully unfurled, 5 of the 12 bird species under study changed their foraging preferences from sycamore to oak and the relative frequency of visits to sycamore dropped from around 50% to 15% (Böhm and Kalko, 2009). If this were also the case in Hainich, it is likely that acoustic surveys began after the peak preference time for sycamore had passed. This would also suggest that sycamore does not necessarily represent a negative influence on bird species richness and abundance throughout the year, just at this particular time.

Differences in the phenology of tree species, and their associated peaks in prey biomass (Veen *et al*., 2010), could also contribute to the positive effect observed for increased tree species diversity. Although the precise leaf-out order for Hainich in 2017 was unknown, the approximate order of broadleaf species assessed would be sycamore, beech, oak and ash (Cole and Sheldon, 2017). Differences in budburst dates between early and late leafing species could potentially exceed three weeks (Cole and Sheldon, 2017) and plots containing several of these species would thus represent a succession of peaks in prey abundance, making them particularly attractive to birds. This situation could be of considerable importance during the breeding season when demand for food is highest but peaks in prey biomass are relatively brief in comparison to the nestling period (Visser *et al*., 2006).

In addition to sycamore, a significant negative effect was also observed for beech, but only for ACI and during the dusk period. Beech, as well as sycamore, has smoother bark than the other three tree species in this study, which may host fewer and less diverse invertebrate prey than trees that have knottier bark such as oaks (Peck, 1989; Korňan and Adamík, 2017). Birds that can build up sufficient overnight fat reserves before dusk are able to sing at a higher rate than those that do not (Thomas, 1999). If the observation for beech was related to foraging success, this could explain why the negative effect on acoustic index values was more pronounced at dusk. In the current study, beech was also the most abundant tree species within the forest, which generally exhibit patterns of being less well favoured by birds in comparison to rare and uncommon species (Böhm and Kalko, 2009; Korňan and Adamík, 2017). Furthermore, beech typically opens its leaves earlier than oak and ash (Cole and Sheldon, 2017), and, as with sycamore, bird activity may have been lower at the time of the survey than in the preceding weeks.

In agreement with previous studies (e.g. Donald *et al*., 1998; Poulsen, 2002; Diaz, 2006), results investigating the hypothesis that mixing broadleaf and conifer trees offered some indication that combining these types of trees could be beneficial for birds. However, further studies are needed to investigate the relative percentage of conifer necessary to gain the highest ecological benefits for birds.

4.4.3 Effects of Other Site Characteristics

In addition to the effects of tree species diversity and species composition, other site characteristics that could potentially influence bird diversity and activity were also accounted for within models. Although the effects of distance to forest edge were uniformly negative (i.e. lower index values with increasing distance from forest edge), they were relatively small and only demonstrated a marginally significant negative trend for BI at dusk. This result was consistent with previous studies (Wilson *et al*., 2006; Šálek *et al*., 2010; Terraube *et al*., 2016; Melin *et al*., 2018), including one in Hainich (Batáry *et al*., 2014), which reported higher bird species richness and abundance at forest edges where increased light penetration, shrub densities and vegetation complexity provide more opportunities for nesting, foraging and shelter. However, in the current study only 4 of the 26 plots were situated within 80 m of the forest edge and very few species would be affected by edge effects beyond this point (Terraube *et al*., 2016), which would explain the absence of any strong effects.

Understorey density and complexity has previously been found to have a positive effect on bird diversity (e.g. Diaz, 2006; Melin *et al*., 2018). Indeed, Batáry *et al*. (2014) found that understorey cover had a significant, positive effect on bird species richness in Hainich. While generally positive, in line with expectations, the magnitude of the effect of understorey was practically negligible for most models. As mentioned above, the majority of survey plots in the current study were based in the forest interior where understorey was predominantly comprised of beech saplings and very few shrubs were present. This could explain the absence of effects observed for understorey as saplings do not produce fruit or flowers, which could attract insect prey, and lack the dense structure suitable for nesting and shelter that bushy shrubs such as blackthorn (*Prunus spinosa*) can provide (Batáry *et al*., 2014; Melin *et al*., 2018).

4.4.4 Implications for Forestry and Forest Plantation Management

As the area of planted forest expands globally, the compositions of tree species within forests are increasingly being determined by humans and informed decisions are therefore required to maximise any potential benefits for biodiversity (Castaño-Villa *et al*., 2019). However, long-term, large-scale monitoring schemes necessary to inform such decisions can be costly, time-consuming and require expert knowledge. The use of PAM, in combination with acoustic indices, thus represents a promising alternative, or supplemental approach, to traditional survey methods. Although the effects that tree species diversity and composition have on bird diversity have been investigated before, this study represents the first time a combination of PAM, acoustic indices and pre-established survey plots with a long diversity gradient has been utilised. Generally, the results for acoustic indices were in agreement with the results from previous studies using traditional surveys (e.g. Peck, 1989; Donald *et al*., 1998; Fuller, 2000; Poulsen, 2002; Diaz, 2006; Böhm and Kalko, 2009). Therefore, this study offers a potential proof of concept that emerging ecoacoustics technologies can be applied to address fundamental conservation and habitat management questions.

As hypothesised, this study found that increasing tree species diversity had a significant, positive effect on acoustic index values used as proxies for bird species richness and abundance. However, tree species composition must also be taken into account in order to maximise any potential benefits for bird biodiversity. Certain tree species (e.g. beech) seem to be less favoured by birds than others and, where possible, these species should not be planted on their own but in mixtures with other tree species. While a wider variety of tree species will typically increase structural heterogeneity and the number of available prey species, combining trees with differing leaf-out phenologies would additionally provide a longer period of peak prey abundance that should benefit breeding birds. The significant, negative effect found for sycamore highlights the importance of performing long-term, continuous surveys to account for the differing phenologies of the tree species being studied. Based on the current study alone, sycamore might appear to be a poor choice when planting for bird diversity when in reality it may provide an important foraging resource earlier in the season when the buds of other trees are still premature (Böhm and Kalko, 2009). Additionally, sycamore was the only tree species not represented as a monoculture within the experimental design and could not be compared with monocultures of the other tree species.

In addition to influencing the abundance of invertebrate prey that feed on leaves, tree phenology would also affect the timing of seed production, another important food source for bird species such as finches and crossbills (Broome *et al*., 2016). It is worth noting that the shedding of seeds by Norway spruce occurs between November and April (Nixon and Worrell, 1999) and may also have presented higher index values than it did if surveys had begun a month earlier. Nevertheless, this research has shown that acoustic indices can produce meaningful results and that questions such as this can potentially be investigated using PAM and acoustic indices.

CHAPTER 5

5. Effects of Different Habitats Created by Rewilding on Bat and Bird Activity and Diversity

5.1 Introduction

In the face of the continuing global declines in biodiversity and increasing habitat loss, traditional conservation practices have produced mixed results and failed to meet targets set for reducing biodiversity loss, prompting the search for innovative, alternate strategies (Deinet *et al*., 2013; Nogués-Bravo *et al.*, 2016; Sandom *et al*., 2016). One potentially promising restoration strategy, 'rewilding', could help to restore biodiversity and multiple ecosystem services; however, as a fairly new discipline, there is an urgent need to supplement the existing empirical research on this topic (Sandom *et al*., 2016; Bakker and Svenning, 2018). The concept of rewilding can be broadly defined as the (re)establishment of self-sustaining ecological functions and processes, rather than specific species or habitats, at the landscape level with minimal human intervention (Gillson *et al.*, 2011). Implementation might simply entail abandoning land previously used for agriculture or development and allowing natural recolonisation to take place unaided, sometimes referred to as 'passive rewilding' (Carver, 2019). While land abandonment is a relatively cost-effective form of rewilding, its outcomes can be unpredictable and may result in colonisation by non-native species (Carver, 2019). Abandoned agricultural land can also be negatively perceived by rural residents as being wasteful, desolate and unattractive (Ruskule *et al*., 2013; Tree, 2018). In forest biomes, land abandonment in the absence of large herbivores to control bottom-up succession through grazing, will produce habitats tending towards woodland climax communities (Sandom *et al*., 2016; Schulze *et al*., 2018; Carver, 2019). This might have negative consequences for biodiversity, particularly in semi-natural habitats, through the loss of open-habitat species (Peco *et al*., 2012; Dyulgerova *et al*., 2015; Delibes-Mateos *et al*., 2019).

As opposed to ‘passive rewilding’, 'trophic rewilding' (re)introduces large-bodied carnivores and/or herbivores to facilitate top-down restoration of ecosystem functions (Sandom *et al*., 2016). In some cases, this will involve species that have previously been extirpated from the area by humans (e.g. grey wolves; *Canis lupus*, brown bears; *Ursus arctos*, and European bison; *Bison bonasus*), which may raise concerns regarding human-wildlife conflicts and the potential for detrimental effects on resident wildlife (Nogués-Bravo *et al.*, 2016; Fernández *et al*., 2017). Indeed, its association with the reintroduction of large carnivores can lead to rewilding as a whole being viewed negatively (Sandom *et al*., 2019). Animal translocations and compensation schemes for predated livestock and crop damage can also be very costly (Deinet *et al*., 2013; Nogués-Bravo *et al.*, 2016). Although these costs can be partly offset by revenue streams from tourism if charismatic or endangered species are re-introduced (Deinet *et al*., 2013), the ecological role of species in the community should be the primary consideration in trophic rewilding (Fernández *et al*., 2017). If the re-introduction of previously extirpated species is not possible or desirable, another approach to trophic rewilding (sometimes referred to as 'naturalistic grazing' or 'near-natural grazing') is based on the introduction of assemblages of modern, domesticated herbivores that mimic the grazing behaviour of their extinct equivalents, e.g. Heck cattle (*Bos taurus*) instead of aurochs (*Bos taurus primigenius*) and Konik horses (*Equus ferus caballus*) in place of tarpan (*Equus ferus ferus*) (Vera, 2000).

The re-introduction of large herbivores aims to influence the natural succession and forest regeneration in a similar way as the large herds of indigenous herbivores would have done in the past, resulting in a more diverse mosaic of wood-pasture habitats (Vera 2000). The presence of large herbivores can influence vegetation structure through herbivory, trampling, rooting, wallowing and by altering nutrient and seed dispersal patterns (Olff *et al*., 1999; Doughty *et al.*, 2016; van Klink and WallisDeVries, 2018; Svenning *et al*., 2019). This process creates a cyclical, non-linear succession in patches where grassland gives way to thorny or otherwise unpalatable shrubs, which in turn shelter saplings from herbivory by large mammals enabling trees to grow in groves and open grassland while also preventing the regeneration of closed-canopy forest (Olff *et al*., 1999; Vera, 2000; Vera *et al*., 2006). Without this dynamic disturbance of natural succession, most habitats would eventually revert to homogeneous forest and the actions of large-bodied herbivores thus produce a more diverse range of habitats than would otherwise be present (Olff *et al*., 1999; Gillson *et al.*, 2011; Bakker *et al*., 2016; Fernández *et al*., 2017; Schulze *et al*., 2018; Svenning *et al*., 2019). By increasing the number of niches and environmental resources available, heterogeneity of habitats and habitat structure enable more species to coexist within the same space and are significant, positive drivers of plant and animal diversity (Tews *et al*., 2004; Stein *et al*., 2014). Furthermore, the varied mosaic of habitat patches created by large herbivores should increase the amount of edge and ecotone habitat available (Kernon Countryside Consultants, 2007; Schulze *et al*., 2018), which typically contain a higher diversity of birds (Batáry *et al*., 2014; Terraube *et al*., 2016), bats (Rachwald *et al*., 2016) and insects (van Klink *et al*., 2016).

Managing habitat using large herbivores may also help mitigate the effects of climate change (Zimov, 2005; Gillson *et al.*, 2011) and invasive plants, although results may vary on a case by case basis (Bakker and Svenning, 2018; Delibes-Mateos *et al*., 2019). Indeed, whether the overall effects of browsing and grazing by large herbivores on habitat diversity are positive, negative or neutral will likely depend on them being present in suitable densities. In forests, for example, too few herbivores will have a negligible or limited impact on structural uniformity whereas overgrazing could reduce tree species diversity and even cause a shift to another, equally homogeneous, type of habitat (Ramirez *et al*., 2018). Excessive grazing can additionally have detrimental impacts on arthropods (Debano, 2006; Littlewood, 2008; van Klink and WallisDeVries, 2018), birds (Petty and Avery, 1990; Newson *et al*., 2012), bats (Altringham, 2016) and other mammals (Schieltz and Rubenstein, 2016) by removing understorey and reducing plant species diversity. In order to maintain a mosaic of habitat types where large herbivores are introduced for trophic rewilding, a suitable balance must therefore be struck, either by controlling the density of herbivores through the introduction of predators or culling, or by creating grazing refuges to allow woody vegetation to regenerate in some areas (Lorimer *et al*., 2015; Smit *et al*., 2015; van Klink and WallisDeVries, 2018; Delibes-Mateos *et al*., 2019). Appropriate densities will vary depending on the species of herbivore, habitat type and the aspect of vegetation affected, for example, densities at which ungulates begin to negatively influence forest regeneration and structure are estimated to be approximately equivalent to 10 and 13 roe deer (*Capreolus capreolus*), or 2 and 3 red deer (*Cervus elaphus*), per km^2, respectively (Ramirez *et al*., 2018). Furthermore, a diverse assemblage of herbivores including browsers and grazers is considered important for maximising the amount of variation in vegetation structure (Olff *et al*., 1999; Sandom *et al*., 2014). Dominance by a single species can potentially also lead to habitat homogenisation when selective foraging negatively impacts certain types or species of plants more than others (Gill, 1992; Côté *et al*., 2004; Bakker *et al*., 2016; Svenning *et al*., 2019); however, effects will vary depending on whether dominant plant species are selectively foraged (Côté *et al*., 2004), the susceptibility of different plant species to herbivory (Gill and Beardall, 2001) and other factors such as soil type and the availability of nutrients and water (Ritchie and Olff, 1999). In some cases, diverse assemblages of herbivores can also negatively impact plant diversity if they have additive (i.e. different herbivores consuming the same plant species) rather than compensatory effects on vegetation (Ritchie and Olff, 1999).

5. Effects of Different Habitats Created by Rewilding on Bats and Birds

The rewilding of uneconomical agricultural land is likely to become an increasingly relevant and important topic with calls to implement two-tier, agri-environmental policies that rewild less-productive farmland and focus food production on more suitable land (Merckx and Pereira, 2015). However, limited published evidence exists on the impact of various rewilding practices on habitat structure and associated biodiversity (Marris, 2009). This chapter will investigate how PAM could potentially help to address this knowledge gap by performing a comparison of bird diversity and bat activity among the different habitat types created by land abandonment and trophic rewilding at the Knepp Castle Estate, West Sussex. The Knepp rewilding project began in 2001 and is based on land formerly used for agriculture (Tree, 2017). The southern area of the estate is of particular interest as it represents a combination of land abandonment followed by the introduction of naturalistic grazing that has proven to be a conservation success story by encouraging biodiversity and attracting rare species (DEFRA, 2018). Indeed, although the experiment has been in effect for less than 20 years, it has already attracted species such as common nightingales (*Luscinia megarhynchos*), European turtle doves (*Streptopelia turtur*), purple emperor butterflies (*Apatura iris*) and Bechstein's bats (*Myotis bechsteinii*), as well as increasing numbers of common species (Knepp Estate, 2018a). Three main habitat types were investigated; (i) those predominated by thorny shrubs such as blackthorn (*Prunus spinosa*) and dog rose (*Rosa canina*), (ii) areas comprised mainly of leafy scrub, predominantly sallow (*Salix caprea, Salix cinerea* and hybrids of these species), and (iii) those with a mixture of both leafy and thorny scrub. Until recently, scrub has generally been regarded as a problematic encroacher of open habitats while also being undervalued as a habitat in its own right by conservationists (Day *et al*., 2003; Tree, 2018). Although attitudes towards its ecological benefits have become more positive of late, negative perceptions persist among landowners and farmers (Day *et al*., 2003; Greenaway, 2011). This study therefore also seeks to further advance our understanding of the possible benefits scrub habitats may provide for bats and birds. The structural characteristics and plant species diversity of each habitat were also assessed to explain the underlying reasons for any differences in bat and bird activity between habitat types. This additionally enabled the relative importance of vegetation structure and diversity for bats and birds to be investigated. Increased plant species diversity and habitat structural heterogeneity can have positive effects for bats and birds by providing a wider range of habitat niches for roosting, nesting and shelter, and by hosting a greater diversity and abundance of prey species (Müller *et al*., 2010; O'Connell *et al*., 2012; Irwin *et al*., 2014). Although bat activity may be influenced by increased prey availability, habitat structure has generally been found to be a more important determinant (Jung *et al*., 2012; Müller *et al*., 2012; Blakey *et al*., 2016). Bats typically have more specialised adaptations (i.e. echolocation and wing morphology) and foraging techniques than birds, which makes them particularly sensitive to habitat structure and will constrain the ability of certain bat species to forage in densely vegetated areas (Müller *et al*., 2012; Froidevaux *et al*., 2016; Renner *et al*., 2018; Barbaro *et al*., 2019). While habitat structure has previously been found to exert a greater influence on bat activity than plant diversity (Barbaro *et al*., 2019; Chapter 3), findings for birds have suggested that either plant species diversity (Barbaro *et al*., 2019; Chapter 4), habitat structure (Müller *et al*., 2010) or even both of these (Hewson *et al.*, 2011) could be important. While vegetation structure and plant species diversity both represent potentially important predictors for bird activity and diversity, this may be an indirect consequence of the increased food resources (e.g. seeds and berries) and prey availability due to higher plant species richness and habitat heterogeneity (Hewson *et al.*, 2011; Ferger *et al*., 2014; Renner *et al.*, 2018). Furthermore, vegetation structure and plant species diversity are not necessarily independent and variations in the canopy architectures of different tree species will influence structure while structural aspects (e.g. canopy openness) can influence plant species composition (Müller *et al*., 2010; Barbaro *et al*., 2019). It is therefore likely that both of these aspects could be of importance to birds. Specific predictions to be tested in this chapter are that:

a) Bat activity will reflect the foraging strategies of different bat species as discussed in Sections 1.5.1 and 3.1. For example, leafy scrub, which is more structurally cluttered, is likely to have fewer open- and edge-space foragers, but more closed-space foragers, whereas more open- and edge-space foragers are likely to be recorded in more open thorny and mixed scrub sites

b) For reasons discussed in Section 4.1, bird species diversity, as reflected by acoustic indices, will be higher in sites with greater structural diversity and higher plant species diversity.

c) Vegetation structure will have a stronger influence on bat activity than vegetation diversity whereas both vegetation diversity and structure are likely to have an impact on birds.

5.2 Materials and Methods

5.2.1 Study Location

Surveys were performed at the 1,400 ha Knepp Castle Estate, West Sussex (51.0° N, 0.4° W). Historically, the Knepp Estate had been used for cattle pasture for several centuries although the heavy clay soil prevented any arable farming until the mid-1800s and even then, it was limited to certain areas (Knepp Estate, 2019a). During the Second World War, farming at Knepp was greatly intensified as part of the 'Dig for Victory' campaign, which led to the ploughing of pasture and widespread scrub removal to create space for crops (Tree, 2017). Subsequently, the Knepp Estate had been managed as an arable and dairy farm, which had remained largely unprofitable until the current owners decided to move into conservation in 2000 (Tree, 2017). Inspired by the publication of Franz Vera's *'Grazing Ecology and Forest History*' (Vera, 2000), they adopted naturalistic grazing as the basis of land management practice at Knepp, with the non-goal-orientated aim of creating greater habitat diversity and dynamism, with the minimum amount of human intervention (Tree, 2017).

The Knepp Estate is divided into 3 main blocks: Northern, Middle and Southern. All surveys were performed in the Southern Block, which covers ~470 ha of the estate. Fields in the Southern Block were gradually taken out of production in stages between 2001 and 2006, starting with the least productive first (Tree, 2018). Unlike the other blocks, the Southern Block was not reseeded with grasses, and delays in obtaining appropriate permits and funding for the Southern Block perimeter fence meant that large herbivores were not introduced until 2009, which enabled various shrub plants to establish themselves (Greenaway, 2011; Tree, 2018). The presence of groves of sallow at Knepp, which require wet, bare clay soil to establish themselves, can also be attributed to the lack of grass reseeding and removing fields from agricultural production in stages, thus increasing the likelihood that at least some fields were open during sallow mast years (Tree, 2018). The varied mosaic of habitats within the Southern Block has also been influenced by the purpose, and crops, for which each field had historically been used; for example, fields previously planted with maize were still devoid of scrub or trees in 2011, despite being abandoned since 2000 (Greenaway, 2011; Tree, 2018).

In 2009, English longhorn cattle (*Bos primigenius*), Exmoor ponies (*Equus ferus caballus*) and Tamworth pigs (*Sus scrofa domesticus*) were introduced to the Southern Block to supplement the existing roe deer as free-roaming herbivores (Knepp Estate, 2018b). Fallow (*Dama dama*) and red deer were also introduced in 2010 and 2013, respectively (Tree, 2018). This diverse assemblage of herbivores has helped to maintain the diversity of habitats, and the mosaic of scrub habitats at the Southern Block of the Knepp Castle Estate generally resembles the patch types that cattle, horses and similar large herbivores would be expected to create (Olff *et al*., 1999; Vera *et al*., 2006). Nevertheless, delaying the introduction of large herbivores and allowing a covering of thorny scrub to develop prior to grazing provided natural refuges for saplings and more palatable woody plants (Tree, 2018), which is considered an important mechanism for establishing cyclical succession dynamics (Olff *et al*., 1999; Vera *et al*., 2006).

Potential survey sites were initially pre-selected based on a previous survey of scrub cover at Knepp (Eernisse, 2017) and then assessed during site visits in spring 2018 to establish which of these offered the best representation of each scrub type. Nine sites were selected in total: three in leafy scrub, three in thorny scrub and three in mixed scrub (Figure 5.1). Sites were separated by a mean distance of ~631 m, with a minimum distance of 60 m between the two closest sites. When examining the effects of habitat characteristics at a small spatial scale, this should have provided sufficient separation for bats and birds for the reasons discussed in Sections 3.2.2 and 4.2.5, respectively. Nevertheless, all results were tested for potential spatial autocorrelations between sites (see Section 5.2.6).

Figure 5.1. Ground cover within a section of the Southern Block of the Knepp Castle Estate in (a) 2001 (at the start of the rewilding project), and (b) 2018 with survey locations shown for leafy (green), thorny (red) and mixed (blue) scrub types (created by R. Beason © Google Earth, 2019). Examples of habitat types are shown for (c) leafy, (d) thorny and (c) mixed scrub habitats (Photos by the author).

5.2.2 Passive Acoustic Monitoring

To investigate the acoustic activity of birds and bats in three of the habitat types (thorny, leafy and mixed scrub) at Knepp, a total of nine AURITA units (for details please see Chapter 2) were installed; a single recorder was placed in three separate locations for each of the three habitat types being investigated. Solo devices (Whytock and Christie, 2016) were configured to continuously record audible frequencies at 44.1 kHz as 16-bit, mono wav files using the default gain settings (CLAC_VOL=31, CLAC_DIG_VOL=152) with a default file length of 30 minutes. Triggered bat recordings were made using the same equipment (RPA2; Peersonic Ltd, Windsor, UK) and settings used in Richmond Park (see Section 3.2) with the exceptions of; recording schedule times (20:30 to 05:30) and max file length (45 seconds). The nine-hour duration was chosen for bat surveys as a compromise between recorder field life, encapsulating sunset and sunrise times, and standardising survey duration throughout the survey period. For most of April, night lengths exceeded 10 hours and recording from before sunset until after sunrise would have reduced the number of nights that could be recorded. Although bats are generally considered to be active during April, this will depend on location and weather conditions (Collins, 2016), and some bats may still be in hibernation (Altringham, 2014). In May and June, when bats were more likely to be active, 9 hours was sufficient to capture activity throughout the whole of the night. RPA2 units were also checked to confirm they were triggering correctly. Prior to deployment, all AURITAs were tested to ensure microphones and electronics were in full working order, and all O rings and cling film seals were replaced. USB power bank batteries were also tested in order to find any that might introduce noise on ultrasonic recordings (see Section 2.3).

Recorders were attached to trees using the method described in Chapter 2 and collected ultrasonic and audible data from 5th April until 12th June 2018, for the analyses of bats and birds, respectively. Field time was limited to approximately 10 weeks by off-line data storage capacity and the time required to process recordings so that performing simultaneous surveys for bats and birds meant that some compromise in survey dates was required to account for differences in their respective phenologies. Studies monitoring bird activity in Europe are typically performed between April and June (e.g. Calladine *et al*., 2013; Batáry *et al*., 2014; Barbaro *et al.*, 2019), although singing activity may peak slightly earlier in March for some species (Catchpole and Slater, 2008). Bat activity tends to peak later in the year, around August, when females and juvenile bats leave maternity roosts (Collins, 2016). Performing surveys from April to June thus captured the majority of the breeding season for birds but may have potentially missed some seasonal peaks in bat activity. To avoid potential animal damage and reduce attenuation due to ground interference, AURITA recorders were mounted at a height of 1.5 m - 2.5 m high and secured using padlocks and metal banding. During the survey period, one bat recorder, one audible microphone (Section 2.3) and one data card failed.

Although all faults were corrected, this created data gaps from 30th May to 5th June, and 29th May to 8th June, for bats and birds, respectively.

5.2.3 Bat Data Processing

Out of the 68 complete nights covered by the survey, there were 45 nights when all nine bat recorders simultaneously captured a complete record for the entire 9-hour survey period. As Knepp was not equipped with a weather station, data were obtained from the Met Office's Weather Observations Website (wow.metoffice.gov.uk) for the Davis Vantage Pro2 Plus (Davis Instruments, California, USA) in Gay Street, West Chiltington, which is ~6km west of Knepp. All recordings were additionally checked for rain when manual species identification was subsequently performed. After excluding nights with rain, high winds (>20 km/h) and low temperatures (<7°C), a total of 26 remained that were suitable for use in analyses.

A bat pass was defined as activity within a 5.46 second time block and any files that were multiples of this length of time were split equally into 5.46 second lengths as per Section 3.2.2. This resulted in a total of 12,946 files for the 26 days under analysis. All bat data were processed using Kaleidoscope Pro v5.1.3 (www.wildlifeacoustics.com) and manually checked by the author. Echolocation calls of *M. brandti, M. mystacinus*, *M. daubentonii* and *M. nattereri* are very similar and can be difficult to reliably identify to species (Parsons and Jones, 2000; Ciechanowski *et al*., 2010); detections of all *Myotis* species were therefore combined into a single category. Larger bats (*N. noctula*, *E. serotinus* and *N. leisleri*) may also produce similar echolocation calls, particularly in cluttered environments (Newson and Berthinussen, 2019) and, as there were very few recordings for these three species, they were also combined into a single group (NSL).

5.2.4 Processing of Acoustic Indices

For audible data, excluding days when batteries and data cards were changed, there were 48 days on which all nine recorders completed their daily schedule. As a preliminary check, dates when rain had been detected for bats were also assessed for audible recordings and removed when rain also occurred during the day, leaving 40 days for which acoustic indices were calculated. After acoustic indices had been calculated, heatmaps of acoustic index values (Appendix R) were inspected for anomalies that could indicate any additional days when adverse weather conditions (rain and high winds) likely to bias acoustic index values and/or influence bird activity occurred (Depraetere *et al*., 2012; Gage and Farina, 2017).

Any such occurrences were confirmed by viewing spectrograms and listening to audio recordings, which resulted in a further 10 days being removed, leaving a total of 30 that were suitable for inclusion in analyses.

The Acoustic Complexity Index (ACI; Pieretti *et al*., 2011) and Bioacoustic Index (BI; Boelman *et al*. 2007) were used in this study as they have demonstrated the best performance as proxies for bird species diversity out of acoustic indices tested in Chapter 4, in addition to their ability to discriminate between biophony and undesirable soundscape elements such as wind and anthropogenic noise. Both indices were generated using the *Soundecology* v1.3.3 package (Villanueva-Rivera, 2015) in RStudio v1.0.153 (RStudio Team, 2016) and R v3.4.4 (R Core Team, 2018). As audible recordings were produced continuously for the duration of the survey, this represented a considerable amount of data (6,480 hours) that required processing. It was therefore decided to process every 5th minute of recordings as this sampling schedule is considered to offer a reasonable representation of continuous recordings (Pieretti *et al*., 2015), while reducing processing overhead by 80%. All audible files were recorded in blocks of approximately 30 minutes (±2 seconds) long. To avoid splitting files into 1-minute sections for processing, *readwave* in *tuneR* package (Ligges *et al*., 2016) was used to selectively load the 2nd, 7th, 12th, 17th, 22nd and 27th minute from each 30-minute file for the processing of indices in R. For both indices, an FFT window size of 1024 and a frequency band of 1.5 to 9 kHz, where most bird vocalisations occurred based on examination of dawn chorus recordings, were specified. Although Knepp is situated within a largely rural landscape, the A24 passes within ~600 m of the survey sites. Examination of background traffic noise in recordings demonstrated a peak frequency of approximately 850 to 1,050 Hz. Processing indices using a lower limit of 1.5 kHz should therefore have excluded the majority of any road noise.

For the reasons discussed in Chapter 4 (Section 4.2.6), three sampling periods representing dawn chorus, daytime and dusk chorus were chosen for analyses and defined relative to sunrise and sunset times. These times were obtained from www.sunrise-and-sunset.com for the closest location, which was Ashington (~4.5km SSW of Knepp). Sunrise occurred at 06:08 ±30 min, 05:15 ±20 min and 04:51 ±3 min in April, May and June, respectively. Sunset times were 19:57 ±23 min in April, 20:42 ±21 min in May and 21:09 ±6 min in June. Heatmaps of acoustic indices revealed that any pre-dawn activity typically occurred within the hour before sunrise (Appendix R). However, as nightingales were active in some sites but not others, and it was desirable to limit any bias due to night-time vocalisations, the start of the dawn sampling period was therefore limited to 50 minutes before sunrise, which still included the majority of dawn chorus activity. Heatmaps also indicated that acoustic activity had generally ceased within the first hour after sunset. The dawn sampling period was thus defined as starting 50 minutes before sunrise and ending 2 hours afterwards, the dusk period as 2 hours before sunset and 1 hour after and daytime as the period between the end of the dawn period and the beginning of the dusk period. Median index values (Eldridge *et al*., 2018) were calculated for each of these three periods at each site, for every date that was included in analyses.

5.2.5 Site Characteristics

The following surveys were performed for a circular area of 30 m radius centred on AURTIA recorders in each site:

1. *Species diversity.* Within each site the number of stems for each species of tree or shrub within the survey area were counted and recorded. Totals were then used to calculate the Shannon diversity index (Shannon, 1948), which was then converted to 'true Shannon diversity' values (i.e. *exp*(Shannon index); Jost, 2006).

2. *Vegetation structure.* Using a telescopic 4 m ranging pole, 25 readings were taken across each site. Readings were taken at the centre of each site (i.e. at the recorder) and at three 10 m intervals (10 m, 20 m and 30 m) every 45° (0°, 45°, 90° etc.) from the direction the recorder was facing. Seven height bands were used (1-2 m, 2-4 m, 4-6 m, 6-8 m, 8-10 m, 10-12 m and >12 m) and the ranging pole was positioned at each survey point to record where vegetation was present within 0.5 m of the pole for each interval. Where vegetation was taller than the ranging pole, an Aofar 700 Laser RangeFinder (Aofar, Jiangsusheng, China) was used to assess the height of any vegetation layers above the pole. Vegetation structure survey results for all sites are presented in Appendix S. Vertical structural diversity (*Vertical SD*) was assessed by calculating the Shannon diversity index score based on the frequency of measurements within each of the seven height bands (Sekercioglu, 2002). Horizontal vegetation profile (*CV height*) was represented by the coefficient of variation (standard deviation/mean) of vegetation height using the maximum height at each of the 25 survey points (Rutten *et al*., 2015).

3. *Understorey cover.* Understorey cover over 1.5 m in height was drawn onto paper site maps and scanned to create digital images. The percentage of cover was then calculated after converting each image to black (understorey) and white (no understorey). The number of black pixels were counted with the histogram function in ImageJ ver.1.51j8 (Rasband, 2017) and divided by the total pixels in the image to produce percentages cover.

4. *Other environmental variables.* For bat species, distance to the closest water body (pond or waterway) can be influential (Bellamy *et al*., 2013) and was measured for each site using the ruler tool in Google Earth Pro v7.3.2.5491 (https://earth.google.com). Although the presence of large mammals can potentially affect bird (Dolman *et al*., 2010; Newson *et al*., 2012) and bat (Sections 3.3 and 3.4) activity, all sites were accessible to the large herbivores present.

A summary of site characteristics is presented in Table 5.1.

Table 5.1. Characteristics of sites used for acoustic surveys in Knepp, 2018.

Site	Scrub type	true Shannon diversity	Vertical diversity	CV Height	Understorey >1.5 m (%)	Distance to water (m)
1	Leafy	2.37	1.77	0.27	0.03	171
2	Leafy	2.75	1.63	0.26	0.16	148
3	Leafy	2.42	1.55	0.23	0.07	283
4	Thorny	5.05	0.93	0.41	0.39	134
5	Thorny	3.0	0.88	0.29	0.55	159
6	Thorny	4.22	0.95	0.32	0.41	215
7	Mixed	4.38	1.2	0.45	0.38	82
8	Mixed	3.37	1.2	0.39	0.6	150
9	Mixed	3.97	1.13	0.47	0.46	157

5.2.6 Statistical Analyses

All statistical analyses were performed using R v3.4.4 (http://www.r-project.org) within RStudio v1.0.153 (RStudio Team, 2016). Generalized Linear Mixed Models (GLMMs) assessing the effects of habitat types and site characteristics on bats and birds were fitted using the *lme4* v1.1-21 (Bates *et al*., 2015) and *glmmTMB* v0.2.3 (Brooks *et al*., 2017) packages. Site characteristics were checked for collinearity (correlation coefficients >0.7; Dormann *et al*., 2013) using the *PerformanceAnalytics* v1.5.2 package *chart.Correlation* function (Peterson and Carl, 2018; Appendix T). Understorey cover was removed from further analyses as it was highly correlated (-0.85) with vertical structural diversity, which provided a better overall measure of habitat structure than understorey. Both measures of vegetation structure were strongly correlated with true Shannon diversity (-0.73 and 0.79 for *vertical SD* and *CV height*, respectively). Therefore, separate models were run with either true Shannon diversity or vegetation structure characteristics to investigate the relative importance of woody vegetation species diversity and structural heterogeneity for bats and birds. Variable Inflation Factors (VIF) of final models were checked using the *vif* function in the *CAR* package (Fox and Weisberg, 2019) and all variables had VIF < 3, which did not indicate any remaining multicollinearity (Zuur *et al*., 2010). Additionally, as the fields in which AURITAs were located were removed from production during different years (2 in 2000, 1 in 2003 and 6 in 2005), a preliminary analysis was performed to determine whether years since removal (i.e. 18, 15 and 13, respectively) was related to true Shannon diversity or vertical and horizontal structural diversity. As no significant patterns were revealed (all p-values ≥ 0.15), time since removal was not included in analyses.

5.2.6.1 Statistical Analyses of Bat Activity

To investigate whether the activity of bat species varied between different habitats, the total number of bat passes per night was specified as the dependent variable with *scrub type* (leafy, thorny or mixed) as a fixed effect. Pairwise comparisons of scrub types based on site characteristics showed that the above scrub types were reasonably distinct, supporting these classifications (Appendix U). Survey site (*site*) and Julian date (*day*) were specified as random effects to account for repeated sampling at the same locations (Bolker, 2015) and possible temporal autocorrelation (Crawley, 2007), respectively.

Full model = *total passes/night* ~ *scrub type* + (1|*site*) + (1|*day*)

Null model = *total passes/night* ~ 1 + (1|*site*) + (1|*day*)

Initially, a Poisson distribution was applied and overdispersion was assessed using the function *overdisp_fun* (Bolker *et al*., 2009); a negative binomial distribution was used when data were overdispersed (Crawley, 2007). AIC and log-likelihood scores were compared to assess whether negative binomial distribution and using both *site* and *day* as random effects improved model performance (Appendix V). The most parsimonious models were assessed for 'goodness of fit' using QQ residual plots and one-sample Kolmogorov-Smirnov (KS), significant outliers and spatial autocorrelation using the *DHARMa* v0.2.4 package (Hartig, 2019; Appendix V). Successful models were then used to assess the overall effect of scrub type for each species/species group by performing likelihood-ratio tests with the equivalent null models where *scrub type* was excluded. Significant and marginally significant differences in bat activity due to scrub type were further investigated using pair-wise comparisons.

A second set of analyses was performed to assess the impact of vegetation structural characteristics and true Shannon diversity. Distance to water was also included as a potential confounding factor to create the initial model structures:

total passes/night ~ *vertical SD* + *CV height* + *distance to water* + (1|*site*) + (1|*day*)
total passes/night ~ *true Shannon diversity* + *distance to water* + (1|*site*) + (1|*day*)

Using the same method as the scrub type models, overdispersion, log-likelihood and AIC scores were checked and the same distributions, random errors and crossed design that had previously been determined still offered the best performance, i.e. Poisson distribution for NSL and *site* only as a random effect for *Myotis*. Independent variables were centred and standardised by one standard deviation (z-transformation) so that estimate effect sizes could be directly compared (Schielzeth, 2010). For any significant relationships, models were repeated using non-standardised values so that predictor effect displays scaled in original units could be created with the R *effects* package (Fox and Weisberg, 2018). Post-hoc tests (QQ-plots, KS-tests, outliers and spatial autocorrelation) were also performed (Appendix V).

5.2.6.2 Statistical Analyses of Bird Acoustic Indices

Acoustic indices were modelled using a Gaussian probability distribution for continuous variables (Quinn and Keough, 2002). Lambert-W transformations (Goerg, 2011) and logarithmic link functions (Quinn and Keough, 2002) were applied to account for non-normal distributions of ACI and BI data. For the reasons specified in the previous section, survey site (*site*) and Julian date (*day*) were included as random effects within a crossed model design. The overall effects of scrub type on acoustic index values were assessed by performing likelihood-ratio comparisons of models with *scrub type* as a fixed effect with null models that had *scrub type* excluded:

Full model = *Index value* ~ *scrub type* + (1|*site*) + (1|*day*)
Null model = *Index value* ~ 1 + (1|*site*) + (1|*day*)

Significant results for any scrub type models were then investigated using pair-wise comparisons. The effects of habitat structure and true Shannon diversity were also assessed with a second set of models:

Index value ~ vertical SD + *CV height* + (1|*site*) + (1|*day*)

Index value ~ true Shannon diversity + (1|*site*) + (1|*day*)

Independent variables were centred and standardised by one standard deviation for direct comparison of estimate effect sizes (Schielzeth, 2010). Models with significant relationships were repeated with non-standardised values so that predictor effect displays created with the *effects* package (Fox and Weisberg, 2018) could be scaled in original units. All models were produced for ACI and BI values during each of the three time periods (dawn, daytime and dusk). Post-hoc QQ-plots, KS scores, outlier and spatial autocorrelation tests were performed for all models using *DHARMa* (Hartig, 2019) with results presented in Appendix W.

5.3 Results

5.3.1 Bat Activity

Out of a total of 12,946 ultrasonic recordings made on nights when weather was suitable and every recorder completed its schedule, 849 were found to contain bat passes. *Pipistrellus pygmaeus* was recorded most frequently (46%), followed by *P. pipistrellus* (31%), *Myotis* spp. (17%) and NSL (6%). A single occurrence of *B. barbastellus* was also recorded at site 5 (thorny scrub) on 17/04/18. Bat pass counts recorded at each site on the 26 survey nights are presented as bar charts of daily totals by site type (Figure 5.2) and total counts for each site (Appendix X).

Scrub type had a significant effect on the activity of *P. pipistrellus* and *P. pygmaeus*, was marginally significant for *Myotis* spp., but had no significant effect on NSL species (Table 5.2). Activity of *P. pipistrellus* and *P. pygmaeus* was significantly lower in sites with leafy scrub in comparison to sites with thorny or mixed scrub (Table 5.3). In contrast, activity of *Myotis* spp. in sites with leafy scrub was significantly higher than those with mixed scrub and also exhibited a non-significant trend for higher activity compared to thorny scrub sites. Although there were no significant differences between thorny and mixed scrub habitats for *P. pipistrellus*, *P. pygmaeus* and *Myotis* spp., activity estimates were always slightly higher in mixed scrub (Table 5.3).

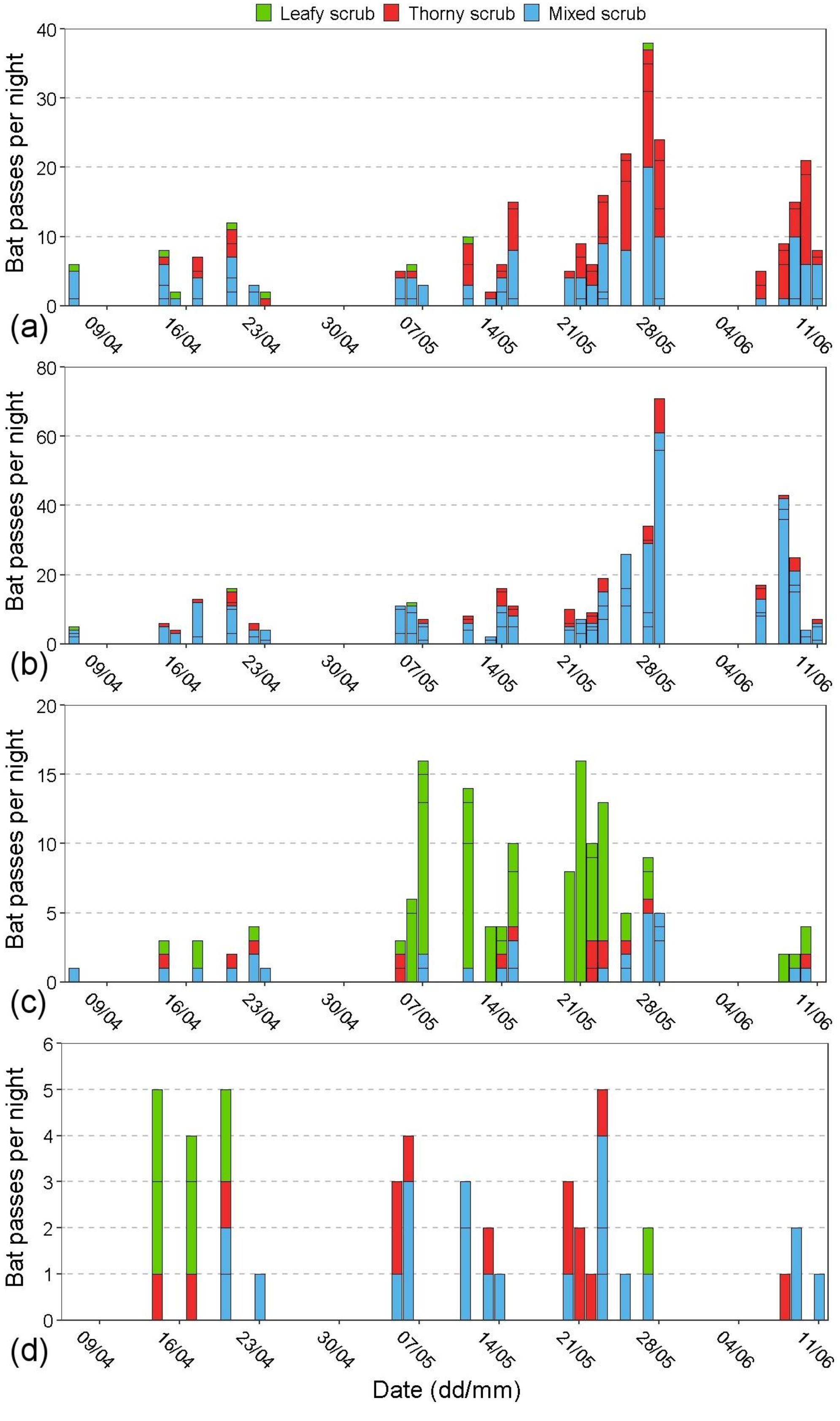


Figure 5.2. Activity of (a) *P. pipistrellus*, (b) *P. pygmaeus,* (c) *Myotis* spp. and (d) *N. noctula*, *E. serotinus* and *N. leisleri* for 26 nights at the Knepp Estate, 2018. Results for separate sites are delineated by horizontal lines. Gaps in the linear time scale are due to either lack of activity, adverse weather or equipment failure.

Table 5.2. Likelihood-ratio tests for the overall effect of site scrub type (leafy/thorny/mixed) on bat activity. Significant results are shown in bold.

Species/species group	Deviance	Chisq	Chi Df	*Pr(*>Chisq*)*
P. pipistrellus	**553.5**	**10.689**	**2**	**0.005**
P. pygmaeus	**592.8**	**10.204**	**2**	**0.006**
Myotis spp.	424.4	4.638	2	0.098
NSL	252.2	2.538	2	0.281

Table 5.3. Post-hoc pairwise comparisons of bat activity between sites with different scrub types.

Treatments compared	Estimate	Std err	*Z* Value	*Pr(*>|*z*|*)*	Sig.
		Pipistrellus pipistrellus			
Mixed - Leafy	2.76	0.72	3.82	<0.001	***
Thorny - Leafy	2.62	0.83	3.17	0.002	**
Thorny - Mixed	-0.15	0.69	-0.21	0.831	
		Pipistrellus pygmaeus			
Mixed - Leafy	4.13	1.09	3.80	<0.001	***
Thorny - Leafy	3.62	1.23	2.93	0.003	**
Thorny - Mixed	-0.51	1.00	-0.52	0.606	
		Myotis spp.			
Mixed - Leafy	-1.30	0.58	-2.23	0.026	*
Thorny - Leafy	-1.37	0.71	-1.93	0.054	.
Thorny - Mixed	-0.07	0.70	-0.10	0.917	

Activity of *Pipistrellus pipistrellus* was significantly lower in sites that had a higher vertical structural diversity but tended to increase with CV height (Figure 5.3a). Similar results were obtained for the activity of *P. pygmaeus* except in this case the relationship with CV height was significantly positive while the negative relationship with vertical structural diversity was non-significant (Figure 5.3b). For *Myotis* spp., higher vertical structural diversity had a significant positive effect on activity, as did distance from water (Figure 5.3c). None of the examined site characteristics had a significant effect on NSL activity (Figure 5.3d). Predictor effect displays for significant results are shown in Figure 5.4.

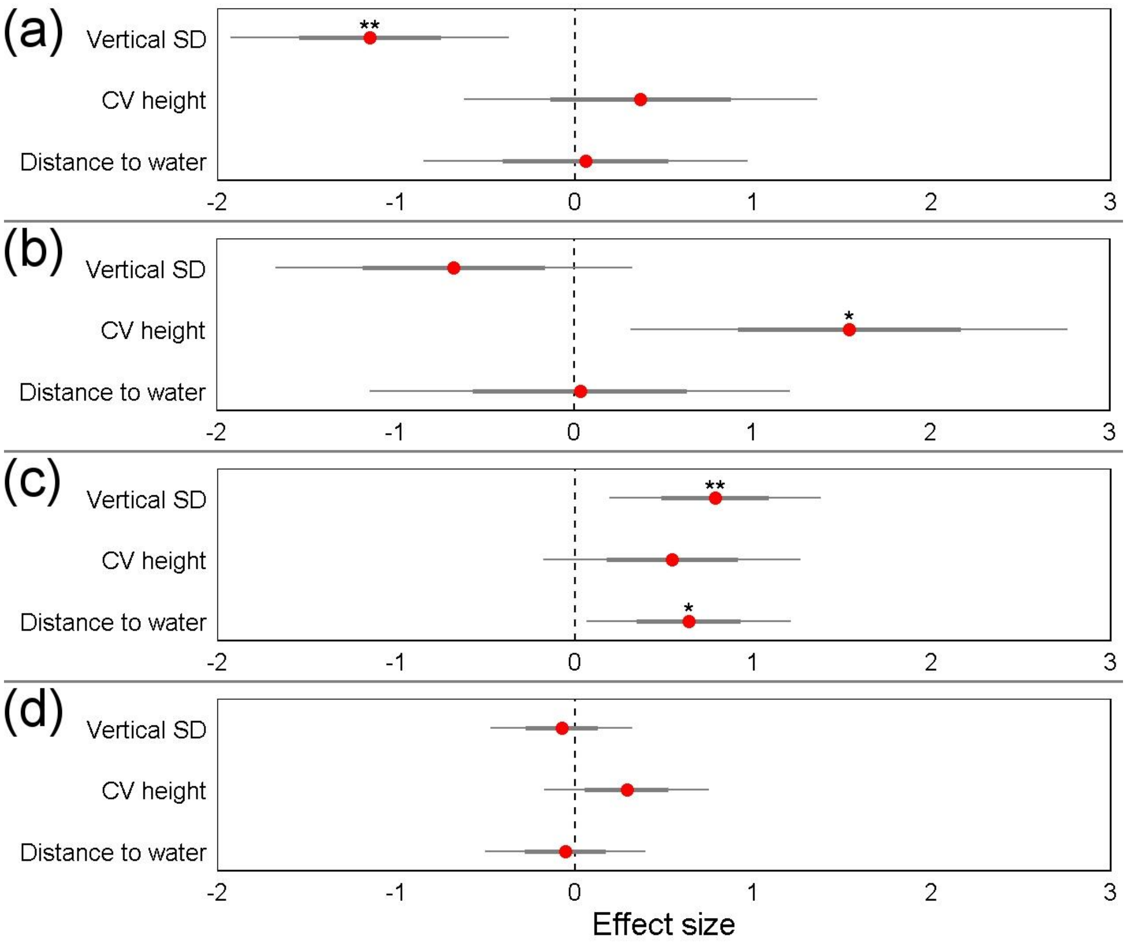


Figure 5.3. Effect size plots for the model exploring the effects of structural site characteristics and distance to water on (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *Myotis* spp., and (d) NSL. Numeric input variables were standardised by 1 standard deviation to enable direct comparison. Effect sizes are represented by red circles; thick grey lines indicate standard errors and thin grey lines show 95% confidence intervals. Significance codes: <0.001 '***', <0.01 '**', <0.05 '*', <0.1 '.'

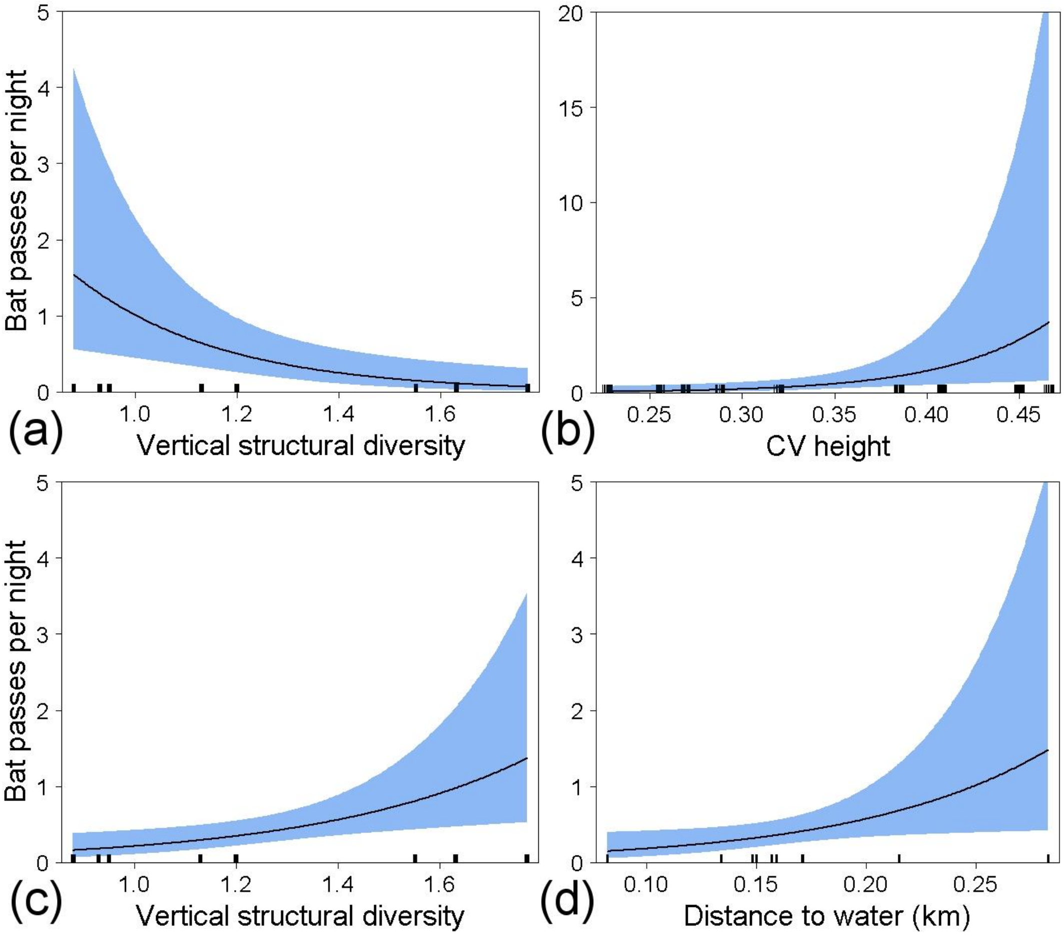


Figure 5.4. Predictor effect displays for significant effects of (a) vertical structural diversity on *P. pipistrellus*, (b) CV height on *P. pygmaeus*, (c) vertical structural diversity on *Myotis* spp., and (d) distance to water (km) on *Myotis* spp. Inner black tick marks represent observations with 95% confidence intervals shown as blue shaded areas. Plots are scaled in original units for easier interpretation.

True Shannon diversity had a significant positive effect on *P. pipistrellus* activity (Figures 5.5a and 5.6) but did not significantly influence any of the other bat species (Figure 5.5). While the effect of distance to water on *Myotis* spp. activity was significantly positive in the model including vegetation structure variables (Figure 5.3c), it was not significant in the model with Shannon diversity (Figure 5.5c), suggesting that the effects of these variables were not independent.

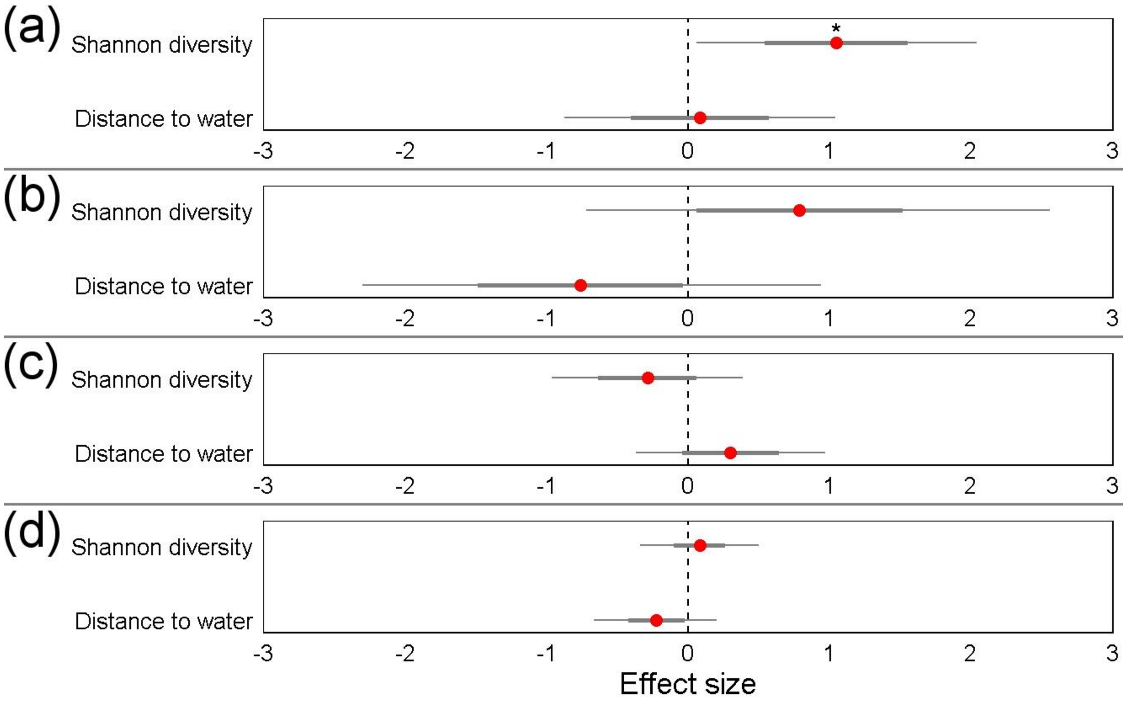


Figure 5.5. Effect size plots for the GLMM exploring the effects of true Shannon diversity and distance to water on (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *Myotis* spp., and (d) NSL. Numeric input variables were standardised by 1 standard deviation to enable direct comparison. Effect sizes are represented by red circles; thick grey lines indicate standard errors and thin grey lines show 95% confidence intervals. Significance codes: <0.001 '***', <0.01 '**', <0.05 '*', <0.1 '.'

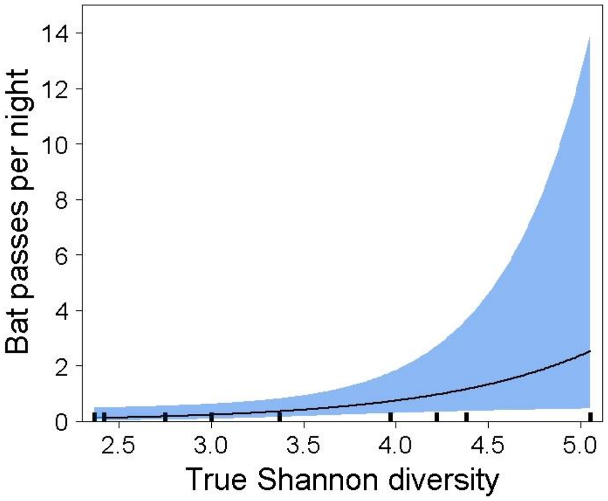


Figure 5.6. Predictor effect display for the relationship between *P. pipistrellus* activity and true Shannon diversity. Inner black tick marks represent observations, 95% confidence interval is shown by blue shaded area. Plots are scaled in original units for easier interpretation.

5.3.2 Bird Acoustic Indices

Scrub type had a significant effect on ACI values during all three time periods while BI values did not differ significantly between scrub types at any time (Table 5.4). Regardless of the survey period (dawn, daytime or dusk) being assessed, ACI values for leafy scrub were significantly lower than in both thorny and mixed scrub habitats but did not differ significantly between thorny and mixed scrub (Table 5.5, Figures 5.7 and 5.8).

Table 5.4. Likelihood-ratio tests for the overall effect of site scrub type (leafy/thorny/mixed) on acoustic index values. Significant results are shown in bold.

Time period	Deviance	Chisq	Chi Df	*Pr(>*Chisq*)*
		ACI		
Dawn	**2844.0**	**15.072**	**2**	**<0.001**
Daytime	**2746.7**	**14.989**	**2**	**<0.001**
Dusk	**2545.2**	**15.233**	**2**	**<0.001**
		BI		
Dawn	1834.2	3.468	2	0.177
Daytime	1690.3	1.536	2	0.464
Dusk	1665.8	2.789	2	0.248

Table 5.5. Post-hoc pairwise comparisons of bird diversity between sites with different scrub types.

Treatments compared	Estimate	Std err	*Z* Value	*Pr(>*|*z*|*)*	Sig.
		ACI (Dawn)			
Mixed - Leafy	0.157	0.028	5.6	<0.001	***
Thorny - Leafy	0.170	0.033	5.1	<0.001	***
Thorny - Mixed	0.013	0.032	0.4	0.675	
		ACI (Daytime)			
Mixed - Leafy	0.093	0.015	6.1	<0.001	***
Thorny - Leafy	0.073	0.018	4.0	<0.001	***
Thorny - Mixed	-0.020	0.017	-1.2	0.248	
		ACI (Dusk)			
Mixed - Leafy	0.071	0.012	5.8	<0.001	***
Thorny - Leafy	0.072	0.015	4.9	<0.001	***
Thorny - Mixed	0.001	0.014	0.0	0.968	

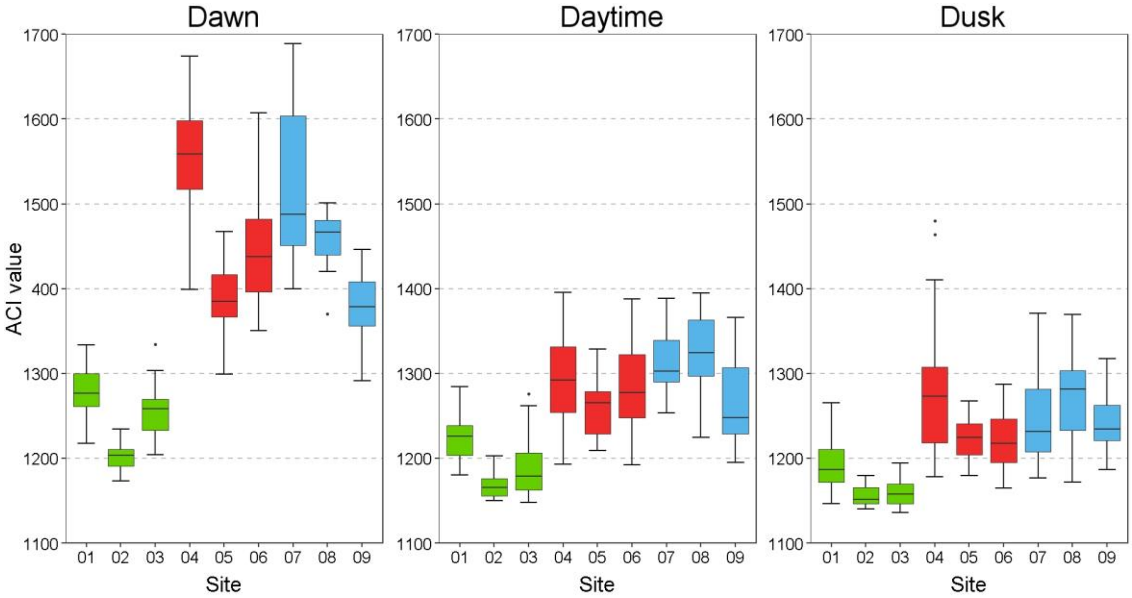


Figure 5.7. Median Acoustic Complexity Index values of the 30 days used in analyses for birds during dawn, daytime and dusk periods at Knepp, 2018. Medians (lines) and interquartile ranges shown. Green = leafy scrub, red = thorny scrub and blue = mixed scrub.

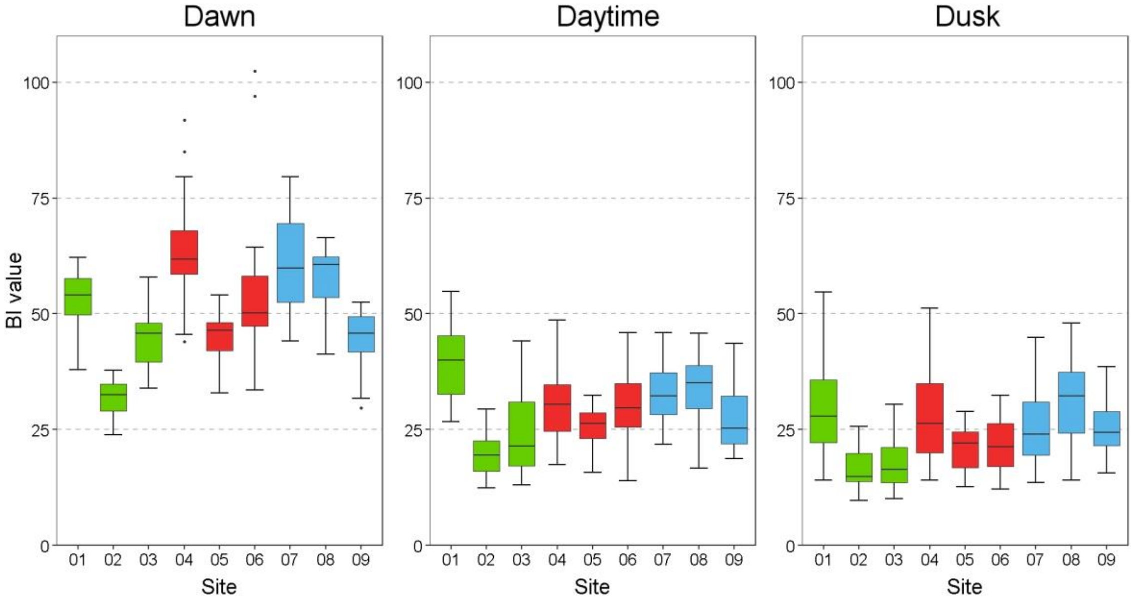


Figure 5.8. Median Bioacoustic Index values of the 30 days used in analyses for birds during dawn, daytime and dusk periods at Knepp, 2018. Medians (lines) and interquartile ranges shown. Green = leafy scrub, red = thorny scrub and blue = mixed scrub.

True Shannon diversity and CV height had significant positive effects on ACI values during all three time periods. Vertical structural diversity had a significant negative effect on ACI at dawn and dusk, and a marginally significant negative effect during the daytime (Table 5.6, Figures 5.9 and 5.10). For BI values, significant positive effects were observed for true Shannon diversity at dawn and CV height at dusk (Table 5.6, Figure 5.11).

Table 5.6. Estimates for GLMMs examining the effects of vegetation structure and true Shannon diversity on acoustic index scores during dawn, daytime and dusk periods. For convenience, results from both sets of models are presented in tandem. Effect sizes are directly comparable between vegetation structure and true Shannon diversity models as all input variables were centred and standardised to one standard deviation.

Characteristic	Estimate	Std err	Z Value	*Pr(>|z|)*	Sig.
ACI (Dawn)					
Vertical structural diversity	-0.050	0.016	-3.1	0.002	**
CV height	0.041	0.016	2.6	0.010	**
True Shannon diversity	0.077	0.016	4.9	<0.001	***
ACI (Daytime)					
Vertical structural diversity	-0.020	0.011	-1.9	0.060	.
CV height	0.027	0.011	2.5	0.011	*
True Shannon diversity	0.034	0.012	3.0	0.003	**
ACI (Dusk)					
Vertical structural diversity	-0.017	0.007	-2.4	0.015	*
CV height	0.023	0.007	3.4	<0.001	***
True Shannon diversity	0.030	0.009	3.4	<0.001	***
BI (Dawn)					
Vertical structural diversity	-0.047	0.075	-0.64	0.525	
CV height	0.095	0.075	1.26	0.206	
True Shannon diversity	0.130	0.062	2.09	0.037	*
BI (Daytime)					
Vertical structural diversity	0.036	0.076	0.48	0.631	
CV height	0.106	0.076	1.40	0.161	
True Shannon diversity	0.057	0.069	0.84	0.402	
BI (Dusk)					
Vertical structural diversity	0.027	0.074	0.36	0.716	
CV height	0.166	0.073	2.26	0.024	*
True Shannon diversity	0.100	0.074	1.35	0.177	

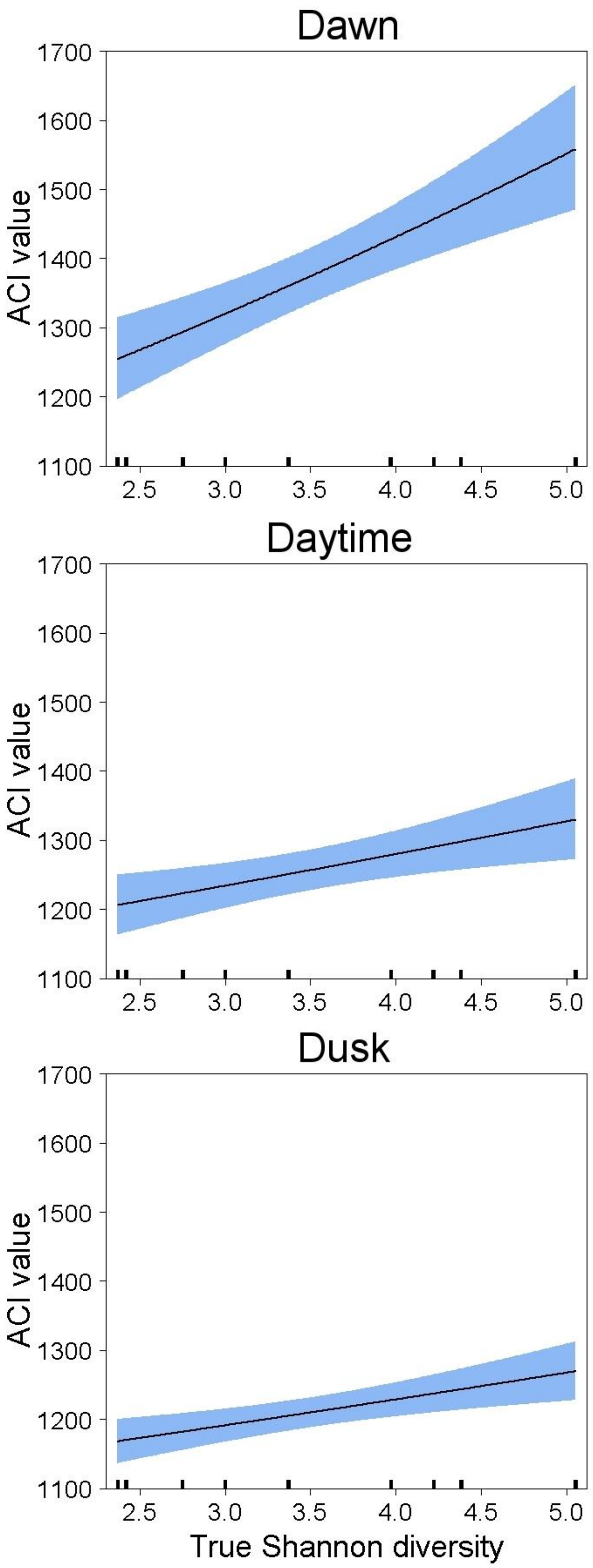


Figure 5.9. Predictor effect displays of relationships between ACI and true Shannon diversity for dawn, daytime and dusk. Plots are scaled in original units, observations shown as inner tick marks and 95% confidence intervals as shaded areas.

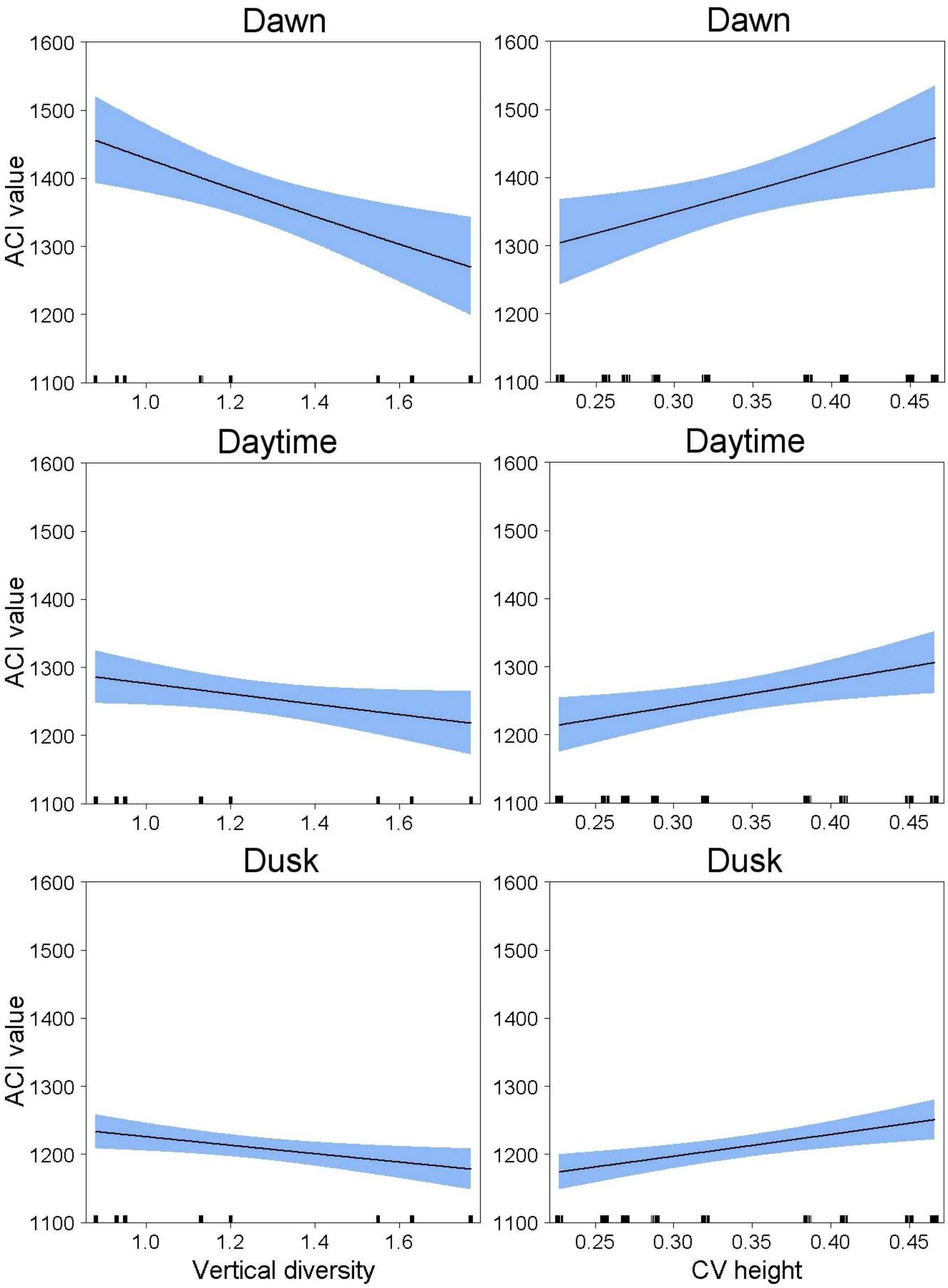


Figure 5.10. Predictor effect displays of relationships for ACI and vertical structural diversity (left) and CV height (right). Plots are scaled in original units, observations shown as inner tick marks and 95% confidence intervals as shaded areas.

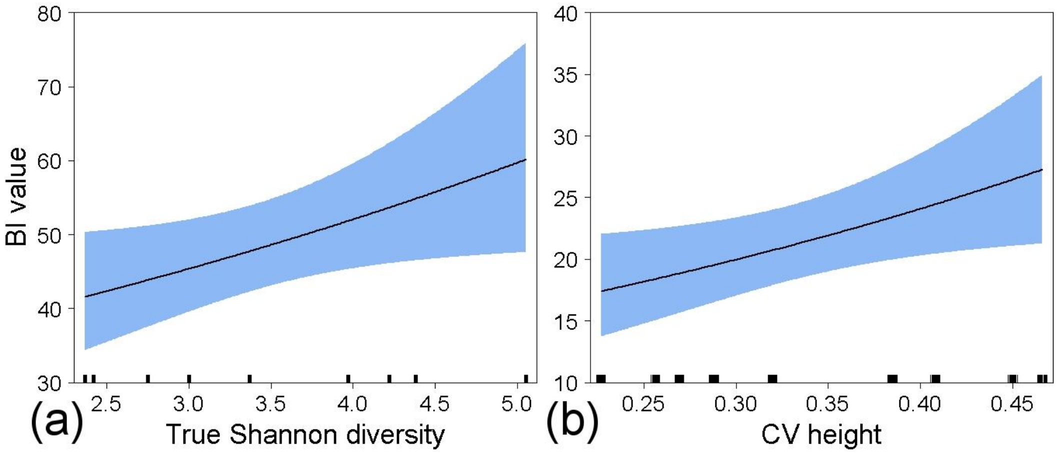


Figure 5.11. Predictor effect displays of relationship between BI and (a) true Shannon diversity (dawn chorus), and (b) CV height (dusk chorus). Inner tick marks represent observations with 95% confidence intervals shown as blue shaded areas. Plots are scaled in original units.

5.4 Discussion

To the best of my knowledge, this study represents the first use of passive acoustic monitoring to assess the effects of different habitat types created by rewilding on two key taxa, bats and birds, which are both considered to be important bioindicators. The activity of bats was generally in accordance with predictions based on habitat preferences and reflected the differing foraging strategies of each species/species group. Investigations into the effect of site characteristics offered further support for the hypothesis that structural diversity is a more important predictor of bat activity than plant diversity. For birds, vegetation structure and plant diversity both appeared to be important determinants of diversity and, to a lesser degree, abundance; however, the direction and strength of effect for structural characteristics varied depending on other influencing factors.

5.4.1 Effects of Different Scrub Habitats on Bat Activity

5.4.1.1. Pipistrelle Species

Both pipistrelle species showed higher activity in mixed scrub, closely followed by thorny scrub, and significantly lower activity in leafy scrub. This is as expected as both species are aerial hawkers, which are better adapted to foraging in edge-spaces than in highly cluttered environments (Müller *et al*., 2012;

Fuentes-Montemayor *et al*., 2013; Altringham, 2014), such as those found under sallow.

Leafy scrub was characterized by high vertical structural diversity, which had a significant negative effect on *P. pipistrellus* activity whereas its effect on *P. pygmaeus* was also negative but not significant. This result may potentially reflect subtle differences in habitat preferences by the two species. *Pipistrellus pygmaeus* is an extremely agile species, which has a stronger association with vegetation than *P. pipistrellus* (Dietz and Kiefer, 2016) and, unlike *P. pipistrellus*, is more active in the interior of forest and woodland than at the edge (Fuentes-Montemayor *et al*., 2013) or in gaps (Froidevaux *et al*., 2016). It is therefore logical that, with its tolerance for vegetation clutter (Suarez-Rubio *et al*., 2018), *P. pygmaeus* would be less negatively affected by more complex vertical vegetation structure than *P. pipistrellus*.

The effect of CV height was generally positive for all bat species although it was only significant for *P. pygmaeus*. As a representation of horizontal canopy roughness irrespective of canopy height (Rutten *et al*., 2015), lower CV height values were associated with flatter canopy profiles and lower levels of bat activity. The external canopy surface can act as a surrogate edge space for species such as pipistrelles (Jung *et al*., 2012; Froidevaux *et al*., 2016) and more heterogeneous canopy surfaces can provide a wider variety of niches with higher prey abundance (Müller and Brandl, 2009) and better protection from predators (Froidevaux *et al*., 2016). Indeed, higher heterogeneity of the canopy profile has been found to positively influence the activity of edge-space foragers (Jung *et al*., 2012; Froidevaux *et al*., 2016) and could explain the significant positive effect CV height had on *P. pygmaeus*. As *P. pipistrellus* is more of a habitat generalist than *P. pygmaeus* (Davidson-Watts *et al*., 2006), its activity was more evenly spread between sites with mixed and thorny scrub (Appendix X), which would have consequently diluted its relationship with CV height. Additionally, Jung *et al*. (2012) found that activity of *P. pipistrellus* was primarily linked to vertical structural variation, which would also agree with the more significant effect found for vertical structural diversity. The split in activity between thorny and mixed scrub for *P. pipistrellus* also illustrates that the mosaic of scrub types not only provides optimal habitat for different species, but also provides opportunities for the same species, particularly generalists, to utilise or switch between different habitats throughout the season.

Pipistrellus pipistrellus was the only bat species to demonstrate a significant relationship with true Shannon diversity. In general, as all bat species except NSL were significantly influenced by some aspect of vegetation structure and the effect of true Shannon index was less significant than the effect of vertical structural diversity for *P. pipistrellus*, habitat structure would appear to be a more important determinant of bat activity than vegetation diversity, as predicted.

5.4.1.2. *Myotis* Species

As hypothesised, activity of *Myotis* species was higher in leafy scrub than in mixed or thorny scrub. Higher vertical structural diversity, which was representative of more cluttered leafy scrub habitats, with vegetation present in a higher number of strata, also had a significant positive effect on the activity of *Myotis* species. These bats are predominantly gleaning species adapted to foraging in cluttered environments (Altringham, 2014) with a high density of trees (Fuentes-Montemayor *et al*., 2013). Müller *et al*. (2013) also recorded significantly more *Myotis* activity within 1 m of the ground, with a drop in activity levels above 7 m. Vegetation profiles of the habitats surveyed in the current study (Appendix S) illustrate that the lower strata (1-4 m) were much more open in leafy sites compared to thorny and mixed ones due to a lack of understorey, thus providing a suitable foraging space for *Myotis* species. The relatively few occurrences of other bat species recorded under leafy scrub (Appendix X) additionally suggests that, with limited competition for resources, this habitat could provide a particularly attractive niche for *Myotis* spp., or at least for those within Knepp.

Despite having a preference for leafy scrub, *Myotis* were also recorded in thorny and mixed scrub types on most nights, which may indicate a degree of habitat switching but could also be a consequence of combining several species with variations in their foraging strategy (Siemers and Swift, 2006; Altringham, 2014). For *Myotis* species, and to a lesser degree *P. pygmaeus* and *P. pipistrellus*, activity was generally lower in April, peaking in May and then falling again in June. Such patterns could be attributed to the annual cycles of UK bats, which leave hibernation sites from March up until May, and tend to give birth to young in June (Altringham, 2014). The high number of nights with unfavourable conditions (19 out of 45) removed from analyses reflects the generally poor weather experienced in April and early May 2018. The more prolonged peak in *Myotis* activity during May compared to other species could potentially be related to the more sheltered conditions under sallow (Entwistle *et al*., 2001). Indeed, although relatively few, the majority of instances when non-*Myotis* species were recorded in leafy scrub also occurred within April to mid-May.

The positive effect of distance to water (i.e. higher activity further away from water sources) was initially surprising for the *Myotis* group, as *M. daubentonii'*s primary foraging strategy involves trawling over water (Altringham, 2014). This could suggest that most of the bats recorded in this group consisted of other *Myotis* species, for which habitat structure was more important than proximity to water. However, the effect of distance to water became non-significant when true Shannon index was included in the model, suggesting that the significant positive effect of water in the model with vertical and horizontal diversity was probably caused by some confounding with another variable.

5.4.1.3 NSL

Activity of NSL species was in general quite low (1-5 passes per night across all 9 sites), which might explain why it did not differ among scrub types and did not display any significant relationships with site characteristics. Contrary to expectations, NSL activity was not significantly lower in highly cluttered sites with leafy scrub. A possible explanation for low NSL activity is that scrub represents suboptimal habitat for NSL bats as serotines often glean near to, or directly from, the ground (Altringham, 2014), and a dense scrub layer would likely inhibit their foraging efficiency (Rainho *et al*., 2010). NSL species in general tend to demonstrate preferences for open spaces such as pasture, meadow and parkland (Entwistle *et al*., 2001).

While no preference for a particular scrub type was observed for NSL when data were averaged across the whole observation period, it appears that these bats used different scrub types in early and late spring/early summer. In April, the majority of NSL recordings NSL occurred at sites with leafy scrub (Figure 5.2d), whereas in May and June these species were recorded mainly in mixed and thorny scrub with only a single occurrence in leafy scrub. The preference for leafy scrub in April is surprising as these sites are extremely cluttered with a high density of sallow stems (Figure 5.1c), which is not a typical open habitat usually preferred by these bat species (Müller *et al*., 2012; Altringham, 2014). One possible explanation could be that sallow provided more sheltered commuting routes than open spaces during adverse weather as discussed above. It is also possible that NSL, which are typically more active at canopy level (Müller *et al*., 2013), may have been easier to detect in early April before sallow were fully in-leaf although foliage is believed to account for <5% of signal attenuation at ultrasonic frequencies (Obrist *et al*., 2011). In general, the low number of occurrences recorded for NSL makes it difficult to draw any firm conclusions.

5.4.2 Effects of Different Habitats on Bird Activity

Of the two acoustic indices examined, ACI showed more pronounced differences between scrub types and was more strongly influenced by habitat characteristics than BI. Given that ACI is a proxy of bird species richness whereas BI is a proxy of bird abundance (please see Section 1.3.3), this suggests that bird diversity was affected by the habitat types created by rewilding more than bird abundance. In all three periods examined, ACI values were uniformly positively affected by the true Shannon diversity index and CV height while vertical structural diversity had a consistent negative effect on ACI. In contrast, vertical structural diversity had no significant effect on BI, whereas true Shannon index and CV height had positive effects on BI values, which were each significant during one of the studied time periods. Although statistical effects for ACI were stronger for true Shannon diversity in comparison to structural aspects, both vertical structural diversity and CV height were also clearly influential. It would therefore appear that, in this study, vegetation structure and diversity were of relatively equal importance as predictors for bird activity.

Reasons for the expected positive relationship between bird diversity and true Shannon diversity have already been detailed in Section 4.4.2. While the relationship between ACI and true Shannon diversity was significant for all time periods, the relationship between BI and true Shannon diversity was only significant during dawn chorus, when vocalisations were more intense and differences between sites were likely to be more pronounced. Similarly, Diaz (2006) found a significant positive relationship between shrub species diversity and bird species richness but no such relationship with bird abundance. While it may seem unusual that increased species richness does not necessarily entail higher abundance, this effect is potentially explained by the 'area-heterogeneity trade-off' (Allouche *et al*., 2012). Allouche *et al*. (2012) suggest that, as habitat heterogeneity increases, the amount of space available for each habitat niche will decrease, thus reducing the size of the population that can be supported. The idea that higher habitat heterogeneity creates a higher structural complexity with more niches to exploit thus leading to higher species diversity (MacArthur and MacArthur, 1961), or the 'habitat-heterogeneity hypothesis', is a key concept in ecology (Tews *et al*., 2004). While the negative relationship found between vertical structural diversity and ACI values may seem counter-intuitive, increased structural heterogeneity does not always have a positive response on bird species richness and effects may vary with the spatial scale or vegetation characteristic studied (Tews *et al*., 2004; Stirnemann *et al*., 2014). In addition, vertical structural diversity was negatively correlated with understorey cover (-0.85) and true Shannon diversity (-0.73), both of which have been found to positively influence bird diversity (e.g. Poulsen, 2002; Diaz, 2006; Batáry *et al*., 2014; Chapter 4).

In the current study, the high vertical structural diversity was characteristic of leafy scrub, followed by mixed and then thorny scrub. The high density of sallow stems found in leafy sites could potentially have impeded accessibility and foraging efficiency due to their highly cluttered nature (Bradbury *et al*., 2005), thus making these sites less attractive (Table 5.5). Birds will also naturally attempt to maximise the transmission efficiency of any vocalisations and so the logical expectation would be for them to sing from higher, more open perches above the canopy layer (Catchpole and Slater, 2008). In leafy plots, the mean vegetation height was 7-8 m compared to 2-4 m in thorny and leafy sites. As all recorders were placed at similar heights (~2 m), this could have potentially meant that birds singing in leafy sites were further away from recorders than in the other sites. If this had been the main reason for lower ACI values in leafy sites, it would be reasonable to expect values for BI to have been similarly influenced. Indeed, based on tests performed in Appendix N, the effect of distance was found to be relatively similar between these indices. However, while ACI values were consistently lower in leafy sites, BI values for leafy sites were more similar, and in some cases higher, than other habitat types (Figures 5.7 and 5.8). Furthermore, when foliage is present, singing at lower heights (~4 m) beneath the canopy layer actually improves transmission efficiency for the calls of some species (Blumenrath and Dabelsteen, 2004). Indeed, different species of birds may use different singing positions based on the transmission efficiencies of their calls at different heights and will also sing from lower down to avoid predation (Catchpole and Slater, 2008).

Another explanation for the negative effect of vertical structural diversity could relate to the relative abundance of vegetation in certain height bands. Melin *et al*. (2018) found that an increased proportion of vegetation over 6 m had a negative effect on bird diversity when vegetation was not also present below 6 m, in the shrub layer. In sites with the highest vertical diversity (i.e. leafy sites), a large proportion of vegetation was recorded above 6 m (Appendix S) and understorey cover was also lowest in these sites (Table 5.1). Leafy sites thus fit the profile described by Melin *et al*. (2018) and the lower ACI values recorded would therefore appear to be in general agreement with their findings. Furthermore, mixed sites contained intermediate levels of vertical diversity yet tended to have higher, or comparably high, ACI values but, unlike leafy sites, a dense shrub layer was also present in mixed sites. It could therefore be argued that the effect of vertical structural diversity is not necessarily negative *per se*, but may be conditional on whether a suitable shrub layer is also present, and whether vertical diversity exceeds a certain point at which access begins to become restricted, as has been hypothesised for bats (Froidevaux *et al*., 2016). Indeed, Carrasco *et al*. (2019) found that although vertical structural heterogeneity had a positive influence on bird species richness at low to intermediate levels, higher levels had a detrimental effect.

In contrast to vertical structural diversity, CV height was positively correlated with true Shannon diversity (0.79) and sites characterised by higher values for CV height (i.e. mixed and thorny scrub) also contained the highest degree of ground cover in the shrub layer, which has been found to positively influence bird diversity (Sweeney *et al.*, 2010; Melin *et al*., 2018). A more heterogeneous vegetation surface can also provide a wider range of microhabitats, hosting a greater abundance and diversity of invertebrate prey species (Müller and Brandl, 2009; Ulyshen, 2011; Zellweger *et al*., 2017). Significant positive relationships between various measures of variation in canopy height and bird diversity have frequently been documented (e.g. MacArthur and MacArthur, 1961; Flaspohler *et al*., 2010; Huang *et al*., 2014; Zellweger *et al*., 2017; Carrasco *et al*., 2019) and results of the current study would therefore appear to be in line with expectations. Nevertheless, as with vertical structural diversity, the effects of horizontal structure may vary based on certain conditions. The relationship between foliage height diversity and bird species diversity may only apply when comparing different habitat types; Willson (1974) and Erdelen (1984), for example, did not find any evidence of this relationship when comparing forest habitats and it only became apparent when scrub habitats were included in analyses. Carasco *et al*. (2019) also found that while increasing canopy height variation had a positive effect on bird species richness, this relationship started to plateau at intermediate values.

5.4.3 Implications for Habitat Management and Rewilding Projects

Evidence of habitat specialisation presented for different bat species in this study further emphasises how the provision of a variety of habitats is important for maximising benefits for biodiversity by supporting a greater number of species (e.g. Tews *et al*., 2004; Rainho *et al*., 2010; Hewson *et al.*, 2011; Fuentes-Montemayor *et al*., 2013; Stein *et al*., 2014). However, based on the results of acoustic indices, it is also worth noting that a greater diversity of habitats may not necessarily be associated with a similar increase in species abundance depending on the amount of available space (Allouche *et al*., 2012). This could potentially be an important consideration for setting realistic expectations when assessing the performance of habitat restoration and creation projects.

Similarly, while early successional habitats such as the scrub at Knepp are characterised by high productivity and structural heterogeneity, and can provide an important source of habitat for threatened bird species and specialists (Swanson *et al*., 2011; Reif *et al*., 2013), late successional stages (e.g. forest) may host a greater number of generalist species (Reif *et al*., 2013). Habitat management decisions should therefore be based on whether objectives aim to increase species richness or abundance, or to provide habitat for a greater number of generalists or a smaller number of more specialised species of higher conservation concern. If a greater abundance of more generalist species is desirable, allowing reclaimed land to progress to climax forest could possibly be more appropriate (Reif *et al*., 2013), while the use of large herbivores to disrupt natural succession could be employed to benefit a smaller but more diverse community of rarer species. A mixture of early- and late-successional habitats could also be created through the use of grazing refuges (van Klink *et al*., 2016) or by maintaining appropriate densities and distributions of mammalian grazers (Ramirez *et al*., 2018). In this case, the relative amount of space allocated to each successional stage should also be considered if specific objectives were required.

It would also appear that greater structural heterogeneity may not always be beneficial for biodiversity beyond a certain threshold or when other conditions are not fulfilled (Stirnemann *et al*., 2014; Froidevaux *et al*., 2016; Melin *et al*., 2018; Carasco *et al*., 2019). While the relative importance of structural features may vary within and between taxa, results for bats were generally as expected and provide further evidence that the structure of trees and shrubs is a more useful predictor of bat activity than vegetation species composition. For birds, this situation was less obvious and would suggest that both structural and compositional aspects should be considered when assessing habitat effects (Hewson *et al.*, 2011).

This study has shown that PAM is capable of simultaneously capturing data for multiple taxa, enabling the effects of habitat to be investigated for two key groups of bioindicators without the need for extra expertise, equipment or duplication of effort i.e. separate surveys for bats and birds. During this investigation, the feasibility of two other potential applications for PAM has also been corroborated. First, the recording of a barbastelle bat indicates the ability of PAM to confirm the presence of rare or cryptic species (Frommolt and Tauchert, 2014). Second, European turtle doves, common nightingales, common cuckoos (*Cuculus canorus*) and the barbastelle bat were all present in recordings made at Knepp, and in addition to establishing their presence, PAM can provide information on the phenology and activity of migrant species (Buxton *et al.,* 2016). In the heatmaps of acoustic indices, for example, nightingale activity was clearly apparent at site 7 (Appendix R) from the 28th April until the 16th of May, and the first cuckoo vocalisations were recorded on the 18th April in 2018. Such information could provide a useful supplement to projects like the BTO's Cuckoo Tracking Project (www.bto.org/our-science/projects/cuckoo-tracking-project). Although satellite tags can provide invaluable information about migration routes, it is only possible to tag a limited number of birds and compiling a long-term record can be challenging and expensive (Buxton *et al*., 2016). The use of PAM at specific locations and migration hotspots could thus provide a more robust and cost-effective means for determining changes in the phenology of migratory species. Furthermore, the ability to identify individuals by their vocalisations (e.g. Zsebők *et al*., 2017) adds the possibility of determining whether the same individuals are returning to the same sites.

While the use of domesticated herbivores controlled by culling rather than predation may be regarded as 'rewilding-lite' (Carver, 2014), in view of the relative expense and negative perceptions involved with translocations and reintroductions (Deinet *et al*., 2013; Nogués-Bravo *et al.*, 2016; Sandom *et al*., 2019), this may nevertheless represent one of the more pragmatic approaches to rewilding. By making use of multiple income streams such as tourism and organic meat production, Knepp provides an interesting model as it demonstrates that this form of rewilding can benefit biodiversity (DEFRA, 2018) and, under some circumstances, may even be more profitable than traditional farming (Tree, 2018). The idea that conservation can be profitable is an important consideration when budgets are limited (Nogués-Bravo *et al.*, 2016; Carver, 2019) and could hopefully encourage more landowners to employ similar practices.

CHAPTER 6

6. General Discussion

6.1 Key Findings

This thesis set out to explore the performance and practicality of using PAM to assess the effects of various habitat management practices. PAM offers similar advantages to camera traps (i.e. non-invasive, long-term monitoring in multiple locations), plus the additional benefits of increasing the area covered by each device and the ability to detect a wider range of different taxa. The importance of PAM as a conservation and biological monitoring tool thus has the potential to match, and even surpass, that of camera traps. However, as a relatively new survey technique, more detailed evaluations into the strengths, weaknesses and limitations of PAM are essential to facilitate its successful application. This thesis considered the full spectrum of PAM activities: the design and deployment of suitable equipment, data capture and storage, and the analysis of data using automated identification and acoustic indices. Three different forms of habitat management were investigated for two different taxa. The following discussion summarises key findings for each of these investigations in relation to the original objectives set by this study and additionally highlights important points relating to the use of PAM in general.

6.1.1 Design, Construction and Testing of an ARU

One of the aims of the thesis was to demonstrate the possibility of constructing an affordable alternative to existing commercial devices capable of monitoring both audible and ultrasonic frequencies. The resulting device, the AURITA, was used during all three field seasons and has proven itself capable of performing the task for which it was developed. Furthermore, the ability to capture both audible and ultrasonic frequencies enabled the assessment, and comparison, of performance for both birds and bats, whereas most other assessments have typically focused on only one of these groups. This chapter additionally highlighted differences in the performance of microphone weatherproofing materials and the possible presence of ultrasonic noise interference when using USB power banks for bat surveys.

Attenuation surveys designed to assess the AURITA's effective detection range for different bird calls demonstrated how detection probability is influenced by distance and angle relative to the recording device. The method developed to quantify the amount of attenuation also provided additional insights into the transmission efficiency of different bird calls and, unlike other methods that rely upon software for species identification and observers (e.g. Yip *et al*., 2017; Pérez-Granados *et al*., 2019), provides a less subjective estimate of detection range, which can be applied to any species. Attenuation tests performed using pure sine waves additionally confirmed the optimum frequency for sound transmission in woodlands to be ~2 kHz (Bucur, 2007).

6.1.2 Effects on Invasive Rhododendron on Bats

In Chapter 3 I applied PAM to study the effects of colonisation of woodland understorey by *R. ponticum* on different bat species in Richmond Park. PAM has rarely been used to assess the effects of invasive species, particularly plants. In general, studies on the effects that non-native invasive vegetation in woodland habitats has on bat communities are relatively scarce and this study represents the first to specifically assess the effects of rhododendron. Additionally, sites cleared of rhododendron were included in analyses to determine how this practice influenced bat activity. Performing surveys in Richmond Park also demonstrated that, with proper precautions, PAM can be utilised in public spaces when necessary.

As hypothesised, the activity of larger, open-space foraging species *N. noctula*, *E. serotinus* and *N. leisleri* (NSL) was greatly reduced in areas where rhododendron was present while other bat species were not negatively affected. However, analyses may not necessarily have included data for all three NSL species and effects could also have been unevenly distributed if several of these species were present. While the clearance of rhododendron had a positive effect on these bats, it did not negatively impact other bat species. Interestingly, the presence of deer had a more pronounced, and highly significant, negative impact on NSL than increased understorey density due to rhododendron, which could be due to the reduction of prey items such as moths. While the negative effects of ungulates on bats and their prey have been documented before (Littlewood, 2008; Fuentes-Montemayor *et al*., 2012; Barbaro *et al.*, 2019), it has also been suggested that mammalian herbivores can potentially benefit some bats, especially open space foragers, by altering habitat structure (Rainho *et al*., 2010; Fuentes-Montemayor *et al*., 2013). The current study therefore provides some initial evidence that, contrary to expectations, the presence of large grazing mammals, specifically deer, may actually have a greater negative impact on the activity of open space foraging bat species.

The Temporal Pass Plots (TPP) developed in this thesis revealed distinct daily and seasonal patterns in the activity of different bat species, which were generally consistent between sites, particularly for *P. pygmaeus* (see Appendix J). Analysis of temporal activity can reveal important information about bat behaviour, phenology and habitat use, and yet this resource remains largely untapped (Newson *et al*., 2015; Kerbiriou *et al*., 2018). TPPs offer a simple and intuitive means of assessing bat activity over time, which can potentially be applied to any form of time-stamped data, and thus opens up new avenues of investigation for which PAM can be used. The first use of TPPs in this study has, for example, potentially been able to reconcile differences in activity patterns observed by two studies (Swift, 1980; Maier, 1992) that were previously thought to have been performed on the same species (*P. pipistrellus*), but which may actually have been on two different species (*P. pipistrellus* and *P. pygmaeus*).

Evaluation of two bat identification software applications (BatClassify and Kaleidoscope Pro) revealed how the use of blanket confidence thresholds without proper evaluation could lead to underestimation of counts and/or introduction of bias for certain species. While BatClassify was capable of outperforming commercial software with proper calibration for *Myotis* and pipistrelle species, it greatly underestimated the number of NSL species present within recordings. Although Kaleidoscope Pro improved this situation for NSL, it was less accurate for other species. Rydell *et al*. (2017) have previously performed comparisons of bat identification software packages, including BatClassify and Kaleidoscope but they did not evaluate performance for NSL species or discuss the calibration of confidence thresholds. Findings in the current study thus offer intriguing new insights into this issue and help to advance research on this topic.

6.1.3 Effects of Tree Species Diversity and Composition on Birds

The study in Hainich represents the first use of PAM and acoustic indices to specifically assess the effects of tree species diversity on bird diversity. The use of FunDivEurope plots additionally enabled assessment of effects of higher levels of tree species richness (up to 4-species mixtures of 5 different tree species) than in previous studies (e.g. Peck, 1989; Donald *et al*., 1998; Diaz, 2006; Felton *et al*., 2010; O'Connell *et al*., 2012). Two months of data were collected at 26 sites during which time the researcher was not even in the same country, further illustrating PAM's potential for long-term, large-scale autonomous collection of data.

In addition to supporting the hypothesis that greater tree species diversity has a strong positive effect on bird species richness and abundance, the study revealed significant negative relationships between bird diversity and the presence of sycamore and beech. While previous studies have reported that beech is typically avoided by most bird species, they also showed that sycamore positively influenced bird species richness (Peck 1989; Adamík and Korňan, 2004; Korňan and Adamík 2017). The negative effects of sycamore observed in Hainich could be explained by switches in foraging preferences based on tree phenology (Böhm and Kalko, 2009).

Evaluations of acoustic index performance illustrated that some of the indices commonly used for assessments of bird diversity are more susceptible to non-biophony soundscape elements than others, and that not all indices are necessarily suitable proxies for bird species richness. This was particularly true for NDSI, which demonstrated a non-linear relationship with bird species richness. The strong logarithmic relationship between acoustic indices and the distance from the recorder was also demonstrated for the first time as part of this chapter (Appendix N). Determining the distance at which vocalisations occur has potentially useful applications when making assessments for fixed radius surveys, and predictable relationships between sound-based metrics and distance could help advance this area of study.

6.1.4 Effects of Habitats Created by Rewilding on Bats and Birds

Investigations at the Knepp Estate provide the first example of PAM being used to assess bird and bat acoustic activity and diversity in different scrub habitats created by rewilding. Additionally, this study is one of the first, if not the first, to demonstrate PAM's capability to simultaneously assess the effects of common habitat characteristics across multiple taxa.

As predicted, habitat preferences for bats were largely determined by the morphology and foraging strategies of different species with activity of *Myotis* species being more positively associated with dense leafy scrub than open thorny scrub, while the opposite was true for pipistrelle species. Vegetation structural characteristics also had a stronger influence on bat activity than plant species diversity, as hypothesised. Analysis of structural characteristics illustrated subtle differences in habitat use by *P. pipistrellus* and *P. pygmaeus*; although both species are considered to be edge space foragers, *P. pygmaeus* was more tolerant of cluttered environments than *P. pipistrellus*. Performing PAM surveys over a period of several months also demonstrated its ability to monitor changes in the habitat preferences of different bat species over time (Figure 5.2).

Although it has previously been suggested that birds may be more influenced by plant species diversity than habitat structure (Barbaro *et al*., 2019), the current study found that both aspects exerted a similar degree of influence on bird diversity. Higher structural heterogeneity is generally considered to be beneficial for bird species diversity (e.g. Peck, 1989; Tews *et al.*, 2004; O'Connell *et al*., 2012);

however, while the effect of increased variation in vegetation height (CV height) on bird diversity was positive, relationships with increased vertical structural diversity were generally negative, contrary to expectations. This result adds further evidence to the suggestion that positive effects due to structural diversity may be conditional on the presence of a shrub layer (Melin *et al*., 2018) and/or the existence of a threshold beyond which the density of habitat structure begins to limit accessibility (Bradbury *et al*., 2005; Froidevaux *et al*., 2016).

Acoustic indices representing bird species richness (ACI) and abundance (BI) exhibited different responses to true Shannon diversity and structural metrics, suggesting that these characteristics had more influence on bird species richness than abundance at Knepp. In Hainich National Park, true Shannon diversity had a significant positive effect on both ACI and BI values; however, plant diversity estimates in Hainich were based purely on tree species whereas scrub at Knepp predominantly consisted of shrubs. Although tree species diversity has been found to positively influence bird species richness and abundance (e.g. Donald *et al*., 1998; Poulsen, 2002), shrub species diversity has previously been found to positively influence bird diversity but not abundance (Diaz, 2006). The fact that previous studies, using traditional bird survey methods, and the current study, based entirely on acoustic indices, produced similar results offers further support for the use of ACI and BI as measures for bird species richness and abundance, respectively. Moreover, comparison of the results for all three study locations (Richmond, Hainich and Knepp) potentially revealed some evidence for the additional hypothesis that higher habitat heterogeneity within a given area increases the number of available niches, supporting higher species richness, but also reduces their size, resulting in lower species abundance (Allouche *et al*., 2012). Although this hypothesis was not included in the original research questions, it would appear to explain, and thus connect, some of the fundamental differences between the sites used in this study.

6.2 Critical Evaluation

Since this project began, there has been rapid development in the field of ARUs and a variety of alternatives have been developed by researchers and academic institutions. Arguably the most notable example of these devices is the AudioMoth (Hill *et al*, 2018), which can be purchased for ~$50 per unit, is small and compact, runs off regular batteries, has a simple user interface and is capable of recording audible and ultrasonic frequencies. Despite being developed less than four years ago, the AURITA now appears relatively dated, expensive and complex to operate (as it is based on two devices that use different data management protocols) in comparison to AudioMoth. Nevertheless, it could still be suitable, or customised, for specific applications and has the benefit of separating data streams for audible and ultrasonic sounds, which facilitates easier processing.

The investigation into the effects of rhododendron in Chapter 3 (Richmond Park) was potentially confounded by the fact that, due to the limited choice of locations, all rhododendron sites were accessible by deer, and none of the locations where rhododendron had been removed were accessible by deer. As a result, the lower activity of NSL in sites with rhododendron could be attributable to the presence of deer, rhododendron effect or a combination of both. Findings for other bat species, which did not demonstrate any significant associations with deer accessibility, were less likely to have been biased by this imbalance. As site characteristics models, which revealed that deer had a stronger effect than understorey density, did not use any grouping factor and treated all sites individually the results from these analyses would be unaffected.

For Richmond, and Knepp, the need to perform surveys in areas with particular habitat characteristics (i.e. rhododendron status or dominant scrub type) limited the choice of suitable locations that were available and meant that some sites were closer together than might otherwise be desirable. However, as the focus of these studies was on the relative differences in bat and bird activity and habitat use at the local, rather than landscape, scale, the fact that the same animals might be recorded at several nearby sites does not affect the interpretation of results. Furthermore, all models included site as a random effect and model residuals were additionally tested for spatial autocorrelation.

The different habitats examined in this study were largely compared in terms of vegetation structure and diversity. Performing invertebrate surveys could have provided additional insights into the potential mechanisms of effects by enabling estimates of prey abundance and diversity to be made. In Richmond, for example, invertebrate surveys could have helped determine whether the absence of the suggested positive effect for rhododendron on *Myotis* species, which would normally be expected to forage in areas with higher understorey density, was due to a reduced prey load in rhododendron in comparison to other habitats. In Hainich, however, with limited field time, over thirty sites to evaluate and the necessity of carrying any equipment over long distances, the performance of more complicated surveys simply was not feasible. The use of a 30 m radius for vegetation surveys at Richmond and Knepp, and 30 m x 30 m plots in Hainich, would seem appropriate as these area sizes have been used by previous studies examining the activity of bats and birds by other studies (e.g. Sweeney *et al.*, 2010; O'Halloran *et al*., 2011; Froidevaux *et al*., 2016; Renner *et al.*, 2018; Dekeukeleire *et al*., 2019).

All ultrasonic recordings for bat surveys in Knepp were manually checked and identified to species or species group, making these results extremely reliable. In Richmond Park, due to the high volume of recordings, one day was chosen at random for each of the 12 sites (2,415 files in total) and manually validated in order to assess the accuracy of BatClassify software used for identification. After classification thresholds used for BatClassify had been iteratively adjusted based on manually identified files to improve their performance and additional validation of NSL species using Kaleidoscope, precision and accuracy statistics exceeded 98% and 97%, respectively, for all species except *P. auritus*. For *P. pygmaeus*, *P. pipistrellus* and *Myotis* spp., recall also exceeded 94% and any results for these species should therefore also generally be robust. For NSL, it was only possible to obtain a recall rate of 55.7%, even after applying both identification packages, and it is therefore likely that these species were under-represented in the results. As the same equipment, settings and identification software were used for the identification of NSL species in Richmond, and BatClassify and Kaleidoscope Pro reference libraries contain calls associated with a range of habitats (Scott, 2012; Wildlife Acoustics, 2019c), it was assumed that underestimations should have been relatively similar across sites. However, the characteristics of echolocation calls used by bats may vary depending on whether they are navigating open or cluttered habitats (Newson and Berthinussen, 2019), which could have potentially had some influence on relative detectability across sites.

Some evidence (Menzel *et al*., 2005; Collins and Jones, 2009; Müller *et al*., 2013) has been presented that performing surveys at different heights may be necessary to completely capture the activity of all bat species present; most notably NSL, which have been found to forage above the canopy. However, Collins and Jones (2009) detected over twelve times the number of total bat passes, and also generally recorded higher numbers of NSL species, at ground level compared to above the canopy. As mentioned above, the intent of this study was to study the effects of local-scale vegetation within a few metres of ground level and the presence of rhododendron or thorny scrub in the understorey would have been unlikely to influence bat activity several metres above in the canopy layer. As all detectors were mounted off the ground at heights of ~2 m, above the level of the majority of understorey, this should have been sufficient to maximise detections at this level (Weller and Zabel, 2002). As a general observation, while placing recorders at several heights may be ideal, compromises may be necessary (Froidevaux *et al*., 2014) as this will not be possible for many short term surveys when installing anything above ladder height requires specialist equipment, not only for deployment but whenever batteries and data cards need changing, and would also require twice the number of recorders to be available.

All evaluations of the effects of habitat and habitat characteristics on birds performed in this study were based on acoustic index values and the robustness of results will thus depend on how accurately these indices represented bird species richness and abundance. As numerous acoustic indices have been created and documented in the literature (up to 69 according to a recent count; Buxton *et al*., 2018a), an initial assessment was therefore performed in order to create a shortlist of indices (ACI, BI, NDSI, AEI and H_t), which have been shown to provide estimates of either bird species richness or abundance in the literature. Recent studies utilising acoustic indices to investigate habitat effects on birds (e.g. Turner *et al*., 2018; Myers *et al*., 2019) have tended to rely upon previously published evaluations of their performance as proof of their validity. In the current study, a two-stage selection process was additionally employed to ensure that any indices used in assessments provided the best performance possible. The first stage (Appendix L), determined whether any of the five indices shortlisted were overly influenced by undesirable soundscape elements. This resulted in the removal of AEI, which was highly susceptible to wind in recordings, and H_t, which was strongly biased towards silence or aeroplane noise for high or low values, respectively. Furthermore, any days with rain or extreme winds were also removed based on weather data and heatmaps of final index values were also checked for anomalies. Several precautionary measures were therefore taken to reduce any likelihood that indices were influenced by anything other than biophony. As surveys were conducted in temperate regions, with few sound-producing diurnal invertebrates, and indices were specifically configured for 1.5 to 9 kHz based on dawn chorus activity, any biophony in the audible frequency range would have consisted almost entirely of bird vocalisations.

A second set of analyses (Section 4.3.1) specifically evaluated the performance of indices as a measure of bird species richness. This revealed a non-linear relationship which demonstrated that, beyond a certain point, NDSI values did not accurately reflect the number of bird species within recordings. ACI displayed the strongest relationship with bird species richness and, as associations between ACI values and bird species richness have frequently been demonstrated by other studies (e.g. Towsey *et al*., 2014a; Buxton *et al.,* 2016; wa Maina *et al*., 2016;

Fairbrass *et al*., 2017; Hilje *et al*., 2017), can therefore be considered as being reasonably reliable. While it was not possible to specifically test BI as a measure of abundance, it generally ranked choruses highly and has previously been found to provide a useful metric for avian activity (Boelman *et al*., 2007; Fuller *et al*., 2015; Eldridge *et al*., 2018; Rajan, 2018). Both indices also displayed expected diel activity patterns with higher values at dawn and lesser peaks at dusk (Appendices K; R).

While the use of acoustic indices enables large amounts of acoustic data to be processed and analysed, any results will inherently be based on the bird community as a whole, or at least the vocalizing species, and it was therefore not possible to investigate how particular functional groups, foraging guilds or individual species might have been affected by the characteristics under investigation. This is a fundamental limitation of any study that uses acoustic indices and constitutes a necessary trade-off to enable the analysis of activity over prolonged time periods at multiple locations.

6.3 General Applicability

The ARU is an essential component of any ecoacoustics study, regardless of species, location or habitat. The AURITA developed for this project is suitable for use for terrestrial investigations in all but the most extreme environments and, apart from subsonic (<20Hz) and high ultrasonic (>192 kHz), capable of monitoring the majority of frequencies. During the course of this project, the AURITA has successfully captured the sounds of target species (birds, bats) as well as non-target groups such as non-flying mammals, Orthoptera and anurans. Incidental recording of non-target species may complicate analyses and require removal (e.g. Newson *et al*., 2015), but can also provide the opportunity to combine surveys for different taxa (e.g. Lacoeuilhe *et al*., 2016; Newson *et al*., 2017).

In terms of the habitats studied, findings from this thesis will primarily apply to forests, parks and scrubland in northern and central Europe, although these will broadly resemble other temperate regions e.g. in North America, Japan and New Zealand, and parts of South America and Australia. As studies for both birds and bats focused on local-scale habitat effects, they may not relate so well to effects at the landscape-scale. Habitat management practices for which these findings are most relevant will include those relating to forests, parks, forest plantations, naturalistic grazing, rewilding and organic farming. Results for specific trees species will obviously only apply to other locations where those species exist. However, the two fundamental aspects of habitat explored in this thesis were vegetation structure and plant species diversity, which have been widely studied for both birds and bats in a range of locations and biomes (see below).

Results for birds in this thesis will fundamentally relate to passerines as the main source of vocalisations in the habitats studied, but this will also be the case for the majority of PAM studies on birds (Depraetere *et al*., 2012; Klingbeil and Willig, 2015). The overall positive effect of plant species diversity on bird diversity is generally well-recognised and is thought to apply regardless of habitat type (e.g. Tews *et al.*, 2009; Castagneyrol and Jactel, 2012). While the effects of habitat structure may vary in their relative importance to birds (Müller *et al*., 2010; Hewson *et al*., 2011; Barbaro *et al*., 2019), structural heterogeneity has frequently been found to influence bird diversity in a variety of temperate (e.g. MacArthur and MacArthur, 1961; Stirnemann *et al*., 2014; Zellweger *et al*., 2017; Carrasco *et al*., 2019) and tropical (e.g. Thinh, 2006; Flaspohler *et al*., 2010; Castaño-Villa *et al*., 2014) environments. Acoustic indices have also been used to assess avian activity in many countries on most continents, although their performance as proxies for bird species richness may be less well suited to tropical habitats (Eldridge *et al*., 2018). Nevertheless, while the relationships found between acoustic indices and bird species diversity are more likely to apply to temperate habitats, the processing methods and other findings (i.e. relationship with distance, susceptibility to non-biophony soundscape elements, NDSI performance) will be fairly universal.

With the exception of non-echolocating bats (e.g. fruit bats) and microchiropterans with specialised, non-insectivorous diets (e.g. sanguinivores and piscivores), findings for UK bats should also be generally applicable to the majority of bat species. Wing morphology and echolocation call attributes are physical adaptations that serve essentially similar functions (flight, navigation, and prey detection and capture) and will be constrained by the same limitations (e.g. manoeuvrability and background clutter separation) regardless of species or country (Norberg and Rayner, 1987). Indeed, the predictable relationships between these attributes, habitat use, and foraging strategy has enabled this highly diverse group of around 1,000 species to be categorized into 7 distinct functional guilds (Denzinger and Schnitzler, 2013). Comparisons between the bat species examined in this study and members of the same foraging guilds on a global scale will therefore be most relevant.

Although the possibility of using PAM to monitor the effects of different habitat management practices was demonstrated in temperate regions, the fundamental methodologies used are widely applicable as they relate to technology and data analysis, namely; recording devices, acoustic indices, automated identification software, Temporal Pass Plots and attenuation analyses.

6.4 Practical Implications

This study has demonstrated that PAM can be applied to simultaneously monitor and study the activity of multiple species and taxa, and, although only birds and bats were considered in this study, the presence of crickets, frogs, foxes, deer and wild boar were additionally heard in recordings. PAM can thus provide detailed information about a wide range of taxa, enabling assessments at the community, rather than species, level, making it particularly well suited to ecological studies. In the last few years, a reasonably extensive range of affordable devices capable of recording high quality audio at practically any frequency desirable has become available (e.g. AudioMoth, Cornell's Swift, Peersonic's RPA2), making PAM more accessible for both small- and large-scale studies. Apart from data loggers used to collect environmental variables (e.g. temperature, water flow, etc.), PAM's ability to collect continuous, real-time data over long time periods is unprecedented. Currently, the main limitation is the ability to extract meaningful information from the vast amount of data PAM studies typically collect. Naturally, the scale of this challenge will vary depending on the study objective and the type and number of species under assessment. As the next logical step following data capture, increasing attention is being focused on workflow automation, particularly species identification, and establishing PAM networks and best practices now, would facilitate easier transition to this technology when it becomes available.

Arguably, of all the species PAM is capable of monitoring, microchiropteran bats are one of the most suitable study organisms for this application as they typically produce sound in order to navigate and detect prey as well as for social purposes. While PAM enables investigations of bat activity to be performed without the need for permits or the risk of disturbing any bats, it has its limitations. The detection of quieter bat species (e.g. *P. auritus* and *B. barbastellus*) remains challenging and, beyond establishing their presence, it is difficult to produce detailed assessments of behaviour and habitat use by these species. Automated identification software currently works well for some bat species, but validation and calibration are essential to achieve the best results. Even though both software packages demonstrated high degrees of precision and accuracy, recall rates were generally lower, especially for Kaleidoscope Pro, which suggests that identification software may tend to underestimate activity. Furthermore, it would seem more likely that most studies would use a single identification package and that the current study represents an unusual case as it applied two separate software packages. Although this only attained 56% recall for NSL, it was a significant improvement on the 19% on just using BatClassify. Equally, if only Kaleidoscope Pro had been used, recall rates for *Myotis* spp. would have been 50% rather than 94%. The use, and cross-validation, of multiple identification software packages could help to compensate for inherent weaknesses of individual packages and should therefore be implemented whenever possible.

Despite the limitations discussed above, the (semi-)automated identification of bats is far in advance of that for birds. As bats are represented by fewer, more distinctly recognisable species vocalizing in a frequency range largely unoccupied by other taxa, this is not necessarily surprising. Nevertheless, this does enable more detailed and precise investigations into connections between different bat species and their habitat characteristics to be performed with PAM data. Indeed, the analysis of bat surveys performed within this study further supports the notion that bat activity and habitat preferences are largely determined by wing morphology and echolocation call structure (Norberg and Rayner, 1987; Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). The ability to predict which species or species groups are likely to associate with, or benefit from, certain types of habitat, enables targeted management to be performed where objectives relate to specific species. Equally, the varied habitats utilised by different bat species highlights the importance of providing a range of suitable habitats if improving their overall diversity is the aim.

The significant negative effect detected for the presence of deer on NSL activity potentially has important implications. Not only are wild deer populations expanding across the UK, but grazing is often employed as a management tool, or for maintaining greater habitat diversity, such as at Knepp. While there is some evidence of negative effects of deer on birds (Dolman *et al*., 2010; Newson *et al*., 2012), little seems to be currently known about the possible effects of deer, or ungulates in general, on different bat species. Although further assessment is required, the use of grazing to manage habitat specifically for bats should be carefully monitored. This is especially true for open space foragers, which are the type of species this practice would most likely seek to benefit by reducing ground vegetation cover (e.g. Rainho *et al*., 2010), yet they also appear to be the group most likely to be negatively affected.

The Hainich study (Chapter 4) offers further evidence that planting a wider variety of tree species can positively influence bird species diversity. However, tree phenology also needs to be considered when deciding which mixtures to plant. Different tree species may be particularly beneficial at a certain time of year and mixing species that come into leaf, produce seeds/fruit or have high prey loads at a particular time of year could provide prolonged benefits throughout the season. Such a mix might, for example, include some early budburst species (e.g. beech, birch and sycamore) in combination with later species (e.g. oak and ash) and evergreen conifers (e.g. spruce and pine). The phenology of thorny scrub (Chapter 5) may also be important by providing a source of food in autumn and early winter when berries ripen. Using PAM to monitor the activity of birds throughout the year could help determine changes in habitat preferences for both trees and shrubs based on the seasonal availability of resources. Where possible native, or near-native, trees and shrubs should be selected with special consideration for those providing benefits that coincide with peaks in breeding seasons, when resources are in highest demand by birds.

The provision of a diverse range of scrub was also found to positively influence birds in Chapter 5 (Knepp). Indeed, dense scrubland is capable of hosting similar levels of bird diversity to forests, while also providing habitat for a greater number of threatened species (Reif *et al*., 2013). Although the importance of scrub habitats has previously been underappreciated or negatively viewed, this situation may be changing (Day *et al*., 2003). Shrubs can provide beneficial cover, nesting and foraging habitat for birds and the importance of a shrub layer for birds has previously been demonstrated (Diaz, 2006; Sweeney *et al.*, 2010; Broome *et al*., 2016; Melin *et al*., 2018). Allowing time lags between different areas being abandoned and the delay in introduction of free-roaming herbivores at Knepp may have been serendipitous as it enabled the establishment of a mosaic of scrub habitats that might not otherwise have been present. Indeed, the introduction of ungulate herbivores such as deer immediately after land clearance can have long-lasting detrimental effects on the diversity of plants, invertebrates and birds (Nuttle *et al*., 2011). Care should also be taken to avoid overgrazing, although it may be also possible to mitigate the removal of understorey where mammalian herbivores are present by planting unpalatable or thorny shrubs such as blackthorn or hawthorn. Ironically, rhododendron also appears to be well suited to this role, particularly in areas under denser canopy cover with its tolerance for low light levels, and, as evidenced in Richmond Park, its resilience to herbivory by deer.

Without acoustic indices, it would not have been possible to process the large volume of audible data collected by this study. As interest in PAM grows, it is likely that more studies will turn to acoustic indices to quantify the activity of various species and communities of species. However, acoustic indices are not without their flaws and should not be interpreted without some assessment of what they are measuring and how this relates to the target subject(s) being measured. The relationship between NDSI values and bird species richness shown by this study, for example, demonstrates that the indiscriminate use of indices without some basic understanding of their underlying mechanisms can produce misleading results. Reliance on previous findings does not necessarily guarantee performance and three out of the five indices evaluated for this study proved to be unsuitable, despite them having at least some degree of support in the published literature (e.g. Joo *et al*., 2011; Fuller *et al*., 2015; Fairbrass *et al*., 2017; Machado *et al*., 2017). Indeed, results of initial tests (Appendix L) in this study also suggested NDSI could be a good proxy for bird species richness. This is not to say NDSI does not work well for the purpose for which it was designed (i.e. to represent the relative degree of anthropogenic noise intrusion; Kasten *et al*., 2012); however, the fact that it is expressed as a ratio should act as some warning that it is unsuitable as a proxy for a continuous variables such as the number of birds or bird species. Another potential issue for acoustic indices is their configuration. Rather than accepting default values, some assessment of the frequencies used by any species of interest, and then adjusting indices to assess these frequencies, while excluding others, should be considered as normal practice.

The additional hypothesis that higher habitat heterogeneity benefits species richness but not abundance (Allouche *et al*., 2012), for which some evidence was found, could also potentially have important practical implications for habitat management where compromises between species richness and abundance may be necessary. ACI values, taken as an average over all sites for the 30 dates included in analyses, were higher at Knepp during all three time periods (dawn, daytime and dusk) than in Hainich. Equally, average BI values were lower at Knepp during all three periods than for Hainich. Although acoustic indices are designed to be directly comparable, there is some degree of uncertainty involved when directly comparing these results, as they were performed using different ARUs. However, both sets of indices were calculated using the same software, frequency bands, settings and, for the purpose of this assessment, based on equal lengths of time - 1 minute. Furthermore, if the recordings produced by different ARUs were fundamentally different, the most likely outcome would be that both indices should either be higher or lower in one location than the other. Hainich is over five times the size of Knepp and the sites studied invariably consisted of forest habitat. At Knepp, a wider range of habitats was assessed within a much smaller area and one of these habitat types consisted of a mixture of two different kinds. It would therefore seem logical that Hainich would be less influenced by the area-heterogeneity trade-off than Knepp, and the larger, more contiguous forest habitat could support larger population sizes and hence produce higher BI values with more pronounced effects.

Differences between bat activity at Knepp and Richmond demonstrated a similar relationship (i.e. higher species richness but lower abundance) to the one found for birds between Knepp and Hainich. Scarcer species such as *M. bechsteinii* and *B. barbastellus* have been recorded at Knepp (Knepp, 2019) but not in Richmond Park (Richmond Biodiversity Partnership, 2010); however, the overall number of passes recorded at Knepp was surprisingly low compared to Richmond. To put this into perspective, the average number of combined passes for all species per night and site was four at Knepp and 217 in Richmond. While surveys were performed at different times of year, and thus may well be influenced by differences in activity due to bat breeding cycles, this difference is substantial enough to suggest it might not merely be the result of phenology. Although Allouche *et al*. (2012) only tested their hypothesis with data for birds, these results could suggest that the area-heterogeneity trade-off may also apply to bats. However, as a whole, Richmond Park is less homogeneous than Hainich, being a more even mixture of wooded areas and open spaces. This makes this explanation less likely, especially as it has only been demonstrated for birds and not bats. Other explanations could relate to differences in the areas surrounding Richmond (residential) and Knepp (agricultural). Bats have previously been found to strongly avoid arable land, being more likely to utilise parkland and urban areas (Walsh and Harris, 1996; Entwistle *et al*., 2001). Compared to Knepp, survey sites in Richmond consisted of larger contiguous woodland patches with more trees, which are also preferred foraging habitat for bats (Walsh and Harris, 1996; Entwistle *et al*., 2001; Bellamy *et al*., 2013). Whatever the reason may be, this result suggests that urban parks and woodlands can potentially contain higher levels of bat activity, if not diversity, than rewilded habitats, at least for common species.

6.5 Future Work

The findings in this thesis have highlighted several areas where further investigation of habitat management practices is recommended. The effects that deer and other mammalian herbivores may have on different bats species is particularly relevant with the increasing use of naturalistic grazing as a habitat management tool and increases in the density of wild deer populations. Evaluating the relative effects of, and which bat species are most affected by, different types or species of mammalian grazers could provide a more detailed picture of potential winner and loser species, enabling more targeted management decisions to be made. This could potentially be achieved by performing PAM surveys in areas with different species and/or densities of mammalian herbivores, and comparable areas from which they are totally excluded. Indeed, some studies (e.g. Smit *et al*., 2014; van Klink *et al*., 2016) have already employed similar approaches using artificial grazing refuges; however, as they were examining grazing effects on invertebrates and vegetation, these were relatively small (>500 m^2) and larger refuges/areas would probably be needed to address similar questions for bats.

The results of this thesis potentially offer further support for the 'area-heterogeneity trade-off' hypothesis (Allouche *et al*., 2012), which could have implications for managing habitats. While creating a wider diversity of habitats is generally encouraged, and may well improve species diversity, whether this practice potentially has negative consequences for species abundance is an important consideration that needs to be better understood. Indeed, most of the findings in this thesis indicate some form of trade-off will usually be necessary as there are few, if any, 'one-size-fits-all' solutions in ecology. Questions relating to thresholds in vegetation structure, the size and number of different habitats to provide, what proportion of broadleaves and conifers, early and late budburst tree species to plant and so forth will all depend on the specific intentions of each project. As stated in the opening line of this thesis, with the growing number of questions on how best to manage our limited resources for the most beneficial outcomes, the need for effective and efficient monitoring technologies is indeed urgent. PAM certainly offers a promising additional tool with which to address these questions; however, there is still some way to go. The following discussion suggests some ways in which further progress can be made.

Current developments in ARU technology suggest that designs are becoming increasingly modular with the intention of expanding the range of complimentary data that can be collected by autonomous units (e.g. Hill *et al*., 2018; Sethi *et al*., 2018; Beason *et al*., 2019). In addition to recording audible and ultrasonic frequencies, the Lunilettronik Soundscape Explorer used in Hainich, for example, already records temperature, relative humidity and light levels alongside acoustic data (IInstEco, 2018). Recently, it has been proposed that simultaneous PAM and camera trap surveys could combine the relative strengths of these two passive techniques (Buxton *et al*., 2018). Although this approach has not yet been widely adopted, the feasibility of collecting coordinated audible and ultrasonic audio in tandem with thermal images using a single, modular system has already been demonstrated by the ATOM (Acoustic and Thermographic Offshore Monitoring; Willmott *et al*., 2015). Combining ARUs with modern camera technology such as that employed by webcams and CCTV could, for example, help to reconcile the patterns in TPPs with the type of bat activity (e.g. foraging, commuting or swarming) they represent and potentially provide insights in relationships between abundance and call frequency. Although the ATOM was a relatively large and complex static installation, digital audio recording and video recording technology have both advanced significantly in terms of affordability, miniaturisation and data capacity making such devices feasible within the near future. Other areas where potential developments would be beneficial, such as power supply and data storage, are not specifically related to audio recording and advancements are likely to be driven by general demand for these technologies, which are fundamental to the majority of consumer electronics.

It is interesting to note that, while most bat recorders (e.g. RPA2, Batlogger A+, SM4BAT) use, or feature the option to use, triggered recordings, this technique is rarely extended to audible recordings. This is possibly due to the development of ecoacoustics being preceded by, and arguably having evolved from, soundscape ecology, which aims to capture the character of acoustic landscapes as a whole (Sueur and Farina, 2015). Use of continuous recordings is understandable when soundscape analysis is the main aim (Bradfer-Lawrence *et al*., 2019); however, PAM is increasingly being used to monitor the presence and activity of specific biological organisms where geophony, anthrophony and the biophony of non-target species are not necessarily of interest. Indeed, camera trap studies do not continuously record images (unless triggered) as a matter of course, why should PAM be any different? From personal experience, continuous audible recordings contain a lot of silence, or at least an absence of biophony, particularly at night. Bat recordings can be triggered almost instantaneously, when the recorder detects any sounds within a particular frequency band that exceed a specified threshold in dB and will continue recording for a pre-set time period or until the sound level falls back below the triggering threshold. It should also be possible to adapt this technique for audible frequencies; Hill *et al*. (2018), for example, used triggered recordings when attempting the establish the presence of the New Forest cicada (*Cicadetta montana*) by configuring their devices to only record in the presence of sound at ~14 kHz, the frequency used by the cicada. However, further examples of this approach being used elsewhere in the literature, other than for bats, remain rare to non-existent. Only recording sounds of interest could extend the field life of ARUs by reducing data storage and power requirements, as many devices tend to consume more power when storing data (Hill *et al*., 2018). When monitoring a particular species (e.g. for establishing presence, assessing conservation strategies, recording migration phenology) is the objective, the use of triggered recordings could greatly reduce processing overhead and analysis times by focusing efforts on data that are more likely to be of interest. However, triggered recordings are likely to be of different lengths, made at irregular intervals, which are not particularly well suited for use with acoustic indices. In cases where manual identification is impractical, the utility of triggered recordings may therefore hinge on further improvements in the automated recognition of non-bat species.

The further development of flexible and reliable automated identification software is essential for fully unlocking PAM's potential for large-scale, long-term studies. Options for bats have progressed somewhat but, as this study highlights, still have some weaknesses that need to be resolved. One possible means of improving accuracy rates could be to program algorithms that actively exclude sources/species known to generate false positives. For example, in this study, it was noticed that the higher harmonics of birdsong around 20 kHz were often classified as NSL bats by BatClassify. Consideration of whether lower frequencies are also present could potentially help to address this issue. Harmonics are produced at fixed intervals based on the fundamental frequency, so a bird singing at 6 kHz would typically generate harmonics around 12 kHz, 18 kHz, 24 kHz etc. whereas a bat using 24 kHz for vocalisations would not produce sound at these lower frequencies. Flagging recordings that contain sound below the known frequency range of the species of interest, particularly at harmonic intervals, could thus improve the robustness of classification accuracy. This could, however, have the potential drawback of generating more false negatives under certain circumstances, such as at dawn and dusk, when bats and birds are both potentially active simultaneously. Nevertheless, further investigation into the use of proactive exclusion by also incorporating frequencies known to cause issues into detection and recognition algorithms could be beneficial. To reduce the probability that recordings were triggered by wind, Hill *et al*. (2018) included sound at 8 kHz, which would not normally be present in a 14 kHz cicada call, in their detection algorithm but there are few, if any, other examples of this approach being employed elsewhere.

It is often suggested (e.g. Stowell and Plumbley, 2010; Kasten *et al*., 2012; Vidaña-Vila *et al*., 2017) that large repositories of reference sounds for various species or species groups, such as www.xeno-canto.org, provide a useful resource for the development and testing of species recognition software. There is no reason why this idea could not be taken a step further by creating a repository for any classifiers and matching templates that have been developed for particular species or software applications for which people are able to create their own classifiers e.g. MonitoR (Katz *et al*., 2016), Tadarida (Bas *et al*., 2017) and Kaleidoscope (www.wildlifeacoustics.com). In the same way that data sets can now be posted and referenced, so could classifiers. Sharing classifiers/template patterns through a repository could incentivise their wider use by the ecoacoustics community, increase cross-pollination of ideas, facilitate more detailed (and arguably less biased) evaluation of classifier performance, highlight which approaches work well for particular species and enable the adaptation and improvement of existing classifiers. Over time, the number of species for which pre-existing classifiers were available could expand to the point where enough classifiers were available to enable assessments of entire communities or locations, or at least reduce the workload of anyone attempting to do so. At present, automated classifiers are typically developed on a per-study basis, either to study the performance of classifiers or for detecting a particular species in recordings. Creating reliable classifiers is a complex and time-consuming task, providing a single repository where any previous work was immediately available could potentially save much duplication of effort.

The Temporal Pass Plots developed for this study illustrate how, in cases where species identification is possible, more detailed assessments of activity and behaviour could also be performed. At present, most bat studies, including this one, base assessments on the total or average number of passes that are recorded within a set time period. TPPs revealed the presence of obvious differences in nightly activity patterns between sites, which would otherwise be considered equivalent based on total or average activity counts (Figure 3.7). Unfortunately, previous research on how such activity patterns should be interpreted is currently both scarce and quite dated. Evaluation by experts in bat behaviour and activity patterns and/or accompanying audio surveys with video capture could help to address this situation. Digital ARUs inherently capture temporal information as file time-stamp metadata, only the will and awareness of how to properly make use of this additional source of information is required. For bats, standardising pass definitions as activity within a set time period (e.g. 5 seconds) would facilitate comparison between sites within a study as well as between studies while also providing a more intuitive measure of activity.

In addition to the general ideas above, over 18 TB of raw data have been collected by this study and the research questions addressed in this thesis are not the only questions it could be used for. Potential ideas include: investigating the impact the calls of invasive bird species (specifically ring-necked parakeets, *Psittacula krameri*) have on the singing activity of native species using Richmond Park data; examining the relationship between light levels and the singing times of forest birds at dawn and dusk, and how different tree species compositions might influence light levels using lux data from Hainich; qualifying the presence, activity and behaviour of visually cryptic species, such as owls and turtle doves, for which PAM may be particularly useful; performing more detailed investigation into the performance of acoustic indices to build upon the findings presented in this thesis and provide further guidance on their appropriate usage; and continuing to develop methods for the visualisation and representation of acoustic data.

Appendix A: Ethics Justification

To the best of our knowledge, ethical clearance should not be required to facilitate the performance of this project. No direct involvement or interaction with human participants is expected and disturbance of wildlife will be kept to a minimum. Indeed, the non-invasive nature of acoustic monitoring is one of its advantages. The only conceivable ethical issue could be the incidental recording of conversations conducted within the range of any sensors. For the following reasons, however, we believe this does not currently constitute an issue requiring ethics approval:

1. Monitoring would predominantly be conducted in locations away from the public. Over half the sites in Richmond are inaccessible to the public, sites in Hainich forest and Knepp were largely remote from public areas where a permit/permission was required for access from the hosting organisation/owner. Before monitoring at any of these locations begins, necessary permission would have to be obtained and any ethical requirements specified by the hosting institution would naturally be complied with at that point in time.

2. As far as we are aware, it is completely legal to record audio data for non-commercial use in public locations within the UK. Advice from London Metropolitan Police (2016) states that "members of the public and the media do not need a permit to film or photograph in public places". Whilst not specifically stating audio, the inclusion of filming inherently implies the accompanying capture of audio data is equally permitted.

3. Recording of human interactions during this study is highly undesirable, in no way related to the objectives or hypotheses being investigated and would therefore be completely accidental. Furthermore, in the unlikely eventuality this did ever happen, data would be entirely anonymous, without accompanying video or imagery, and will mostly be analysed using autonomous methods.

Appendix B: R Scripts

R script used to split longer bat files into 5.46 second lengths and append modified dates and times to filenames

```
library("seewave")
library("tuneR")
library("tools")
setwd("G:/split")
outdir <- "G:/Temp/"
filetotal <- dir()
filelist <- list.files()
totalfiles <-length(filetotal)
print(filelist)
for(i in 1:totalfiles){
tfile <- file.path(filelist[i])
mtimea <- file.info(tfile)$mtime
batfile <-readWave(tfile)
flength <- duration(batfile)
stime <- 0
etime <- 5.46
while (flength > etime ) {
mtimeb <- mtimea
tfilenamenoext<- file_path_sans_ext(filelist[i])
mtimea <- gsub(":","_",mtimea)
tfilenamea <- paste(outdir, tfilenamenoext," ",mtimea,".wav",sep="")
batfilea  <- extractWave(batfile, from=stime, to=etime, xunit="time")
writeWave(batfilea, tfilenamea, extensible = FALSE)
stime <- stime + 5.46
etime <- etime + 5.46
mtimea <- mtimeb + 5.46
}
}
```

Appendix B

R script to append original modified date to filenames without splitting files

```
library("tools")
setwd("G:/rename")
filetotal <- dir()
filelist <- list.files()
totalfiles <-length(filetotal)
for(i in 1:totalfiles){
tfile <- file.path(filelist[i])
mtimea <- file.info(tfile)$mtime
mtimea <- gsub(":","_",mtimea)
tfilenamenoext<- file_path_sans_ext(filelist[i])
tfilenamea <- paste(tfilenamenoext," ",mtimea,".wav",sep="")
file.rename(tfile, tfilenamea)
}
}
```

Appendix C: BatClassify Confidence Rating Performance

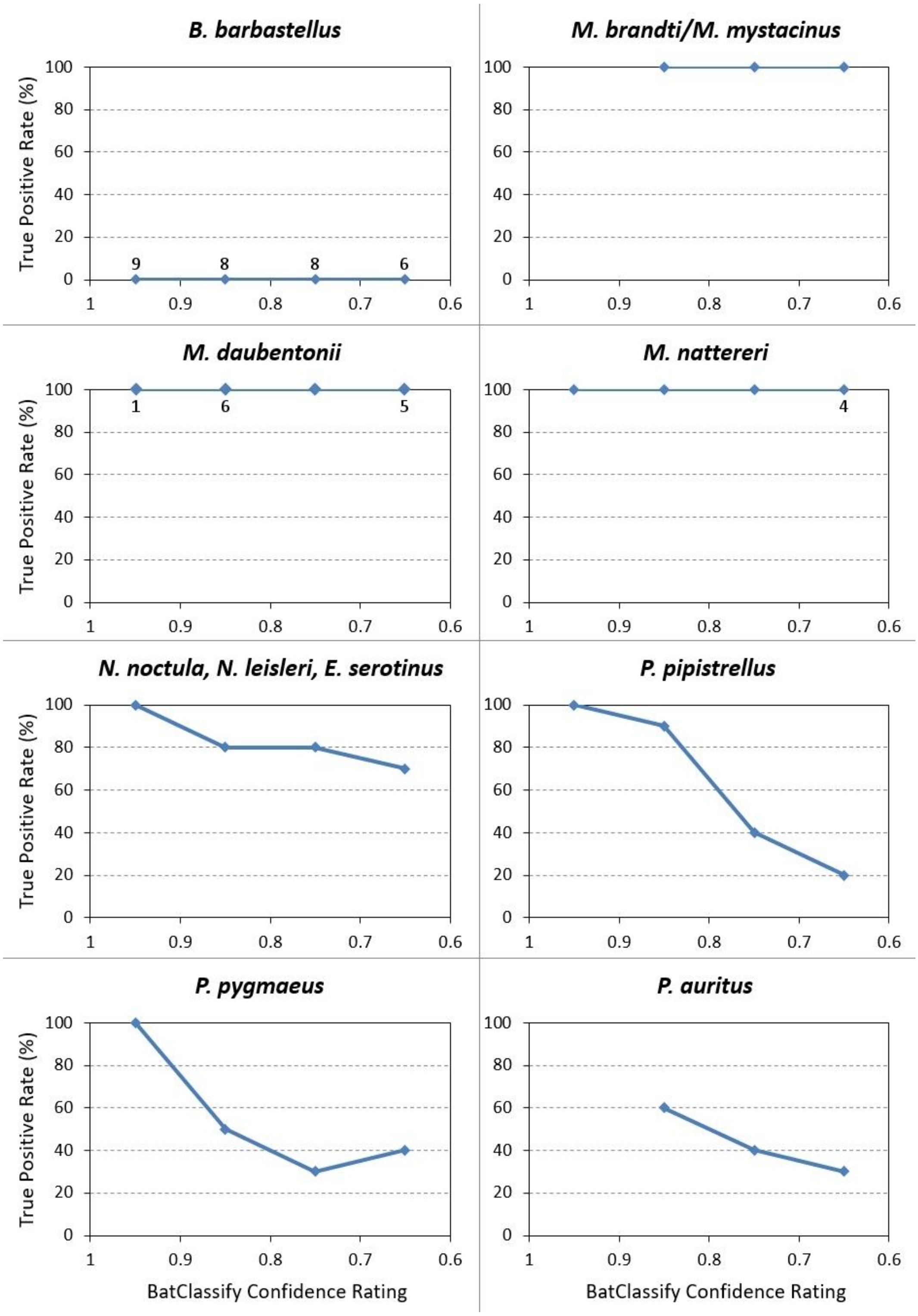


Figure C1. Evaluation of BatClassify confidence ratings for an initial sample of ten randomly chosen files rated within each threshold band (1-0.91, 0.9-0.81, 0.8-0.71 and 0.7-0.61) for each species or species group. Plots are presented using the same classification groupings as BatClassify. The number of files evaluated are shown for threshold bands when less than ten or omitted when none were available.

Appendix D: Classification Accuracy Statistics for Kaleidoscope Pro

Table D1. Accuracy statistics generated for Kaleidoscope Pro v5.1.3 by manual validation of 2,415 bat files, using one night per site chosen at random. NSL represents *N. noctula*, *E. serotinus* and *N. leisleri* and *Myotis* spp. represents *M. brandtii, M. mystacinus*, *M. daubentonii* and *M. nattereri*. Classifications were performed using the recommended settings for bats (8-120 kHz range, 2-500 ms length, 500 ms max. inter-syllable gap, minimum number of pulses =2), UK region species classifiers and -1 More sensitive (Liberal) selection setting.

Species/Species group	Precision[1]	Accuracy[2]	Recall[3]
P. pipistrellus	100%	90.3%	77.6%
P. pygmaeus	99.1%	94.2%	86.5%
Myotis spp.	90%	99.2%	50%
NSL	88.9%	96.9%	51.8%
P. auritus	66.7%	99.8%	50%

[1] Precision = true positives / (true positives + false positives)

[2] Accuracy = (true positives + true negatives) / total files

[3] Recall = true positives / (true positives + false negatives)

Appendix E: Location, Tree Inventories, Ground Cover and Canopy Survey Details for Richmond Park, 2016

Table E1. Location details of acoustic recording sites in Richmond Park in 2016.

Site	Area name	Rhododendron status	Public access	Deer access	Latitude	Longitude	Facing	Elevation (m asl)	Unit height (cm)
1	Pens Pond	Present	N	Y	51.43852	-0.27860	250°	28	217
2	Pens Pond	Present	N	Y	51.43851	-0.27825	210°	29	257
3	Spankers Hill	Present	Y	Y	51.44032	-0.26407	260°	34	285
4	Spankers Hill	Present	Y	Y	51.44024	-0.26324	220°	30	265
5	Spankers Hill	Absent	Y	Y	51.44110	-0.26263	170°	26	281
6	Prince Charles' Spinney	Absent	N	N	51.43599	-0.26828	170°	27	160
7	Isabella Plantation	Absent	N	N	51.43554	-0.27468	80°	40	170
8	Queen Elizabeth Plantation	Absent	Y	Y	51.44357	-0.28401	145°	39	250
9	Sidmouth Wood	Removed (2014/15)	N	N	51.44598	-0.28772	315°	52	200
10	Sidmouth Wood	Removed (2013/14)	N	N	51.44571	-0.28727	45°	51	225
11	Sidmouth Wood	Removed (2012/13)	N	N	51.44564	-0.28734	165°	51	220
12	Sidmouth Wood	Removed (2011/12)	N	N	51.44522	-0.28771	255°	51	225

Latitude and longitude readings taken using a Garmin eTrex Legend HCx GPS. Site elevations obtained from Google Earth. Unit heights given from ground level to the bottom of the recorder case.

Table E2. Characteristics of acoustic survey locations in Richmond Park, 2016.

Site	Shannon index	Mean DBH (cm)	DBH Std. dev. (cm)	Tree species richness	Living trees	Dead trees	Canopy cover (%)	Understorey >1.5 m (%)	Rhododendron >1.5 m (%)	Distance to water (m)*
1	0.80	52.4	27.6	3	35	2	96	0	63	202[1]
2	0.89	39.3	23.9	4	46	3	81	0	34	199[1]
3	0.61	69.0	16.2	3	20	1	81	0	75	218[2]
4	0.00	75.4	11.6	1	20	0	86	0	53	200[2]
5	0.22	77.4	13.6	2	17	2	72	0	0	99[2]
6	1.81	23.9	14.5	11	41	0	69	9	0	601[3]
7	0.74	27.0	23.3	5	84	1	83	9	0	250[4]
8	1.44	44.8	21.3	8	43	3	80	0	0	252[5]
9	0.79	47.6	33.3	3	28	4	56	1	0	558[5]
10	1.14	43.3	27.8	4	38	3	78	35	0	519[5]
11	0.99	45.7	28.6	4	33	1	75	34	0	519[5]
12	0.47	72.3	19.1	3	23	0	81	31	0	525[5]

* Nearest water body used to calculate distance: 1=Pen ponds, 2=Spankers hill pond, 3=Martin's pond, 4=Thomson's pond, 5=Leg-of-mutton pond

Table E3. Percentage of different ground cover types at acoustic recording sites in Richmond Park, 2016.

Site	Saplings	Bracken	Bracken/ bramble mix	Bramble	Dead wood	Grass	Holly	Bare ground	Rhododendron
1	0%	3%	0%	0%	5%	0%	0%	29%	63%
2	0%	0%	0%	0%	13%	0%	0%	53%	34%
3	0%	9%	0%	0%	0%	2%	0%	14%	75%
4	0%	32%	0%	0%	2%	3%	0%	10%	53%
5	0%	67%	0%	0%	1%	0%	0%	32%	0%
6	9%	37%	21%	25%	0%	1%	0%	7%	0%
7	0%	0%	63%	0%	1%	0%	9%	27%	0%
8	0%	11%	0%	16%	8%	38%	0%	27%	0%
9	1%	19%	60%	4%	1%	0%	0%	15%	0%
10	35%	2%	50%	1%	1%	7%	0%	4%	0%
11	34%	3%	52%	0%	1%	7%	0%	3%	0%
12	31%	0%	28%	29%	1%	6%	0%	5%	0%

Appendix E

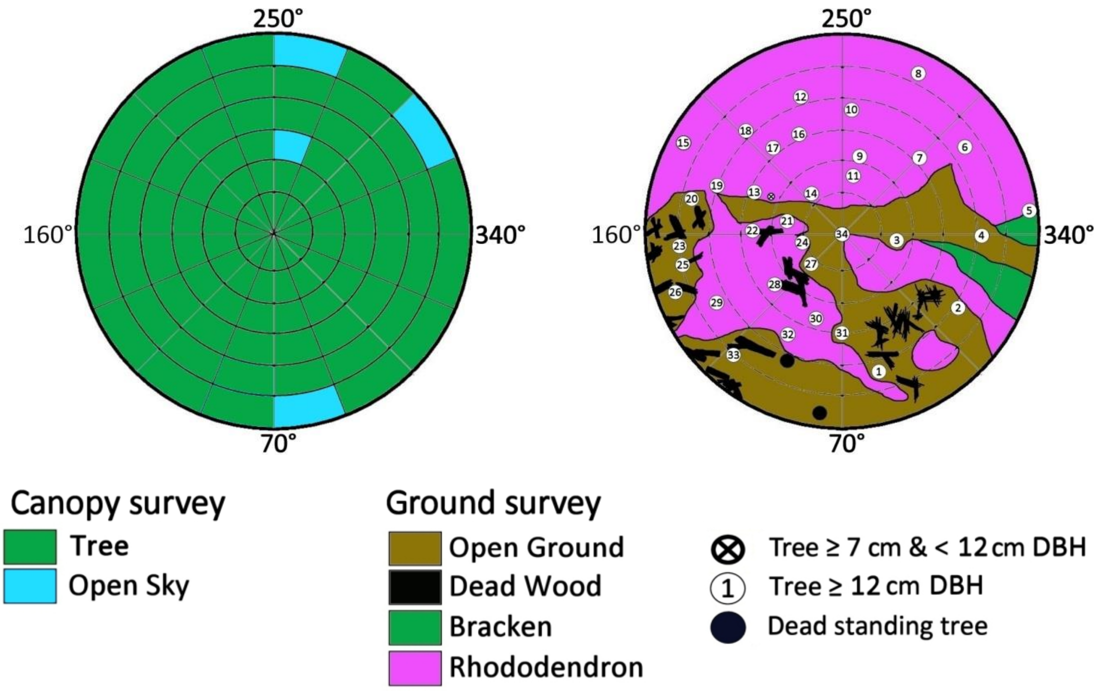


Figure E1. Site 1 vegetation map, 2016.

Table E4. Site 1 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	8.18	19
Betula pendula	0.67	15
Castanea sativa	0.72	1

Appendix E

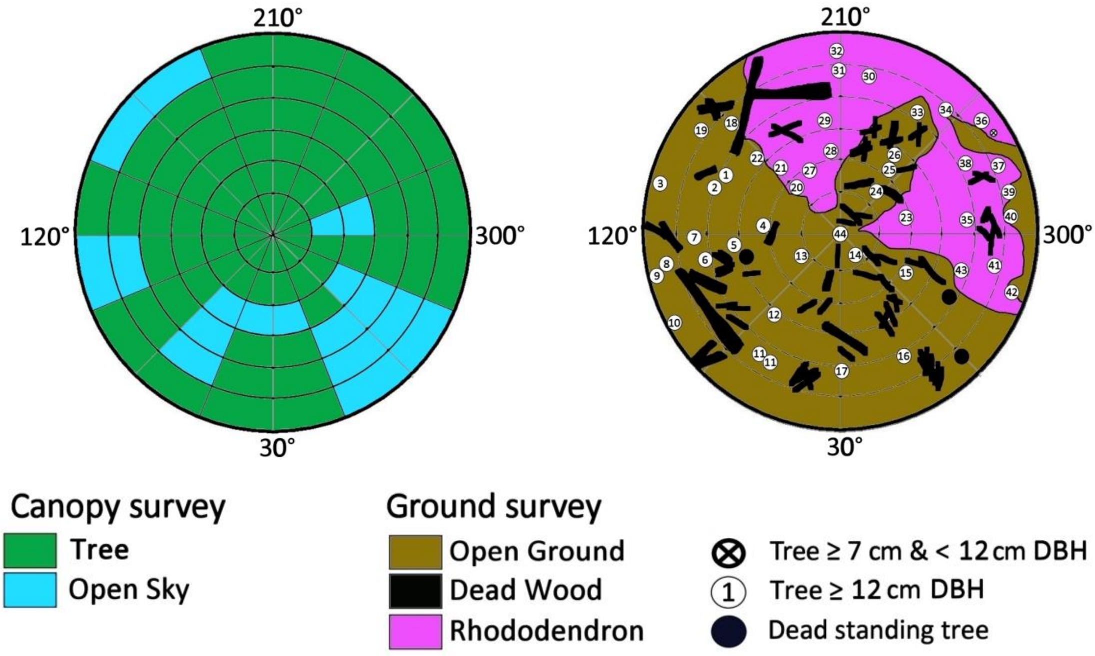


Figure E2. Site 2 vegetation map, 2016.

Table E5. Site 2 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Betula pendula	1.64	30
Quercus spp.	5.16	12
Carpinus betulus	0.67	3
Quercus rubra	0.1	1

Appendix E

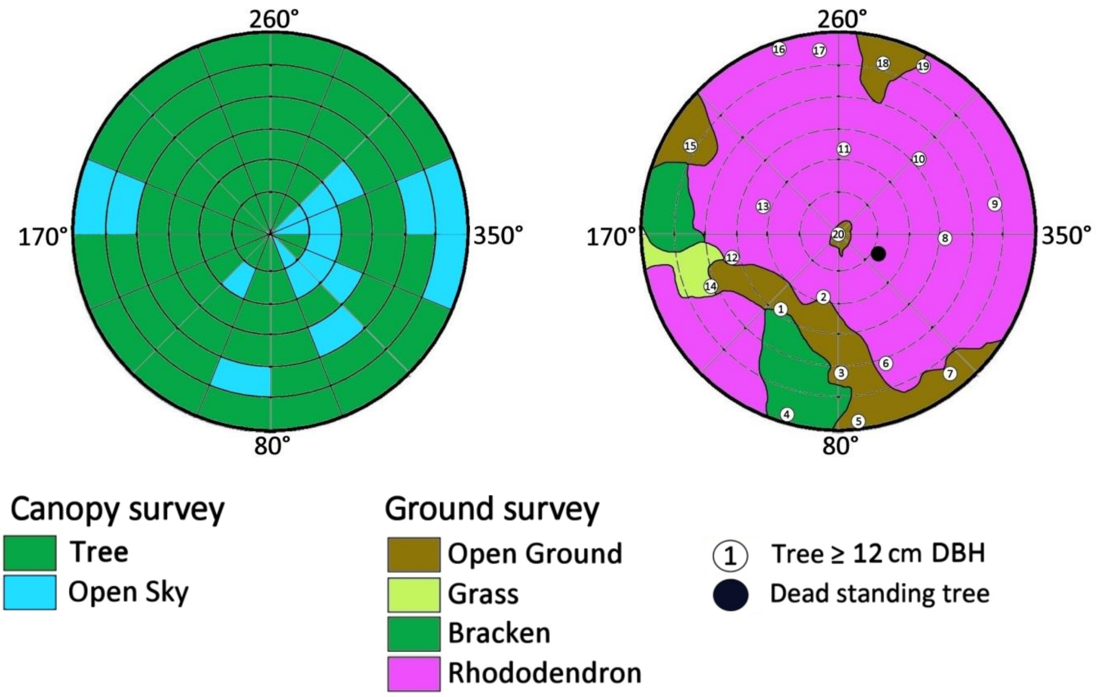


Figure E3. Site 3 vegetation map, 2016.

Table E6. Site 3 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	7.08	16
Castanea sativa	0.59	3
Fagus sylvatica	0.19	1

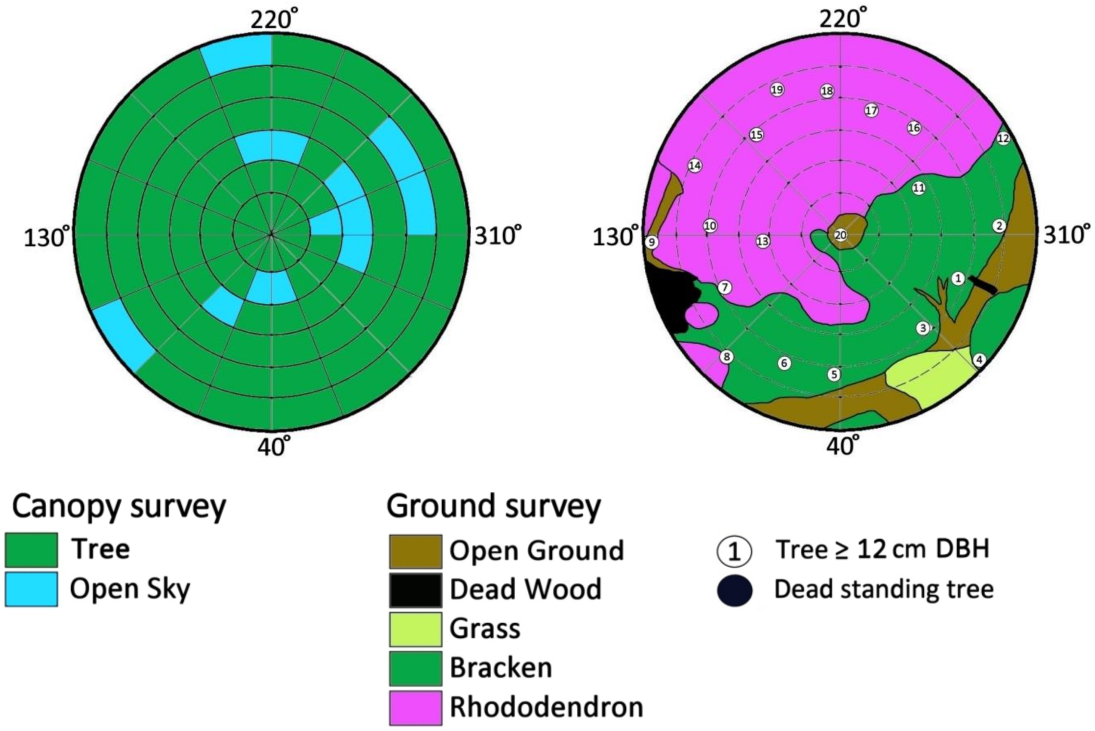


Figure E4. Site 4 vegetation map, 2016.

Table E7. Site 4 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	9.13	20

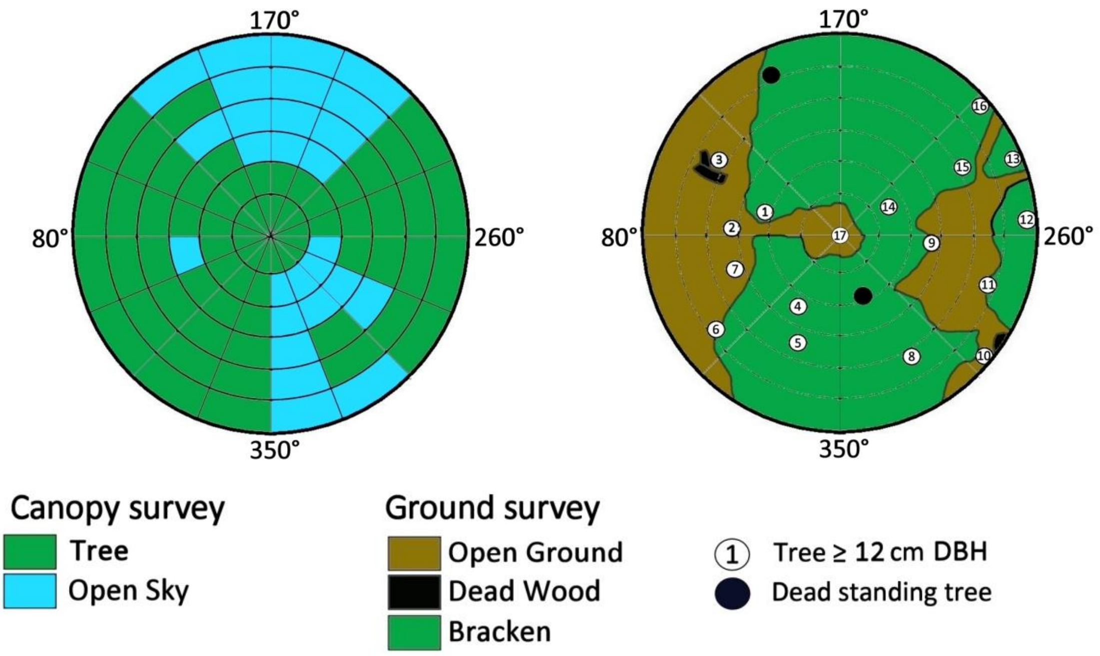


Figure E5. Site 5 vegetation map, 2016.

Table E8. Site 5 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	7.58	16
Castanea sativa	0.65	1

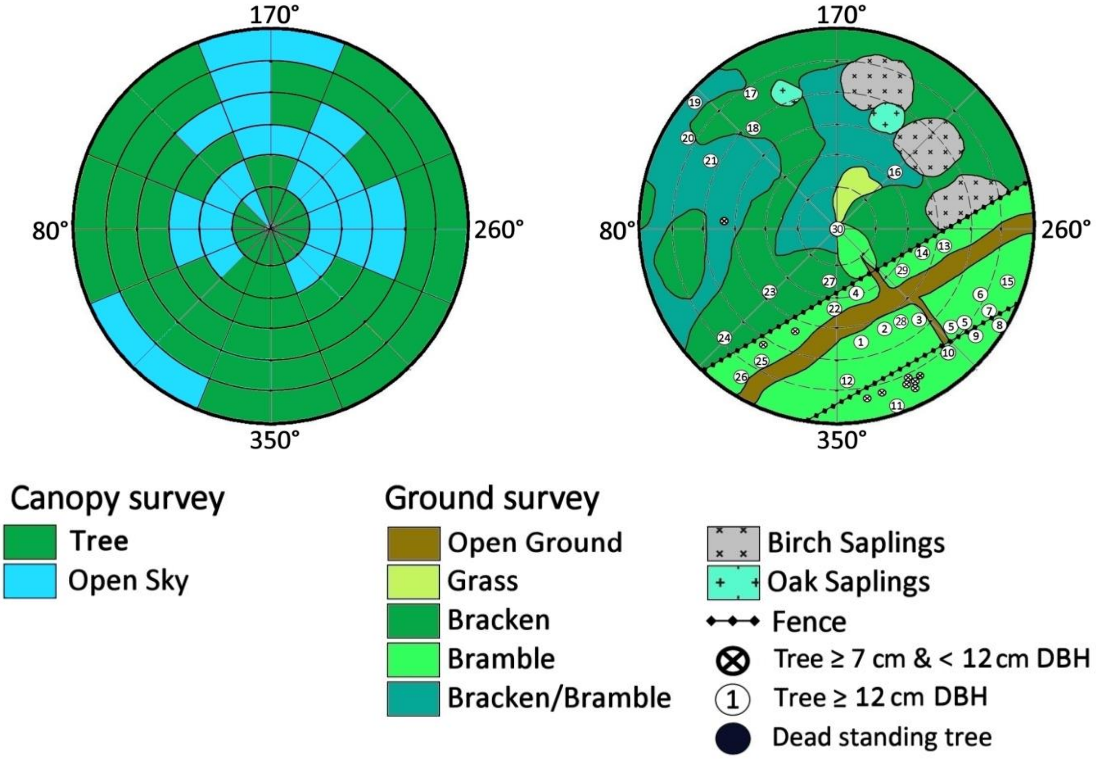


Figure E6. Site 6 vegetation map, 2016.

Table E9. Site 6 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Betula pendula	0.46	16
Crataegus monogyna	0.22	10
Quercus spp.	0.7	5
Fraxinus excelsior	0.17	2
Fagus sylvatica	0.43	2
Carpinus betulus	0.14	1
Pinus nigra	0.1	1
Crataegus prunifolia	0.01	1
Malus sylvestris	0.02	1
Sorbus intermedia	0.17	1
Prunus avium	0.08	1

Appendix E

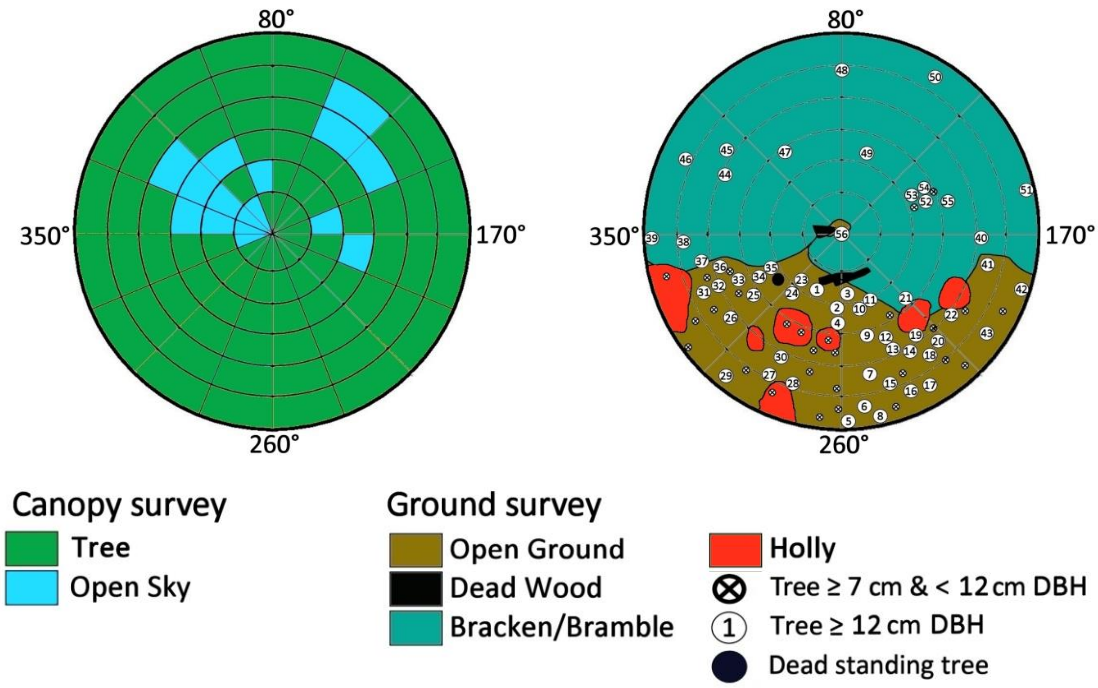


Figure E7. Site 7 vegetation map, 2016.

Table E10. Site 7 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Fagus sylvatica	2.6	66
Quercus spp.	5.59	11
Prunus avium	0.05	4
Betula pendula	0.06	2
Salix caprea	0.03	1

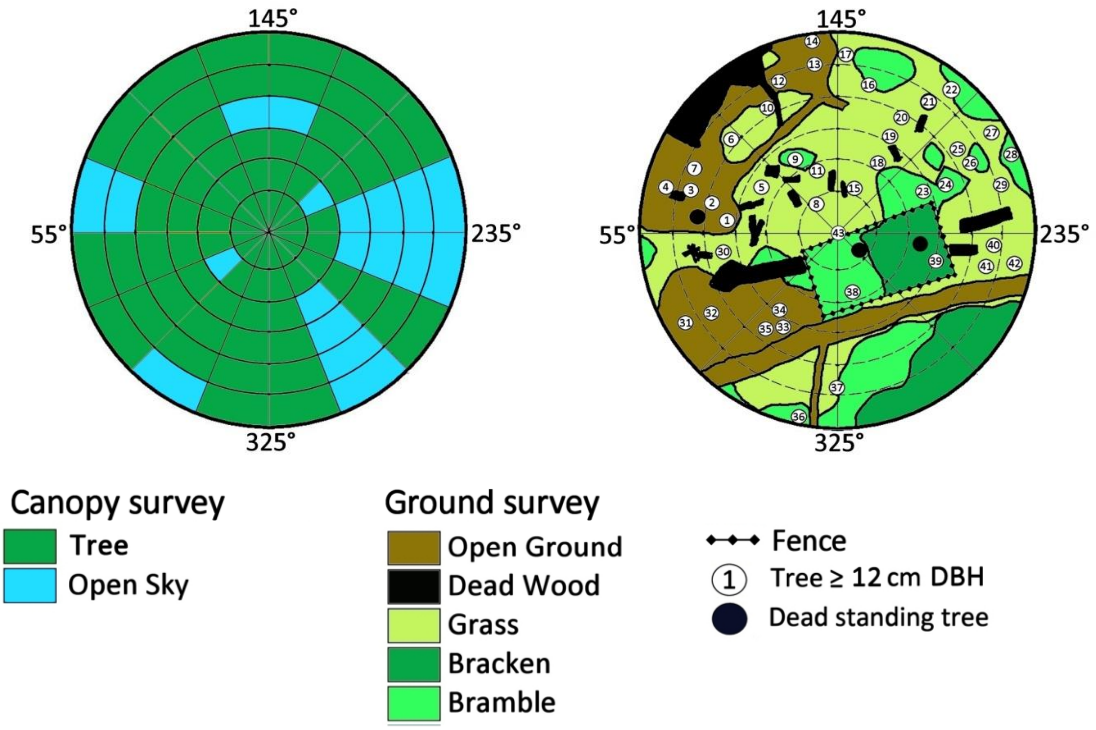


Figure E8. Site 8 vegetation map, 2016.

Table E11. Site 8 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	5.98	24
Betula pendula	0.65	6
Fagus sylvatica	0.43	5
Castanea sativa	0.52	3
Quercus rubra	0.29	2
Fraxinus excelsior	0.33	1
Acer pseudoplatanus	0.03	1
Crataegus monogyna	0.05	1

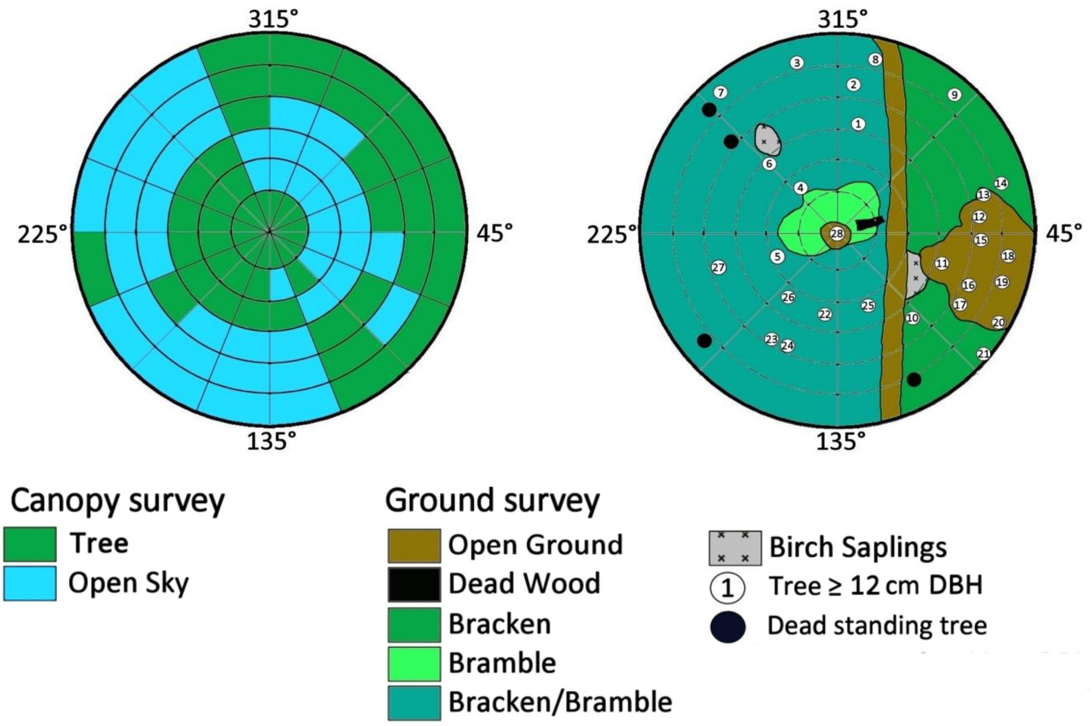


Figure E9. Site 9 vegetation map, 2016.

Table E12. Site 9 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	3.89	20
Betula pendula	0.12	5
Castanea sativa	3.33	3

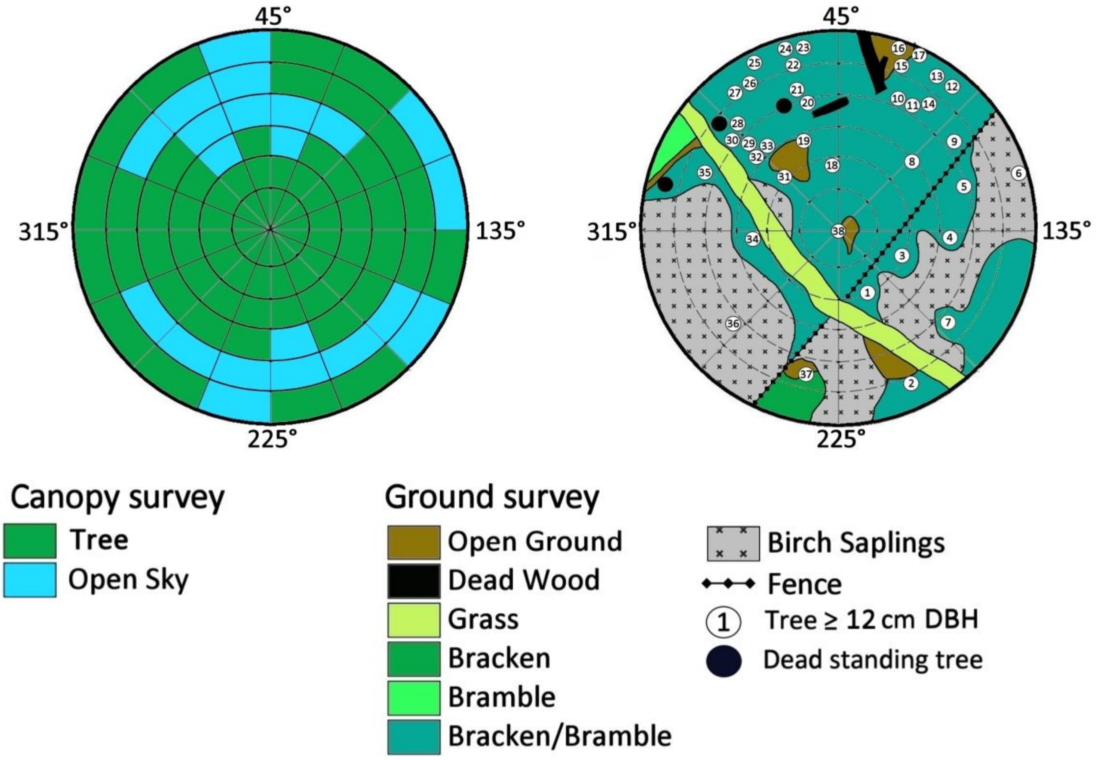


Figure E10. Site 10 vegetation map, 2016.

Table E13. Site 10 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	6.37	16
Betula pendula	0.47	14
Castanea sativa	0.91	7
Fagus sylvatica	0.07	1

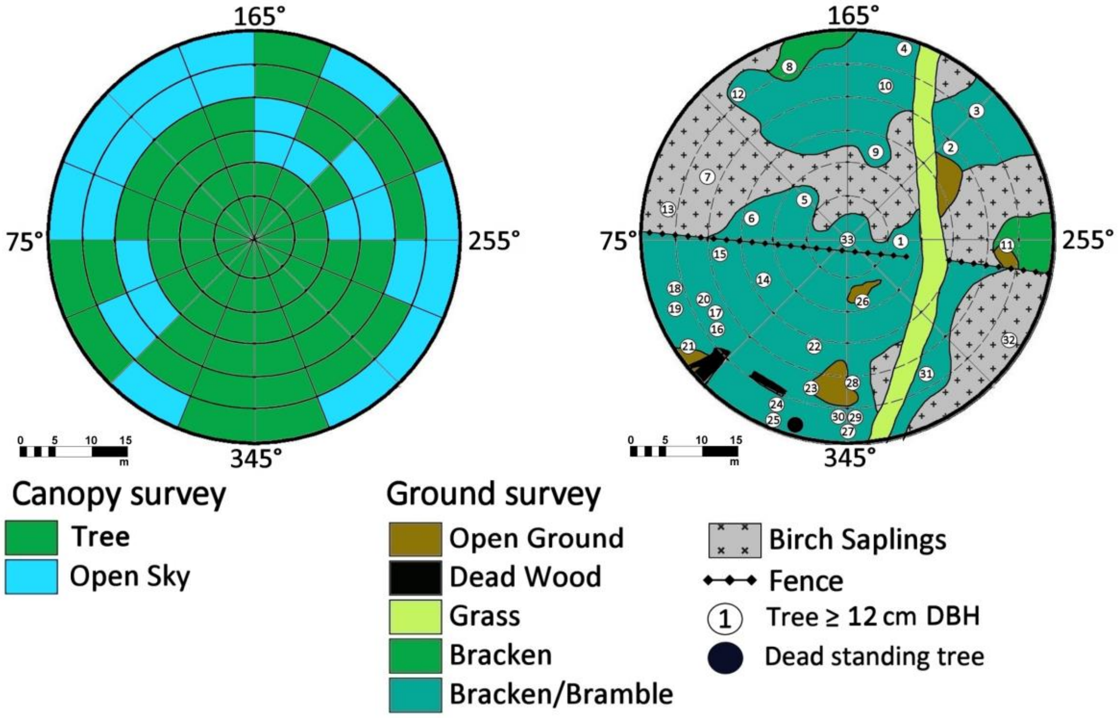


Figure E11. Site 11 vegetation map, 2016.

Table E14. Site 11 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	6.57	15
Betula pendula	0.54	15
Castanea sativa	0.29	2
Fagus sylvatica	0.07	1

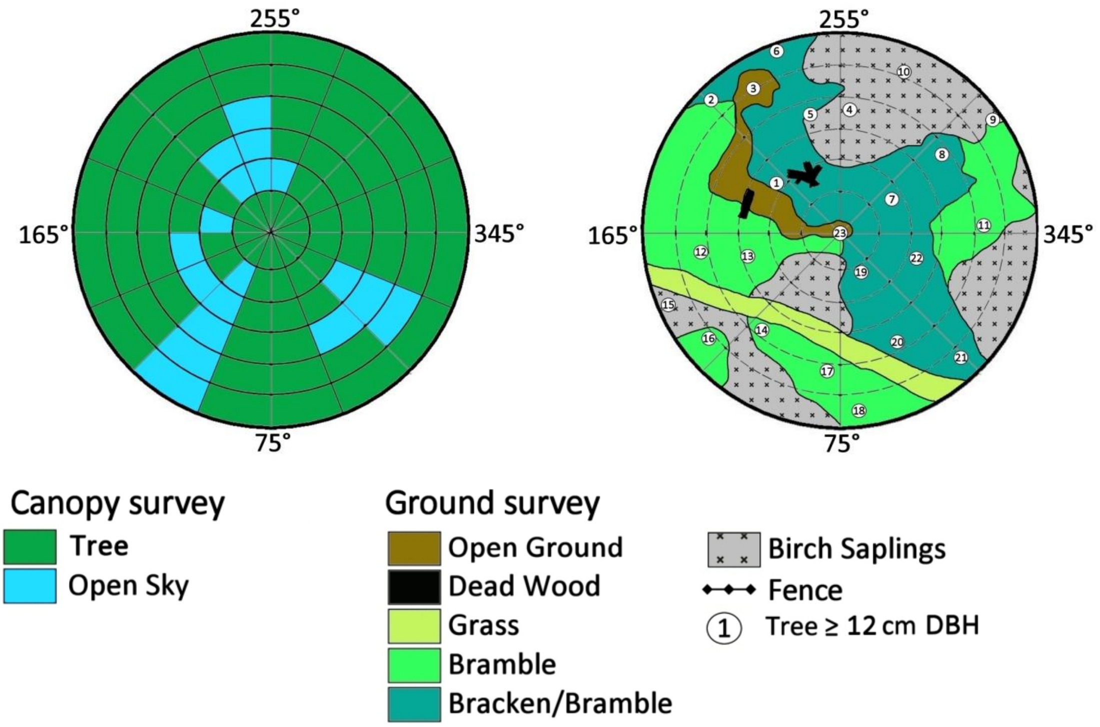


Figure E12. Site 12 vegetation map, 2016.

Table E15. Site 12 tree inventory, 2016.

Tree species	Basal area (m^2)	# of trees
Quercus spp.	9.55	20
Betula pendula	0.07	2
Pinus pinea	0.45	1

Appendix F. Treatment GLMM Selection and Validation for Richmond Park

Table F1. AIC scores and overdispersion ratios used to assess possible error distributions and random effects for treatment models.

Structure[1]	Random[2]	Overdispersion[3]	res.df	loglik	AIC	ΔAIC	weight
			NSL				
NB	S D	0.81	258	-614.7	1241.4	0	1
NB	S	1.19	259	-634.4	1278.7	37.3	<0.001
P	S D	6.65	259	-1054.7	2119.3	877.9	<0.001
P	S	21.47	260	-2204.2	4416.5	3175.1	<0.001
			P. pipistrellus				
NB	S D	0.92	258	-1296.8	2605.5	0	1
NB	S	1.04	259	-1338.7	2687.3	81.8	<0.001
P	S D	31.65	259	-4804.9	9619.8	7014.3	<0.001
P	S	64.91	260	-8519.1	17046.1	14440.6	<0.001
			P. pygmaeus				
NB	S D	0.93	258	-1450.9	2913.8	0	1
NB	S	0.86	259	-1495.4	3000.7	86.9	<0.001
P	S D	35.69	259	-5197.5	10405.1	7491.3	<0.001
P	S	71.02	260	-9774.8	19557.7	16643.9	<0.001
			Myotis spp.				
NB	S D	0.93	258	-534.9	1081.8	0	0.891
NB	S	0.98	259	-538	1086	4.2	0.109
P	S D	1.86	259	-586.7	1183.4	101.6	<0.001
P	S	2.46	260	-618.4	1244.7	162.9	<0.001
			P. auritus				
Bi	S	0.75	260	-83.9	175.7	0	0.73
Bi	S D	0.76	259	-83.9	177.7	2	0.27

[1] Structure key: P = Poisson, NB = Negative binomial, Bi = Binomial

[2] Random effects key: S = site, D = day.

[3] Overdispersion shown as ratio of residual deviance to residual degrees of freedom, should be ~1 (Crawley, 2007).

Data were overdispersed for all four Poisson structure models, which in each case was corrected by using a negative binomial distribution (Table F1). It was also apparent that including day number as a random effect improved model fit in all cases except for *P. auritus*. Both *P. auritus* models produced virtually identical results and indicated that date accounted for very little variance ($2.96e^{-9}$) when included. For NSL, *P. pipistrellus* and *P. pygmaeus*, models using negative binomial distribution with site and day as random effects clearly provided the best performance. For *Myotis* spp.

performance of negative binomial models with and without day as a random effect was more similar. In all cases, the most parsimonious model (lowest AIC) was chosen. Goodness-of-fit was assessed for final models with QQ plots of scaled residuals for observed vs. expected values and one-sample Kolmogorov-Smirnov tests, created using the *DHARMa* package (Hartig, 2019), which was set for 10,000 simulations. None of the model residual tests demonstrated significant deviations from uniformity or outliers (Figure F1).

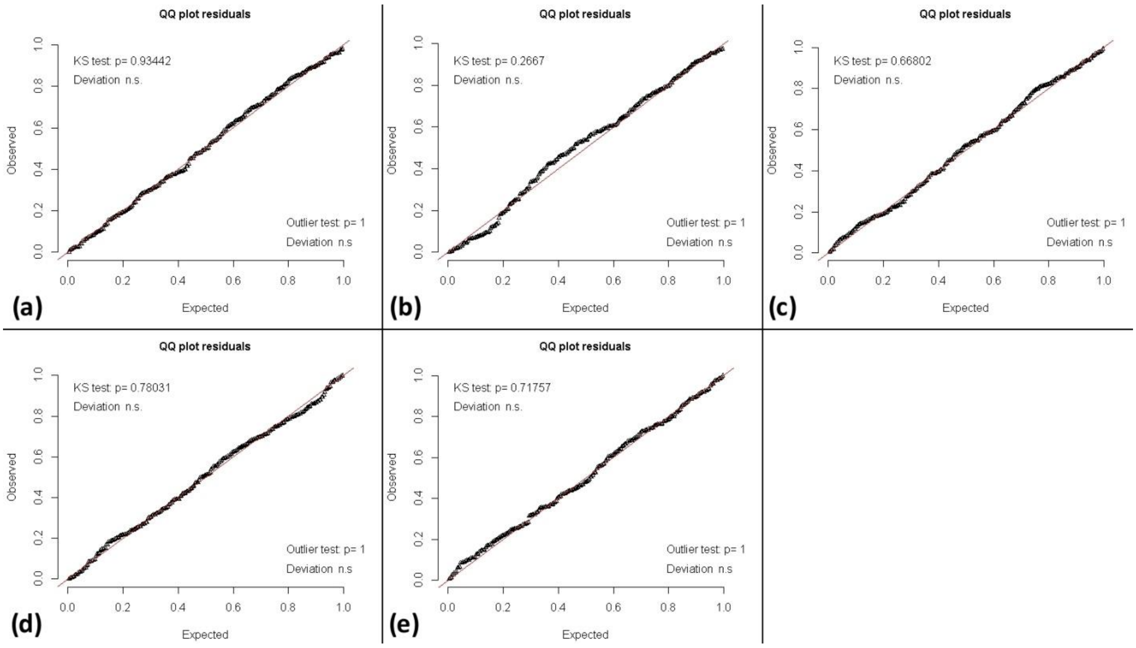


Figure F1. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores of treatment GLMMs for (a) *P. pipistrellus* (b) *P. pygmaeus* (c) *Myotis* spp. (d) NSL and (e) *P. auritus* generated by *DHARMa* using 10,000 simulations.

Appendix G: Correlation Table of Site Variables for Richmond Park

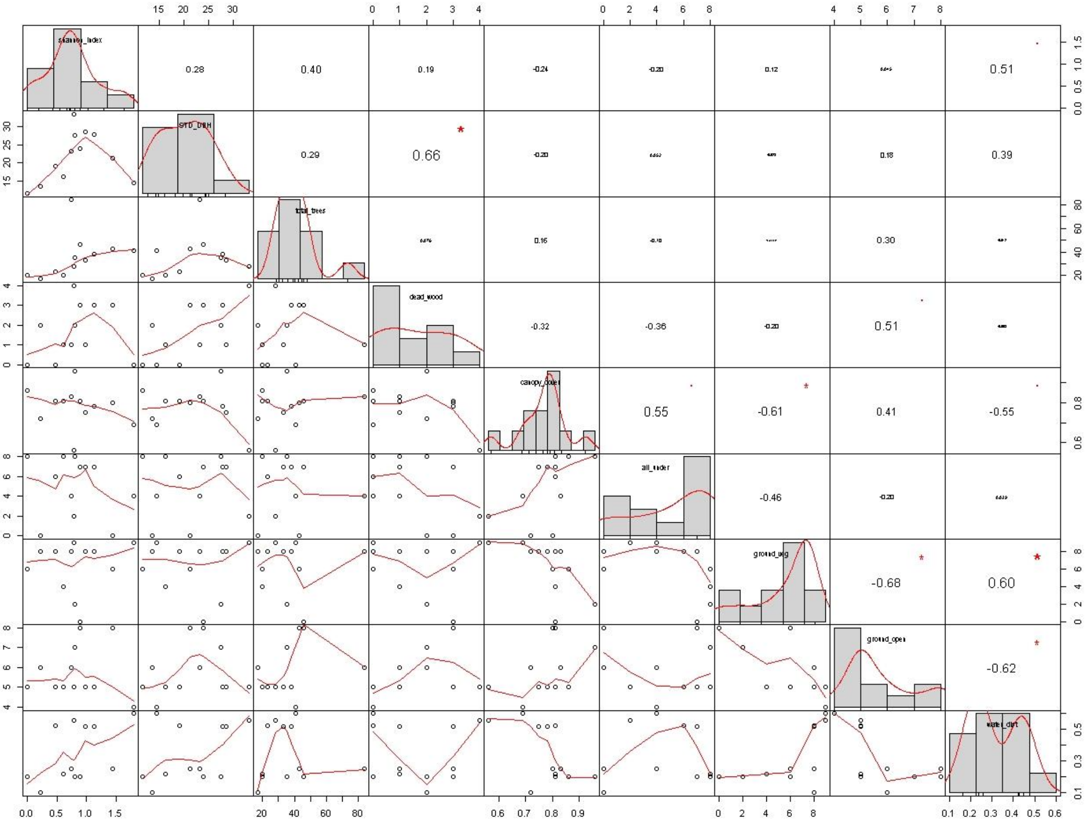


Figure G1. Correlation chart of the 9 final site characteristic variables (left to right): Shannon index, std. dev. DBH, # living trees, # dead trees, % canopy cover, woody understorey, dense ground vegetation, open space and distance to water.

Appendix H. PCA Reduction and Model Averaging Selection Process for Site Characteristics GLMMs in Richmond Park

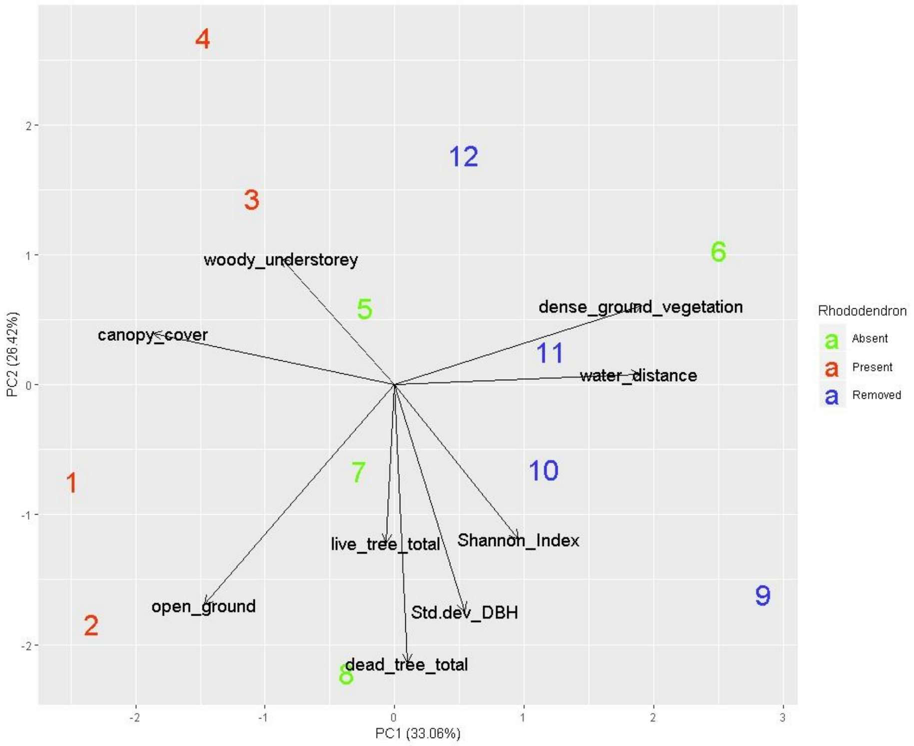


Figure H1. PC1 and PC2 loadings obtained using PCA from nine site characteristic variables in Richmond Park, 2016.

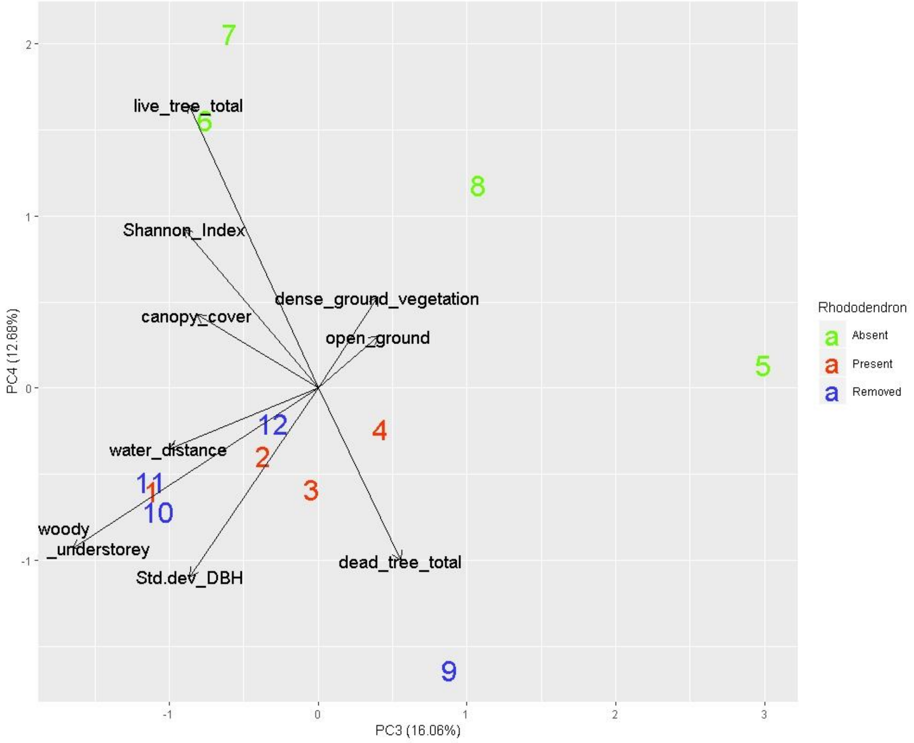


Figure H2. PC3 and PC4 loadings obtained using PCA from nine site characteristic variables in Richmond Park, 2016.

Reasonably distinct separation between sites with (1-4) and without (5-12) rhododendron was demonstrated by Figure H1. Loading directions for PC1 and PC2 accounted for 59% of variance and indicated rhododendron sites were primarily characterised by higher values for woody understorey and canopy cover, less dense ground vegetation and closer proximity to water in comparison to other sites. Within the rhododendron sites, the main differences were related to open ground and tree characteristics total trees, standard deviation, Shannon index and dead trees. This variation is due to the different trees species compositions (Tables E4 to E7) in the two areas where rhododendron was surveyed; Pen ponds (sites 1 and 2) contained a mixture of smaller (Silver birch) and larger trees while Spankers Hill (sites 3 and 4) predominantly consisted of large oaks. Rhododendron sites clustered more closely together for PC3 and PC4, which explained 28% of variance, although three sites where it had been removed exhibited similar characteristics (Figure H2). A summary of the variances explained by all nine PCs is provided in Table H1.

Table H1. Eigenvalues and % variance explained by initial Principal Component Analysis results for nine site characteristics in Richmond Park, 2016.

Component	Eigenvalue	% of variance	Cumulative %
PC1	2.975	33.06	33.06
PC2	2.378	26.42	59.48
PC3	1.445	16.06	75.53
PC4	1.141	12.68	88.21
PC5	0.626	6.95	95.16
PC6	0.244	2.71	97.87
PC7	0.122	1.35	99.22
PC8	0.055	0.61	99.84
PC9	0.015	0.16	100

The first four principal components, which all had eigenvalues exceeding 1 and accounted for ≥10% of total variance, were retained (Table H1). Altogether, these four PCs explained over 88% of the total variance contained within the original variables. Rotation is often applied to PCA results to improve their interpretability by rotating their axes in order to more evenly distribute variance between the retained PCs (Jolliffe, 2002). Orthogonal rotation was selected and performed using the *varimax* function in the R *stats* package (R Core Team, 2018). Component loadings of the resulting PCs are shown in Table H2. Loadings closer to 1 or -1 represent higher correlations between variables and components, while zero loadings indicate no correlation exists (Quinn and Keough, 2002). A relative comparison of how many variables are loading onto each PC, and how strong these loadings are, is provided at the foot of each table based on ratings suggested by Comrey and Lee (1992) where 0.71 or above is considered “excellent”, “very good” at 0.63, 0.55 is “good”, 0.45 is “fair”, and 0.32 or lower is "poor".

Table H2. Principal component loading values for Richmond park site variables, 2016. Loadings exceeding ±0.71 (excellent) are shown in bold.

Survey variable	PC1	PC2	PC3	PC4
Shannon index	0.270	-0.252	0.103	**0.746**
Std. dev. DBH (cm)	0.137	**-0.884**	-0.137	0.249
Living trees (#)	-0.183	-0.008	0.016	**0.881**
Dead trees (#)	-0.270	**-0.871**	0.347	0.001
Canopy cover (%)	-0.608	0.313	-0.632	0.110
Woody understorey >1.5 m (Domin)	0.044	0.040	**-0.976**	-0.127
Dense ground vegetation (Domin)	**0.761**	0.199	0.490	0.065
Open ground (Domin)	**-0.885**	-0.311	0.107	0.215
Distance to water (km)	**0.904**	-0.253	-0.060	0.234
Ratings based on Comrey and Lee (1992)				
Excellent	3	2	1	2
Very good	0	0	1	0
Good	1	0	0	0
Fair	0	0	1	0

In Table H2, PC1 represented the amount of ground vegetation, with higher values indicating greater coverage of dense vegetation (bramble and bracken) and less open ground. High values also represented further distances to the nearest water body. PC2 was associated with more homogeneous tree sizes (less deviation in DBH) and fewer dead trees. PC3 represented lower levels of woody understorey and was less strongly associated with lower levels of canopy cover. Higher values for PC4 were associated with greater numbers of trees and more diverse communities of tree species. Scores for the four PCs, following rotation, are presented for each site in Table H3.

Table H3. Principal component scores obtained for Richmond park site variables, 2016.

Site	PC1	PC2	PC3	PC4
1	-1.1078	-0.5974	-1.3723	0.0905
2	-1.4788	-0.9541	-0.5677	0.2580
3	-0.1513	0.4598	-0.7266	-0.8961
4	-0.2117	1.3573	-0.6441	-1.2674
5	-0.6778	0.6957	1.8835	-1.3747
6	1.4853	1.0987	0.3374	1.2492
7	-0.4343	0.8330	0.2459	1.7991
8	-1.0973	-0.2600	1.3893	0.9733
9	1.1146	-1.9215	1.1196	-0.7369
10	0.7821	-0.9559	-0.5257	0.2681
11	1.0056	-0.4212	-0.6712	0.1354
12	0.7713	0.6656	-0.4682	-0.4986

Table H3 confirms what was seen earlier in Figure H2, that although woody understorey and canopy cover (PC3) mostly closely characterised rhododendron sites, there were also some sites where rhododendron had been removed with similar values for this component. For PC2 and PC4, the difference in tree characteristics at the two rhododendron sites is evident in the reversal of positive and negative scores between sites 1 and 2, and 3 and 4. Finally, PC1 presents some similarity between rhododendron sites but, again, this is not exclusive and comparable values exist within three sites (5, 7 and 8) where rhododendron was absent.

Following PCA, models were created for all possible combinations (*n*=64) of the 5 variables in combination with site or site and day as random effects. Except for *P. auritus* (binomial), a negative binomial distribution was used, as data were already known to be overdispersed. The most parsimonious models ($\Delta AIC_C < 2$) for each species/species group were selected for model averaging (Table H4). Different threshold values, for example $\Delta AIC_C < 6$ (Richards, 2008) and 95% summed confidence weight (Burnham and Anderson, 2002), have been suggested for candidate model selection. These thresholds were also evaluated but would have entailed inclusion of half, or more, of the candidate models for *P. pipistrellus*, *Myotis* spp. and *P. auritus* using $\Delta AIC_C < 6$, for example. Additionally, the ΔAIC_C score for both the *P. pipistrellus* and *P. pygmaeus* full models was 2.1, suggesting that by this point all variables were of roughly equal importance. For *Myotis* spp. and *P. auritus*, the null model had the lowest ΔAIC_C, and increasing the number of candidate models would therefore seem unlikely to reveal any additional relationships.

Table H4. AIC_C scores of candidate characteristic models selected for model averaging.

Model components[1]	Random[2]	df	loglik	AIC_C	ΔAIC_C	weight
NSL						
3.d	S D	6	-618.4	1249.1	0	0.265
d	S D	5	-620.3	1250.9	1.81	0.107
2.3.d	S D	7	-618.3	1251	1.95	0.1
P. pipistrellus						
1.2.3.d	S D	8	-1292.3	2601.3	0	0.075
2.3	S D	6	-1294.6	2601.6	0.36	0.063
1.3.d	S D	7	-1293.7	2601.8	0.58	0.056
2	S D	5	-1295.8	2601.8	0.59	0.056
2.3.4	S D	7	-1293.8	2602	0.76	0.051
Null	S D	4	-1297	2602.2	0.98	0.046
1.d	S D	6	-1295	2602.3	1.07	0.044
1.2.d	S D	7	-1293.9	2602.3	1.08	0.044
1.2.3	S D	7	-1294	2602.4	1.12	0.043
3	S D	5	-1296.1	2602.5	1.21	0.041
2.4	S D	6	-1295.1	2602.6	1.3	0.039
1.2.3.4	S D	8	-1293	2602.6	1.32	0.039
1.2	S D	6	-1295.3	2602.8	1.58	0.034
4	S D	5	-1296.5	2603.2	1.94	0.028
3.4	S D	6	-1295.5	2603.2	1.98	0.028
P. pygmaeus						
1.3.4.d	S D	8	-1446.4	2909.4	0	0.171
1.3.d	S D	7	-1447.4	2909.8	0.44	0.137
3	S D	5	-1450	2910.2	0.82	0.114
Myotis spp.						
Null	S D	4	-536.7	1081.6	0	0.136
4	S D	5	-536	1082.3	0.77	0.092
2	S D	5	-536.4	1083.1	1.56	0.062
3	S D	5	-536.5	1083.3	1.7	0.058
P. auritus						
Null	S	2	-84	172.1	0	0.096
2	S	3	-83.4	172.9	0.76	0.066
3	S	3	-83.6	173.2	1.13	0.055
4	S	3	-83.8	173.7	1.62	0.043
d	S	3	-83.9	173.8	1.63	0.041
1	S	3	-84	174	1.91	0.037

[1] Components key: 1 = PC1, 2 = PC2, 3 = PC3, 4 = PC4, d = deer.

[2] Random effects key: S = site, D = day.

Appendix I. Bat Pass Totals for Richmond Park and Characteristics GLMM Results

Table I1. Total pass counts recorded over 22 nights in July and August at Richmond park, 2016. NSL represents *N. noctula*, *E. serotinus* and *N. leisleri,* and *Myotis* spp. represents *M. brandtii/M. mystacinus*, *M. daubentonii* and *M. nattereri*.

Site	*P. pipistrellus*	*P. pygmaeus*	*Myotis* spp.	NSL	*P. auritus*
Rhododendron present					
1	4785	4732	151	11	0
2	224	3045	14	5	7
3	1306	1231	11	11	0
4	4170	4194	121	103	5
Rhododendron absent					
5	1122	1489	32	94	1
6	2569	575	6	258	1
7	315	3441	12	79	0
8	567	1538	103	39	6
Rhododendron removed					
9	368	1429	52	188	6
10	2204	4461	135	1080	3
11	726	3216	52	275	0
12	3766	2312	256	347	2
Total	22122	31663	945	2490	31

Table I2. Parameter estimates of averaged Characteristics GLMMs with full average results given. Bracketed numbers are the total candidate models used for averaging (next to species) and the relative importance of characteristics included in averaged models (next to variables). Note: missing characteristics were not included in any of the candidate models selected for averaging. Significance codes: <0.001 '***', <0.01 '**', <0.05 '*', <0.1 '.'

Characteristic	Estimate	Std err	Z Value	*Pr(>|z|)*	Sig.
		P. pipistrellus (15)			
(Intercept)	3.569	0.508	7.009		
PC1 (0.49)	0.668	0.941	0.709	0.478	
PC2 (0.65)	0.544	0.557	0.974	0.330	
PC3 (0.58)	-0.447	0.52	0.859	0.391	
PC4 (0.27)	-0.166	0.372	0.444	0.657	
Deer present (0.32)	0.486	0.843	0.575	0.565	
		P. pygmaeus (3)			
(Intercept)	4.942	0.411	12.013		
PC1 (0.73)	-0.922	0.716	1.287	0.198	
PC3 (1.00)	-0.710	0.249	2.842	0.004	**
PC4 (0.41)	-0.205	0.312	0.655	0.512	
Deer present (0.73)	-0.922	0.740	1.245	0.213	
		Myotis spp. (4)			
(Intercept)	0.696	0.339	2.046		
PC2 (0.18)	-0.086	0.338	0.255	0.799	
PC3 (0.17)	-0.688	0.312	0.219	0.826	
PC4 (0.27)	-0.203	0.476	0.425	0.671	
		NSL (3)			
(Intercept)	2.196	0.447	4.894		
PC2 (0.21)	-0.050	0.290	0.170	0.865	
PC3 (0.77)	0.944	0.720	1.309	0.190	
Deer present (1.00)	-2.977	0.611	4.848	<0.001	***
		P. auritus (6)			
(Intercept)	-2.558	0.451	5.649		
PC1 (0.11)	-0.030	0.256	0.116	0.908	
PC2 (0.20)	-0.150	0.424	0.353	0.724	
PC3 (0.16)	0.115	0.400	0.286	0.775	
PC4 (0.13)	-0.065	0.326	0.197	0.844	
Deer present (0.12)	0.050	0.289	0.173	0.863	

Appendix J: Temporal Pass Plots for Richmond Park

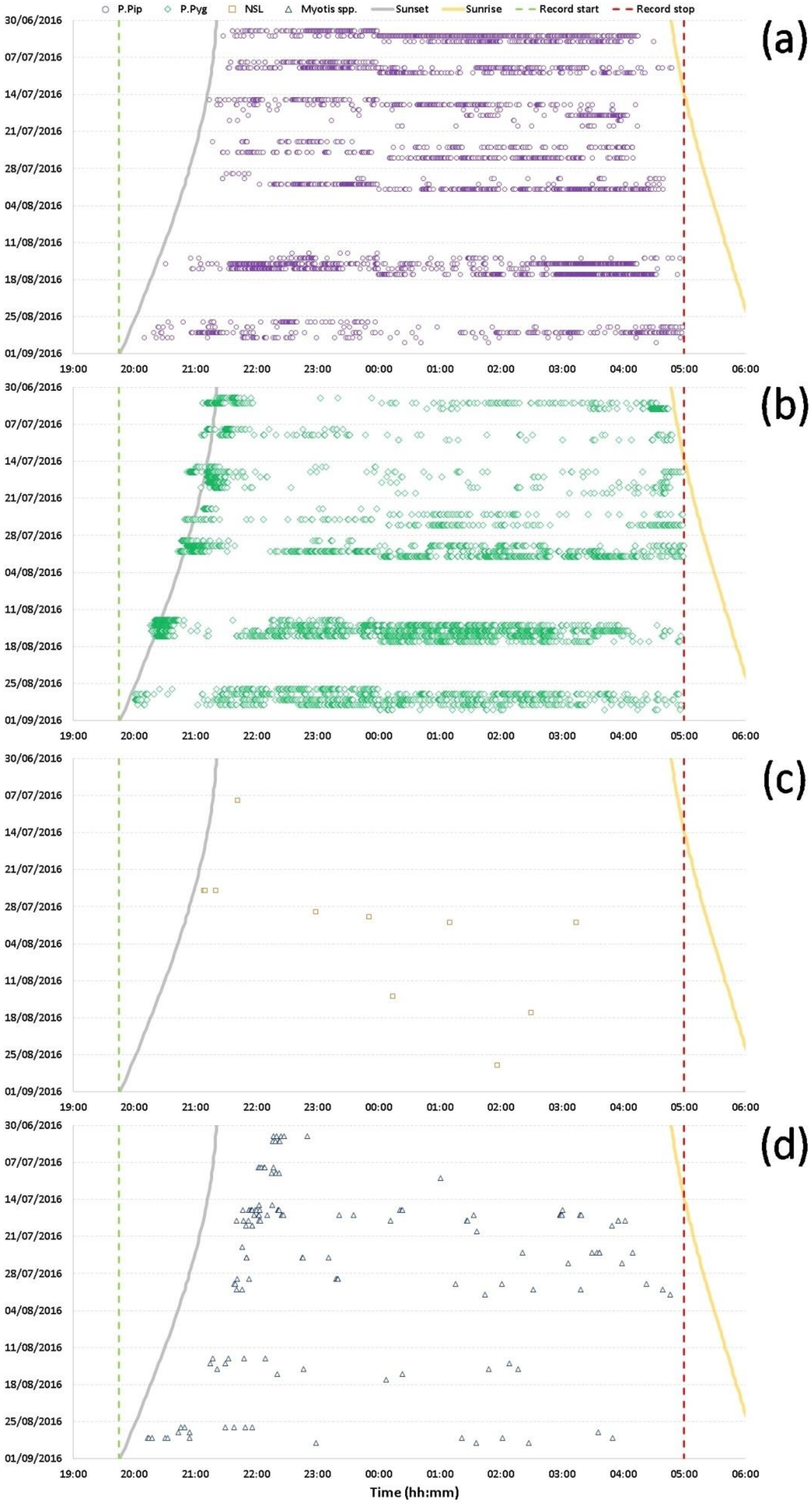


Figure J1. Temporal Pass Plots for site 1, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

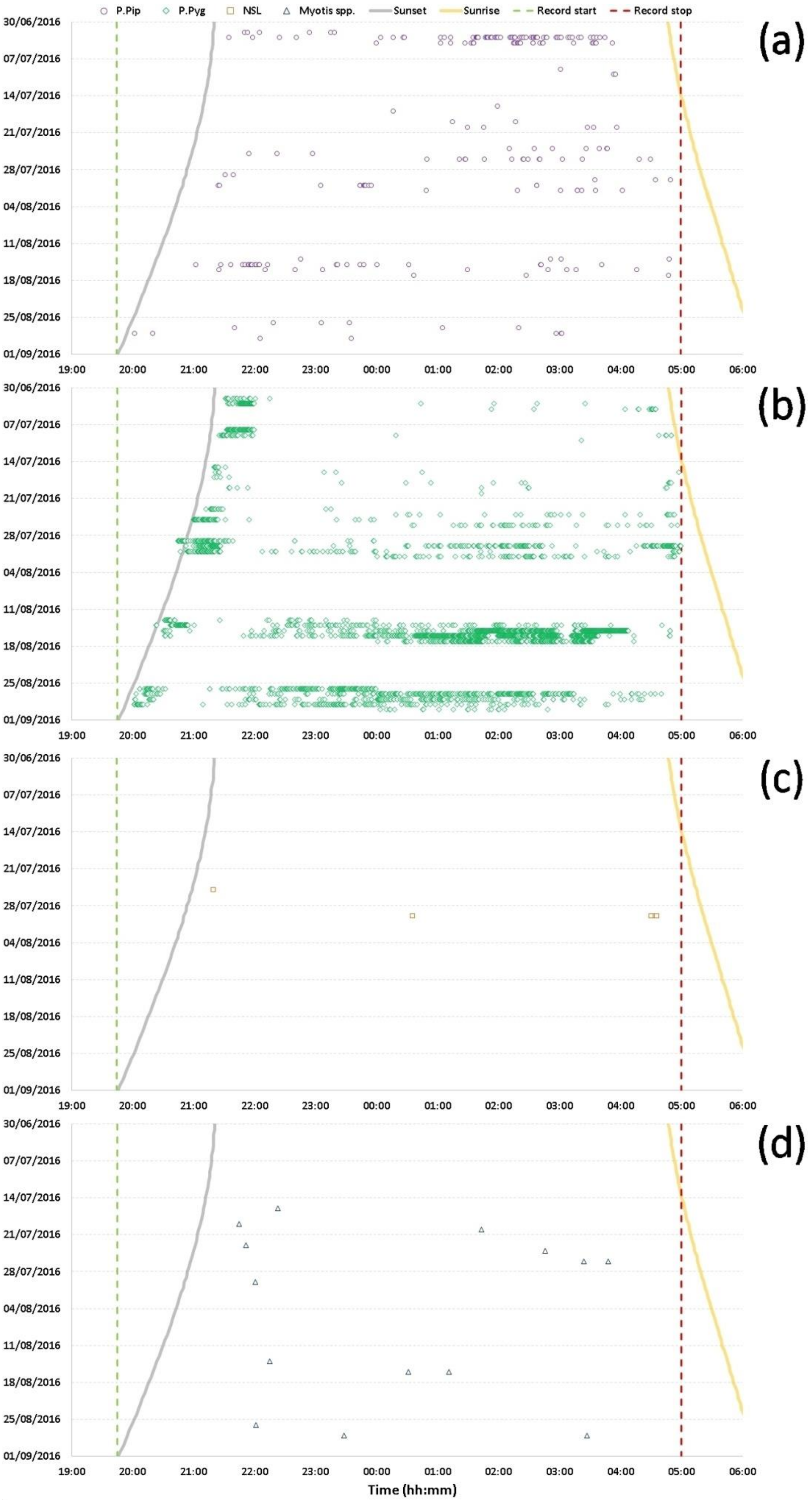


Figure J2. Temporal Pass Plots for site 2, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

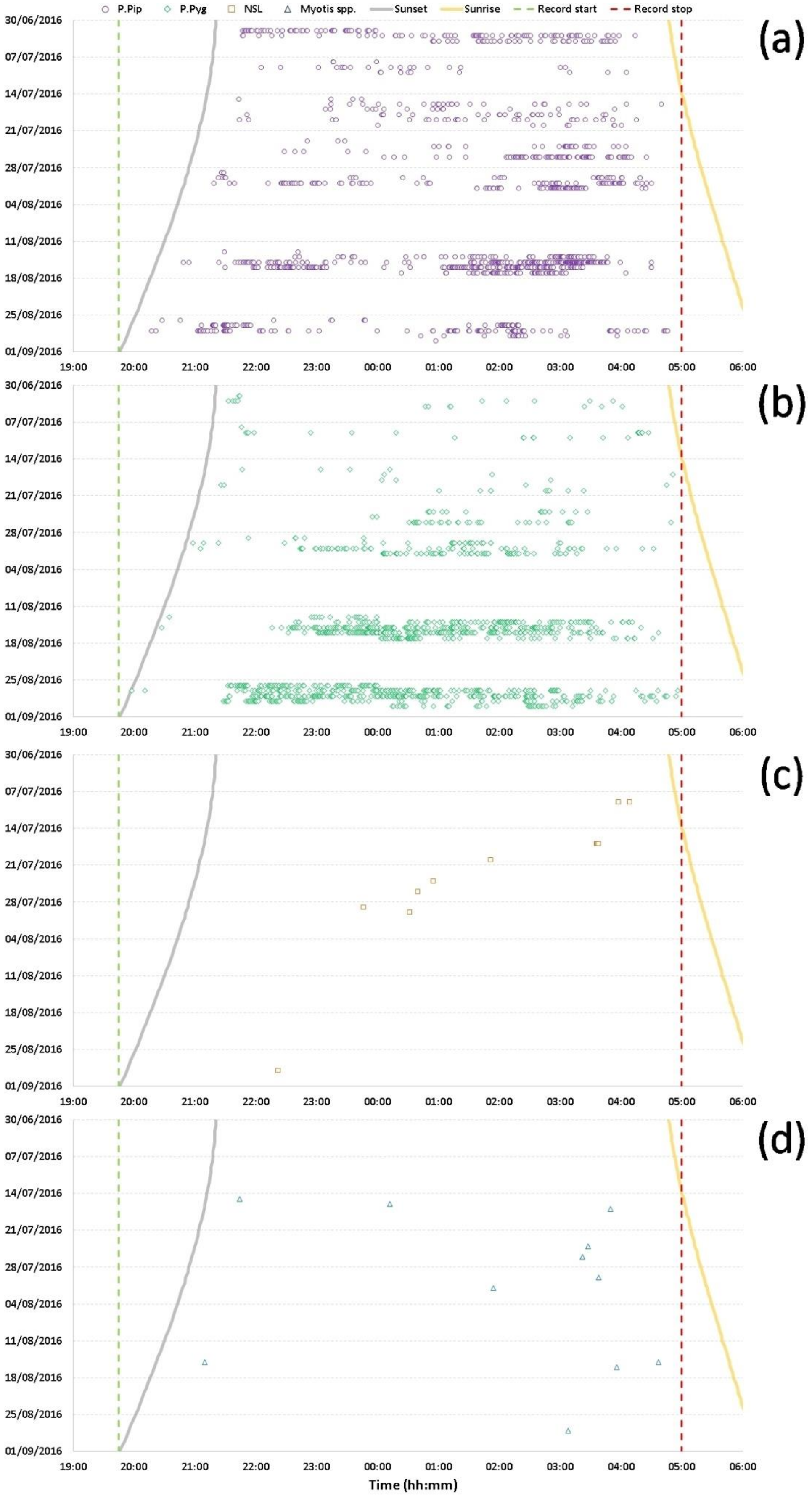


Figure J3. Temporal Pass Plots for site 3, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

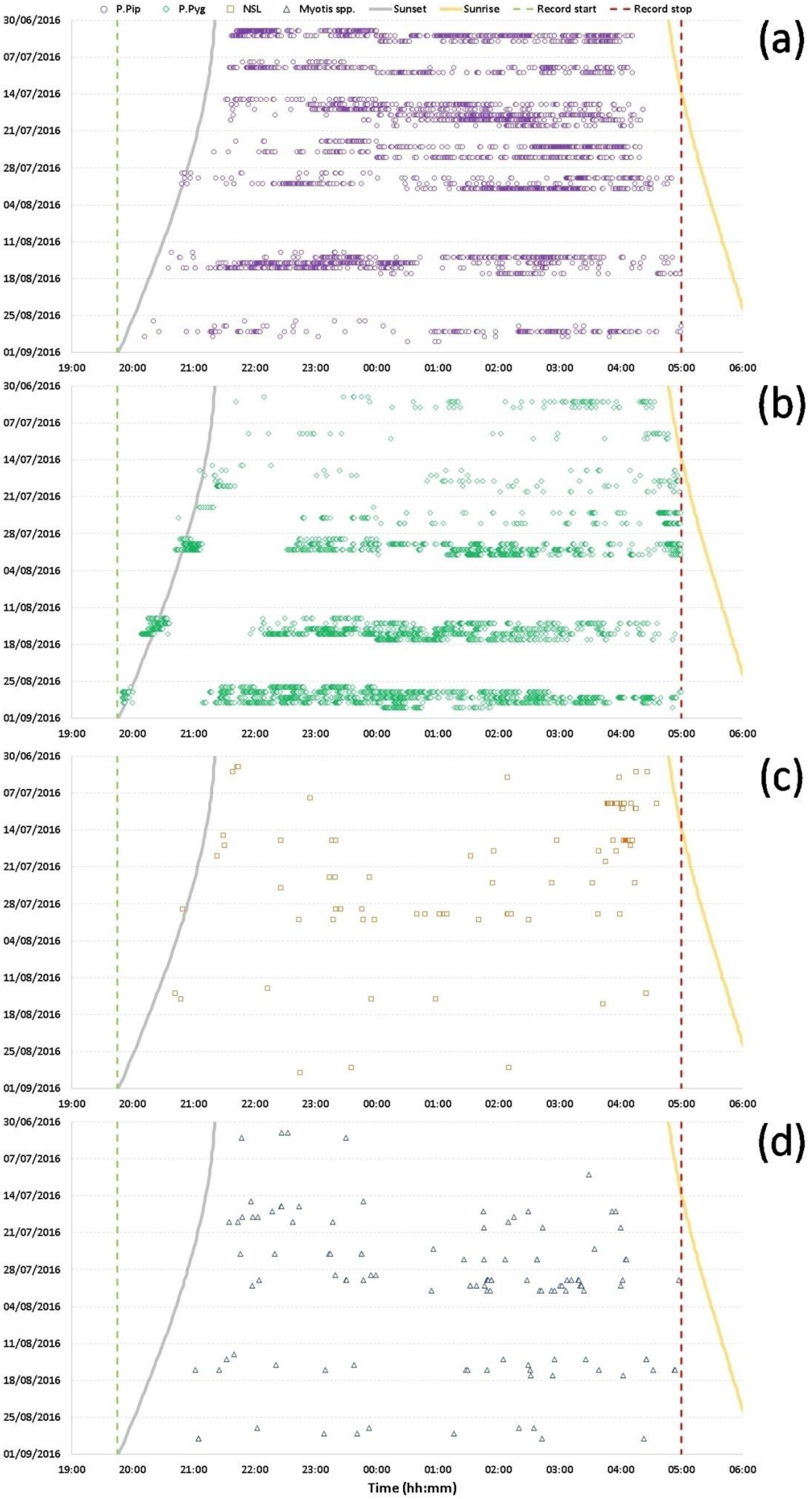


Figure J4. Temporal Pass Plots for site 4, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

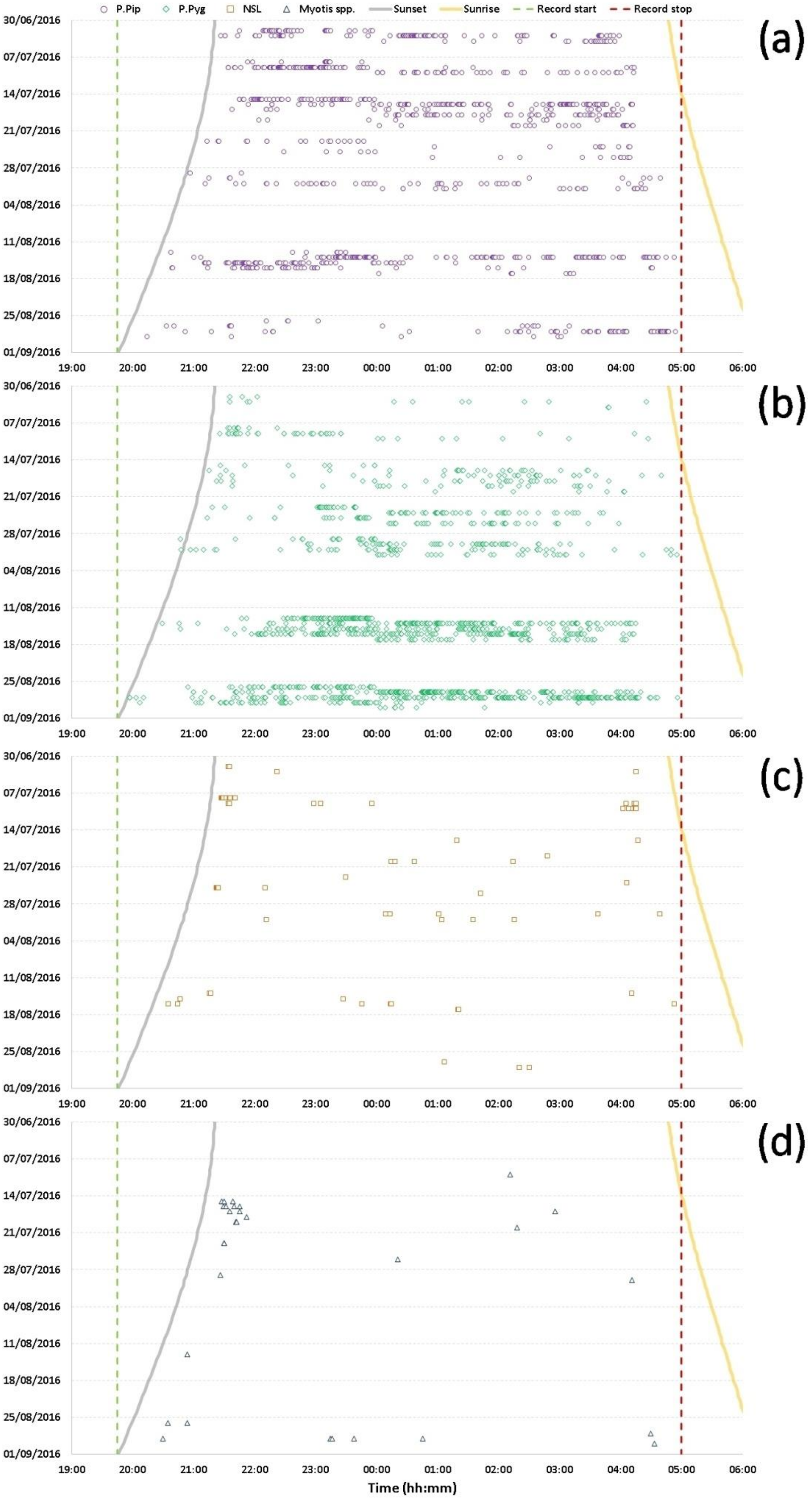


Figure J5. Temporal Pass Plots for site 5, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

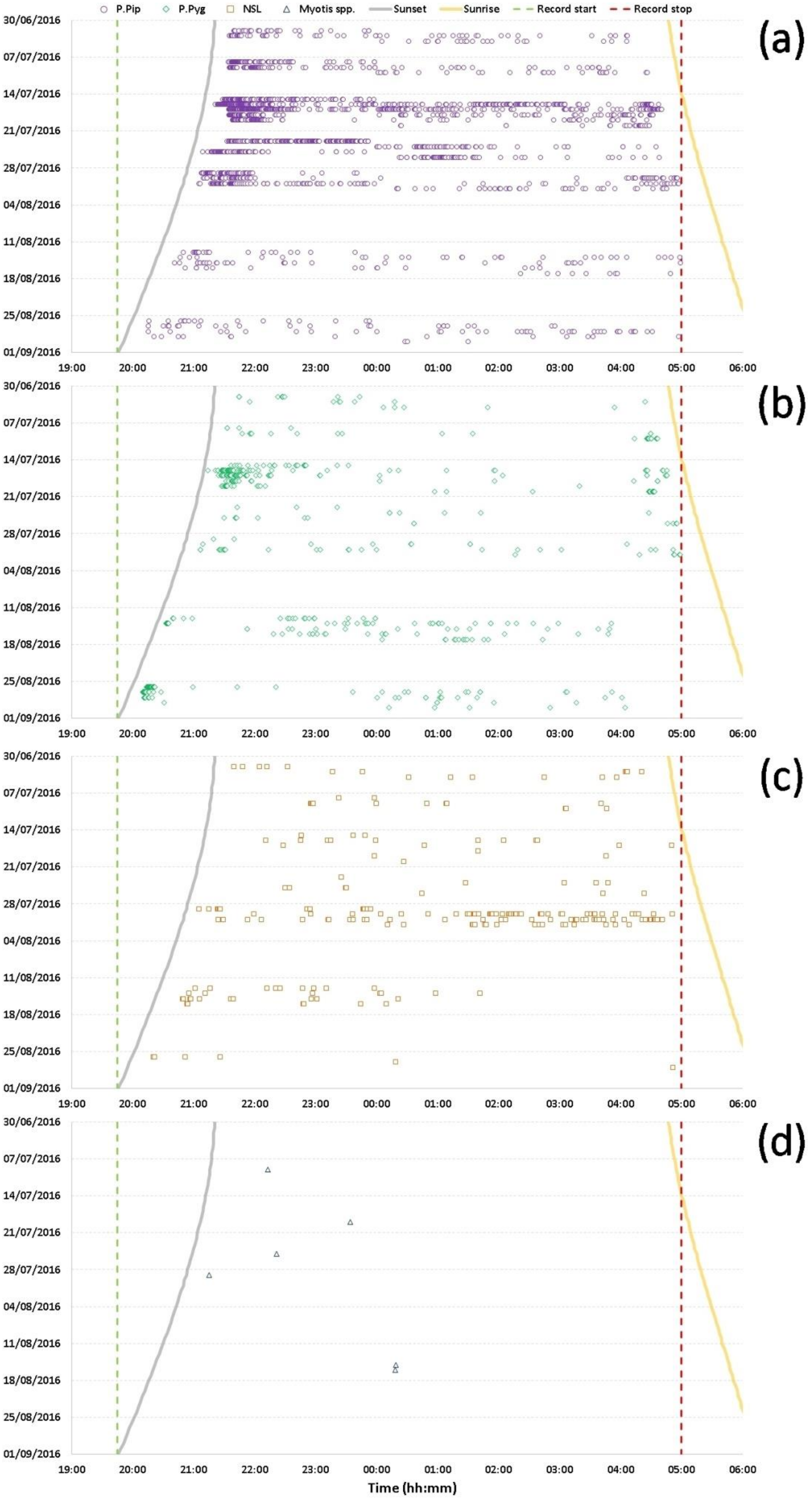


Figure J6. Temporal Pass Plots for site 6, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

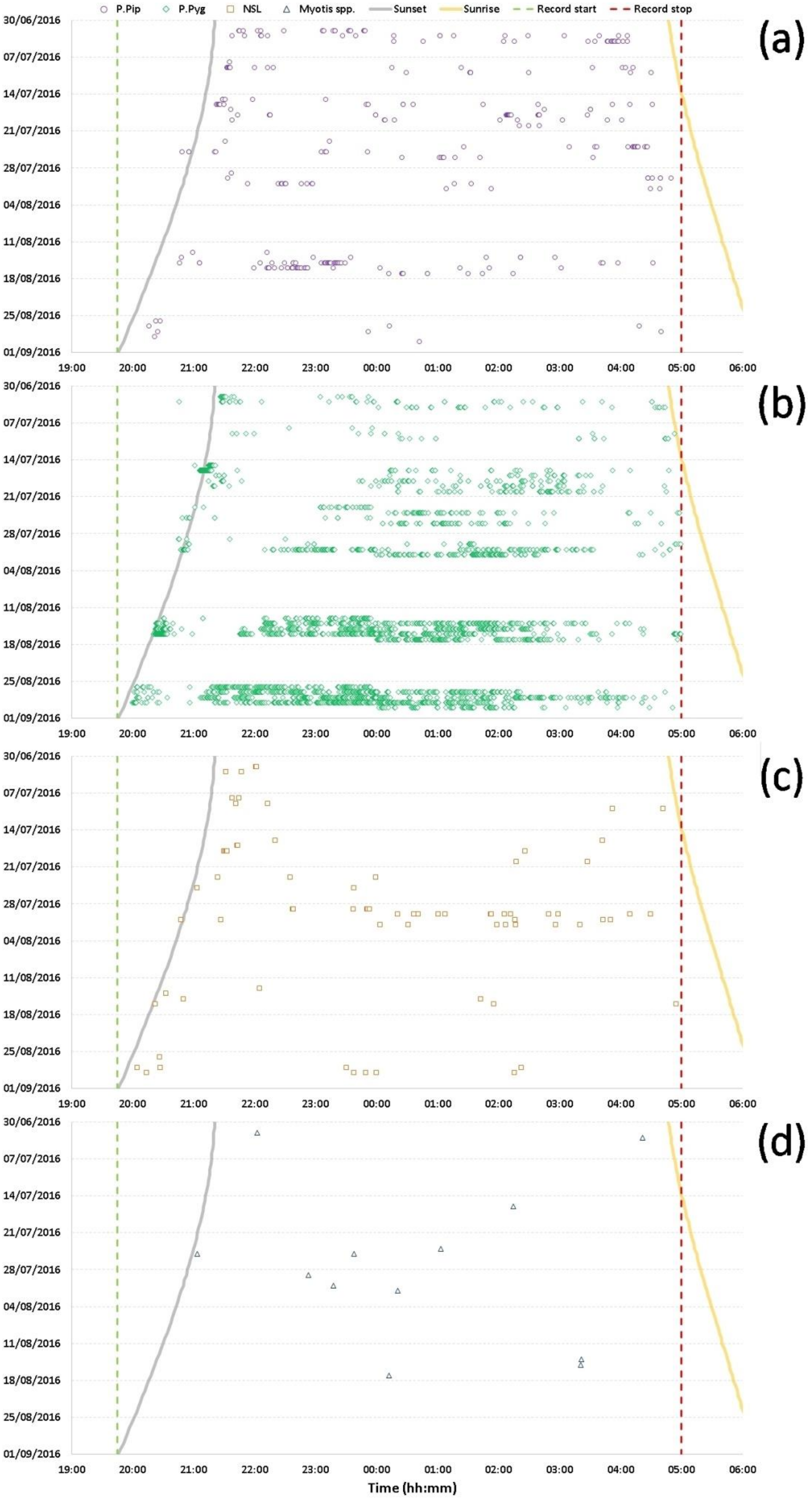


Figure J7. Temporal Pass Plots for site 7, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

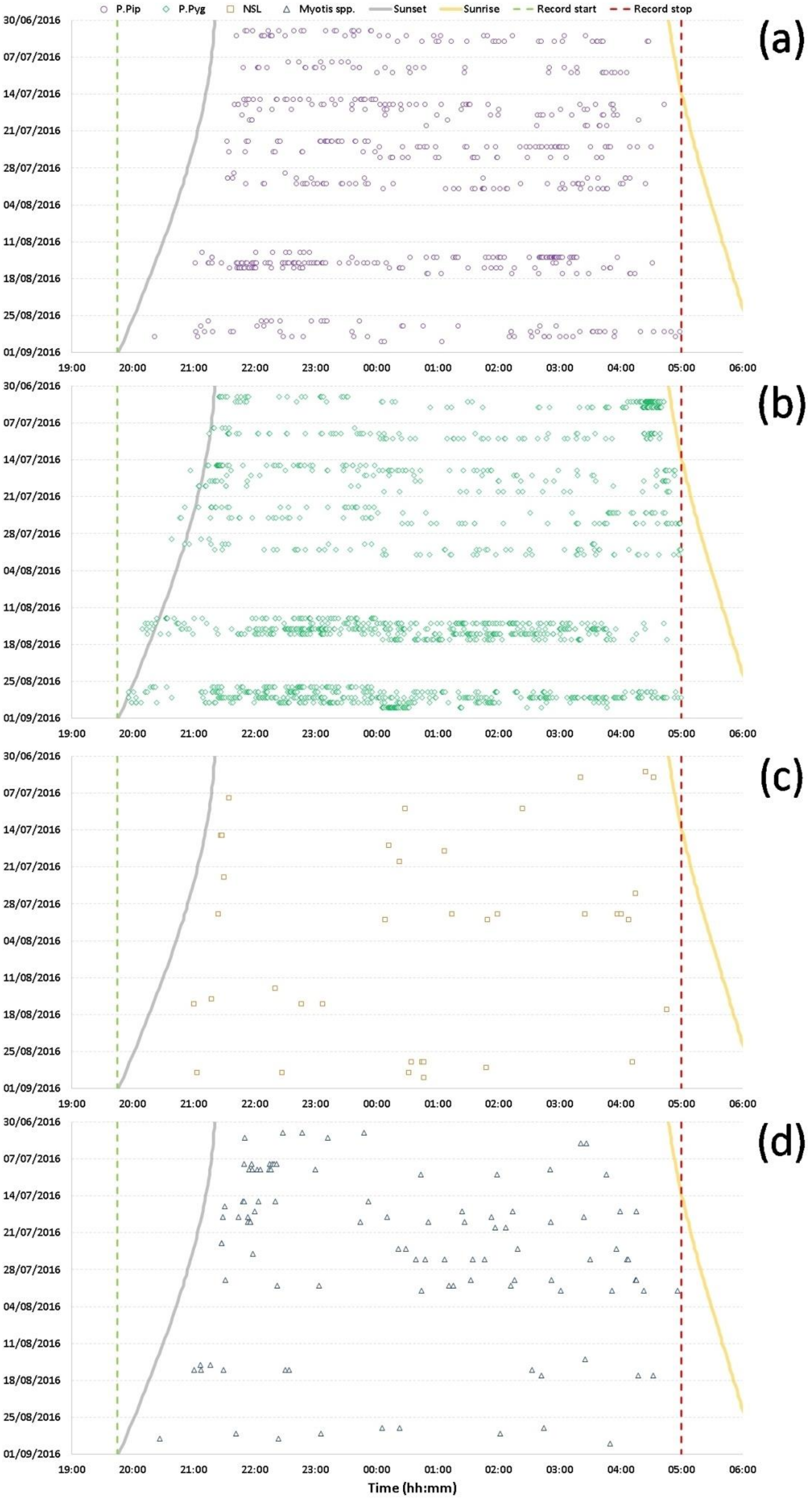


Figure J8. Temporal Pass Plots for site 8, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

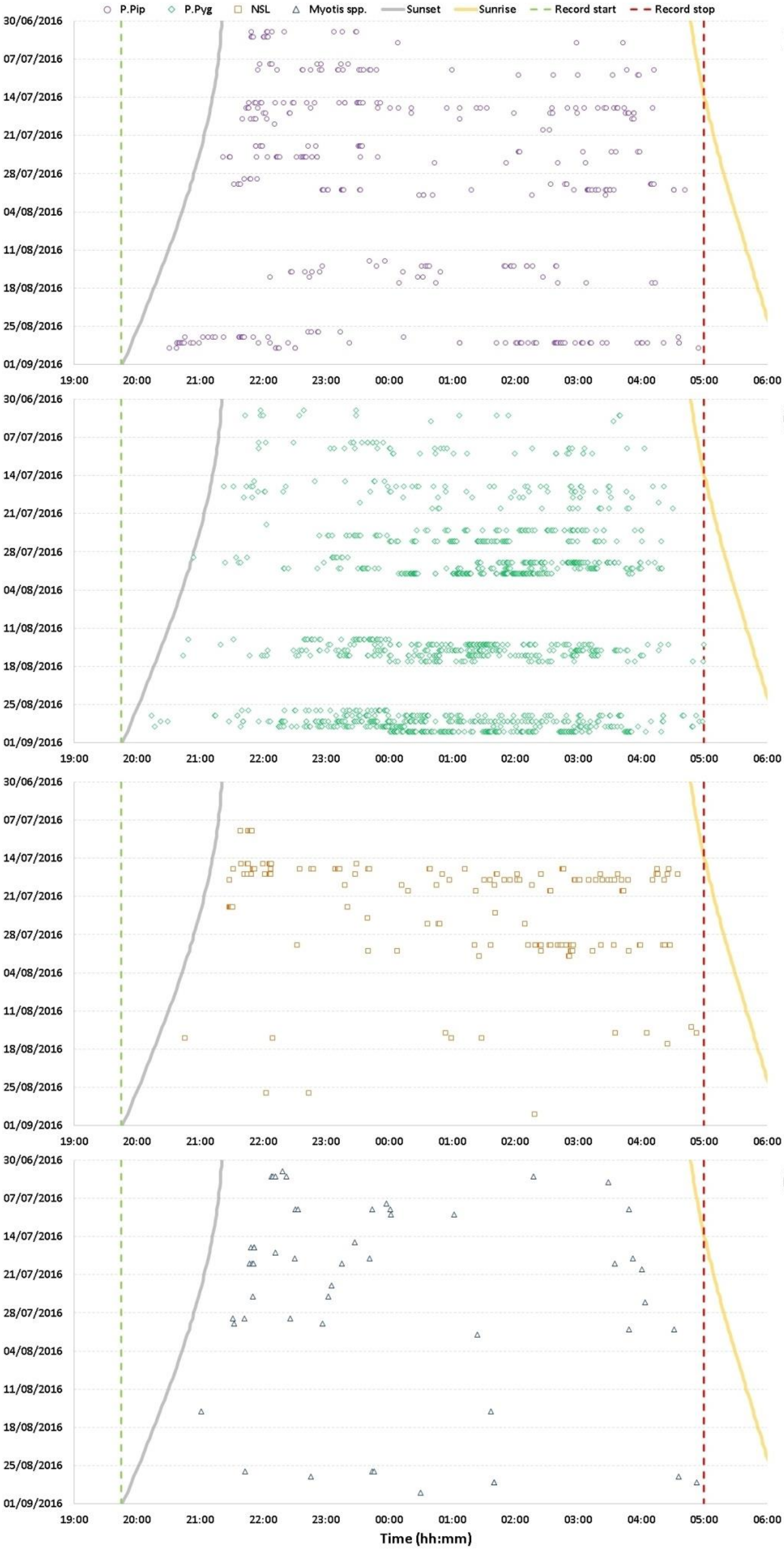


Figure J9. Temporal Pass Plots for site 9, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

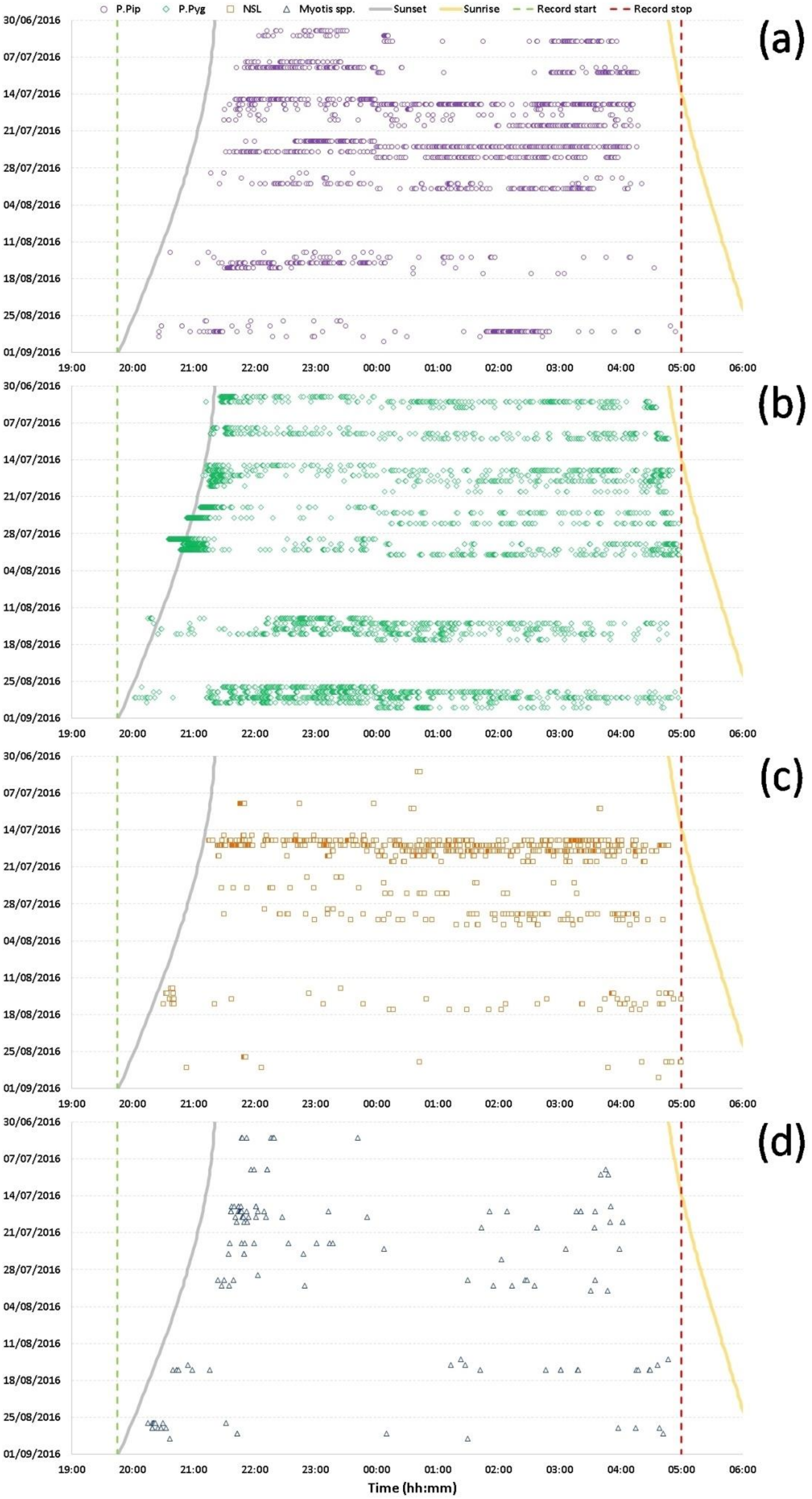


Figure J10. Temporal Pass Plots for site 10, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

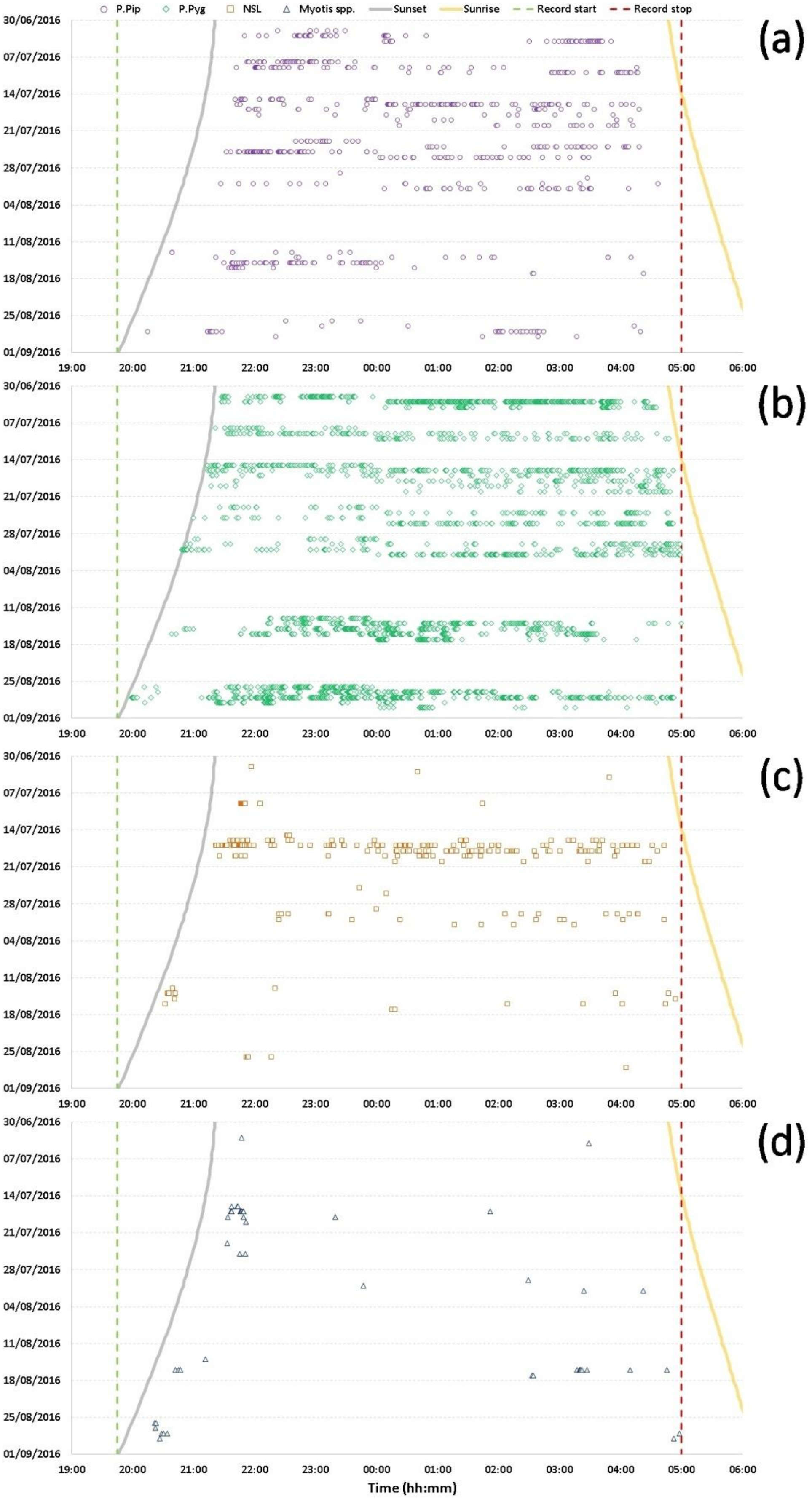


Figure J11. Temporal Pass Plots for site 11, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula*, *E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

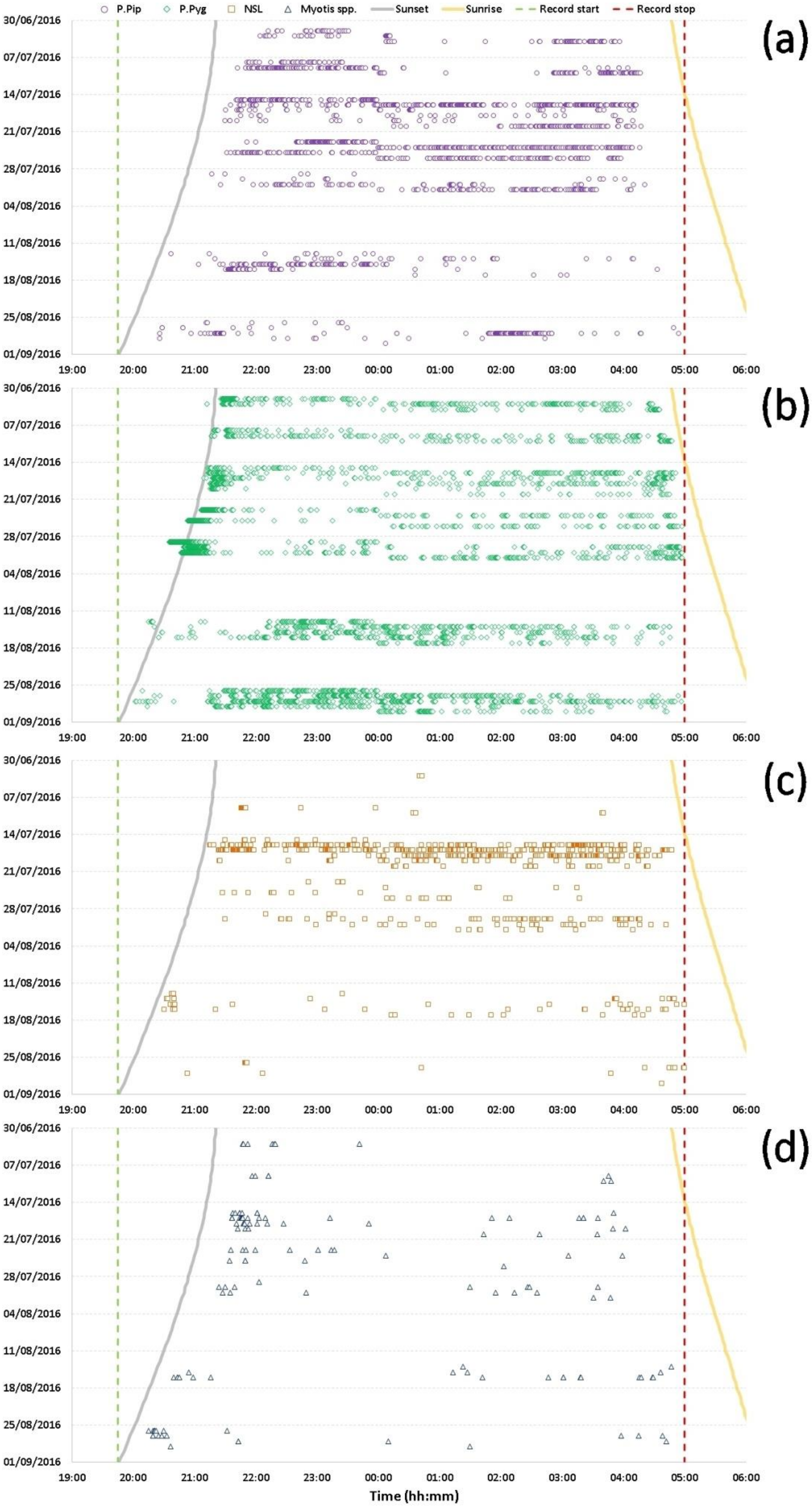


Figure J12. Temporal Pass Plots for site 12, Richmond Park for (a) *P. pipistrellus*, (b) *P. pygmaeus*, (c) *N. noctula, E. serotinus* & *N. leisleri*, and (d) *Myotis* spp.

Appendix K. Examples of Acoustic Indices Heatmaps for Hainich, 2017

Heatmaps produced in Excel 2016 (Microsoft Corp) by arranging acoustic index values in a grid with time on the x-axis and date on the y-axis. Conditional formatting was then applied to this grid using green as the lowest value, red as the highest and yellow as the 50% percentile. Heatmaps provided a convenient means of checking the entire survey period for data gaps and other issues that may not otherwise be apparent (Figure K1).

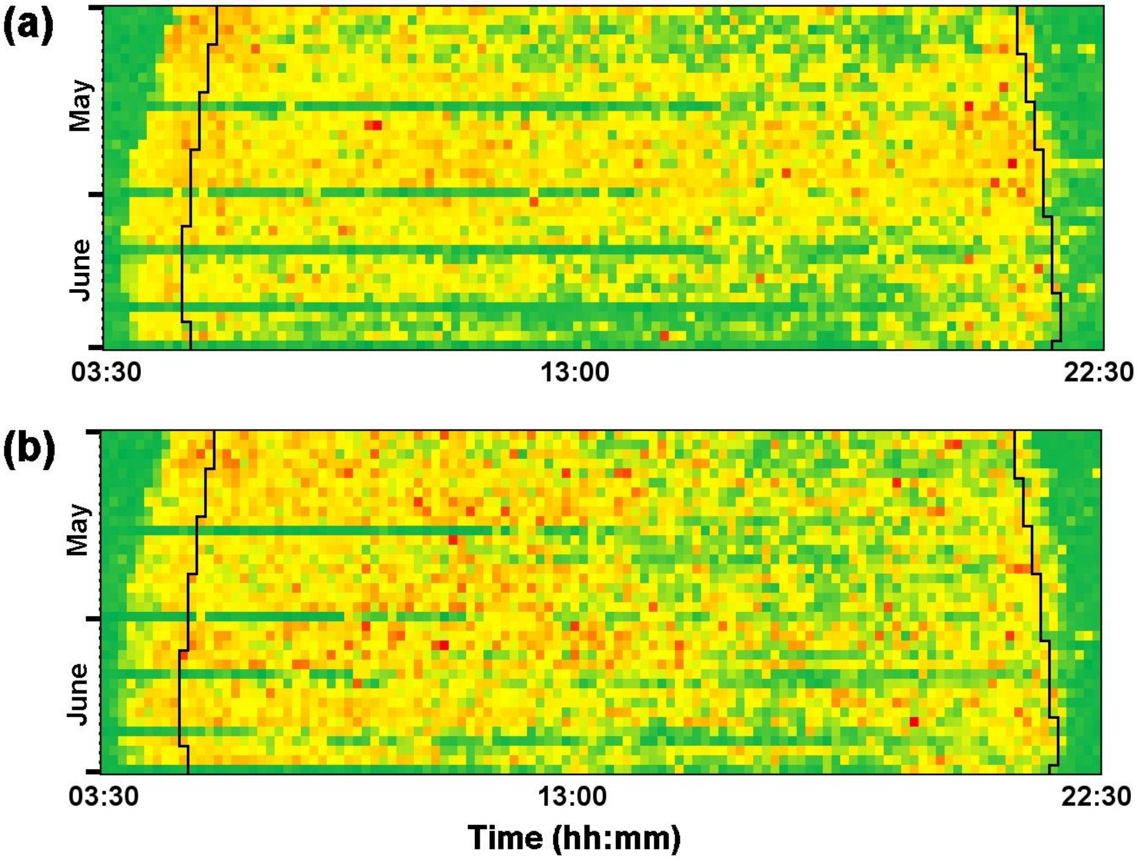


Figure K1. Examples of heatmaps used to inspect ACI values for gaps and anomalies shown for sites (a) GER24, and (b) GER29. Each pixel represents the ACI score of a 1-minute recording, taken every 10 minutes. Lower values (green) can be seen at night with higher values (red, orange and yellow) occurring at dawn chorus and during the day. Changes in seasonal activity, due to earlier sunrises and later sunsets (shown as vertical black lines), were also apparent as an inverse hourglass shape. Long green lines throughout the day represent uncharacteristically low index scores, usually indicating adverse weather conditions. Note: heatmaps are scaled based on highest and lowest values recorded within each site and are not directly comparable.

Appendix L. Ranking of Soundscape Elements by Acoustic Indices

Table L1. Results of acoustic indices tested on a sample group of 60 1-minute recordings; 30 containing biophony (ten each for dawn chorus, dusk chorus and individual birds) and 30 containing non-biophony (ten each of wind, aeroplane noise and silence). The numbers of each file type ranked in the top 30 results are listed for each index. Indices are shown from best (top) to worst (bottom) performance.

Index	Value	Dawn chorus	Dusk chorus	Individual bird(s)	Plane	Wind	Silence
NDSI	High	10	10	10	0	0	0
ACI	High	10	10	9	0	1	0
BI	High	10	9	8	0	3	0
AEI$^{(-50\ \mathrm{dBFS})}$	Low	10	10	3	0	7	0
AEI$^{(-70\ \mathrm{dBFS})}$	Low	9	10	3	0	7	1
H_t	High	3	5	10	0	2	10
H_t	Low	7	5	0	10	8	0

Appendix M. Bird Species Richness Assessments for Acoustic Indices

Table M1. Results of bird species richness assessments performed for the 30 1-minute recordings made in Hainich, 2016, used to evaluate acoustic index performance.

Date	Time	Site	Type	Author assessment*	L. Nouri assessment*	Agreed richness
07/05	04:10	GER34	Dawn	CC, C?, P?, TM, TT, ??, ??	CC, C?, PA, PM, SA, TM, TT, ??	8
07/05	04:10	GER33	Dawn	C?, CP, TM, TP, TT, ??	CC, C?, CP, TM, TP, TT	6
07/05	04:10	GER28	Dawn	Co, FC, PC, P?, TM, TT	Co, FC, PA, PC, TM, TT	6
07/05	04:20	GER06	Dawn	C?, ER, FC, P?, TM, TT	C?, ER, FC, PM, TM, TT	6
08/05	04:20	GER35	Dawn	ER, FC, P?, TM, ??	Cy, C?, FC, SA, TM	5
09/05	04:10	GER02	Dawn	ER, FC, P?, TM, TP	Cy, ER, FC, TM, TP	5
17/05	04:10	GER07	Dawn	ER, FC, PM, P?, RI, TM, TP	FC, PA, PM, Py, SA, TM, TP	7
21/05	04:10	GER05	Dawn	Cy, PM, TM	Cy, ER, TM	3
21/05	04:10	GER13	Dawn	C?, ER, FC, TP, TT, ??	ER, FC, PP, SA, TP, TT	6
21/05	04:10	GER04	Dawn	C?, ER, FC, TM, ??	C?, ER, FC, P?, TM	5
08/05	13:50	GER07	Bird(s)	RR, TM, TT	RR, TM, TT	3
15/05	20:00	GER01	Bird(s)	ER, TM	ER, TM	2
17/05	12:10	GER07	Bird(s)	P?	PA	1
20/05	12:40	GER07	Bird(s)	ER, ??	ER, SA	2
31/05	19:50	GER01	Bird(s)	FC	FC	1
11/06	02:40	GER02	Bird(s)	TM, TP	TP	2
16/06	20:00	GER25	Bird(s)	TP	TP	1
16/06	20:10	GER01	Bird(s)	ER	ER	1
30/06	19:50	GER14	Bird(s)	FC	FC	1
03/07	19:50	GER34	Bird(s)	TT	TT	1
31/05	20:10	GER04	Dusk	DM, ER, FC, TM, ??	DM, ER, FC, TM, ??	5
01/06	20:10	GER28	Dusk	ER, PC, TM, TP, ??	ER, PC, P?, TM, TP	5
04/06	19:50	GER02	Dusk	ER, P?, TM, TP, ??	DM, ER, SA, TM, TP, ??	6
05/06	20:10	GER21	Dusk	ER, FC, SE, TM, TP	ER, FC, SE, TM, TP	5
05/06	20:20	GER33	Dusk	TM, TP, TT	TM, TP, TT	3
07/06	20:00	GER06	Dusk	BB, ER, TM, TP	BB, ER, TM, TP	4
14/06	20:00	GER05	Dusk	FC, P?, TP	FC, P?, TP, ??	4
16/06	19:50	GER07	Dusk	ER, FC, P?, TP, ??	CC, FC, SA, TP, ??	5
16/06	19:50	GER25	Dusk	ER, P?, TM, TP	CC, ER, TM, TP	4
17/06	20:20	GER34	Dusk	ER, TM, TP, ??	ER, TM, TP, p?	4

* BB (*Buteo buteo*), CC (*Coccothraustes coccothraustes*), Co (*Corvus corone*), Cy (*Cyanistes caeruleus*), C? (*Certhiidae* sp.), DM (*Dendrocopos major*), ER (*Erithacus rubecula*), FC (*Fringilla coelebs*), PA (*Periparus ater*), PC (*Phylloscopus collybita*), PM (*Parus major*), PP (*Phoenicurus phoenicurus*), Py (*Pyrrhula pyrrhula*), P? (*Paridae* sp.), p? (*Parulidae* sp.), RI (*Regulus ignicapilla*), SA (*Sylvia atricapilla*), SE (*Sitta europaea*), TM (*Turdus merula*), TP (*Turdus philomelos*), TT (*Troglodytes troglodytes*), RR (*Regulus regulus*), ?? (Unknown sp.).

Appendix N. Effect of Distance on Acoustic Indices

To assess the effect of distance, index scores were calculated for recordings of playback calls of the European robin (90 dB) made at set distances (2 m, 4 m, 8 m, 16 m and 32 m) in Richmond Park in 2016 (Section 2.5). Although these recordings were made using the AURITA devices in open park woodland, attenuation in recordings made by the Lunilettronik Soundscape Explorers in the denser forest of Hainich would more likely be even greater than in Richmond (Trimpop and Mann, 2014). As sound attenuation is a physical law, the same principles, if not the exact index values, would apply equally to Hainich. Recordings were of equal length (3.4s) and chosen to contain very little background noise; acoustic indices were also calculated using the frequency band in which only the robin call was present (2.4 to 9 kHz) to further limit possible interference from other sources. Index results of recordings were then plotted against the distance at which they were recorded and fitted with a logarithmic regression line (Figure N1).

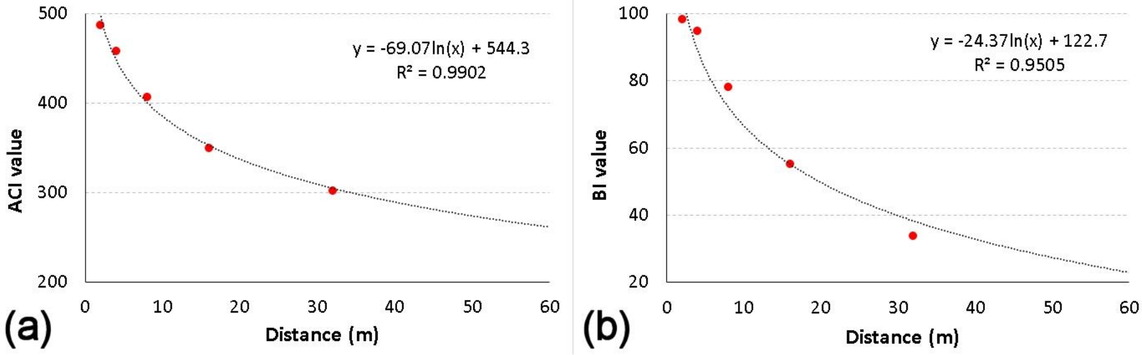


Figure N1. The effect of distance of vocalisations from recording devices has on acoustic indices for (a) ACI, and (b) BI. Index values were calculated based on the same recording, the song of a European robin, played at the same SPL at different distances from the recording device. The trendline (dotted black line) reflects the logarithmic attenuation of sound, extrapolated to a distance of 60 m.

In both cases, index values displayed almost perfect logarithmic relationships with distance (R^2=0.99 and R^2=0.95 for ACI and BI, respectively). Higher index values thus appear to represent a mixture of both acoustic activity and the distance from the recorder at which this activity took place. Indeed, this may explain some of the variation seen in Figure 4.3, where bird species were identified in recordings irrespective of their distance. Although the relationship between acoustic indices and bird diversity metrics may be subject to some variation due to attenuation effects, this analysis suggests that index scores will reflect higher levels of activity within, or nearby, the areas of interest.

Appendix O: Correlation Table of Site Variables for Hainich

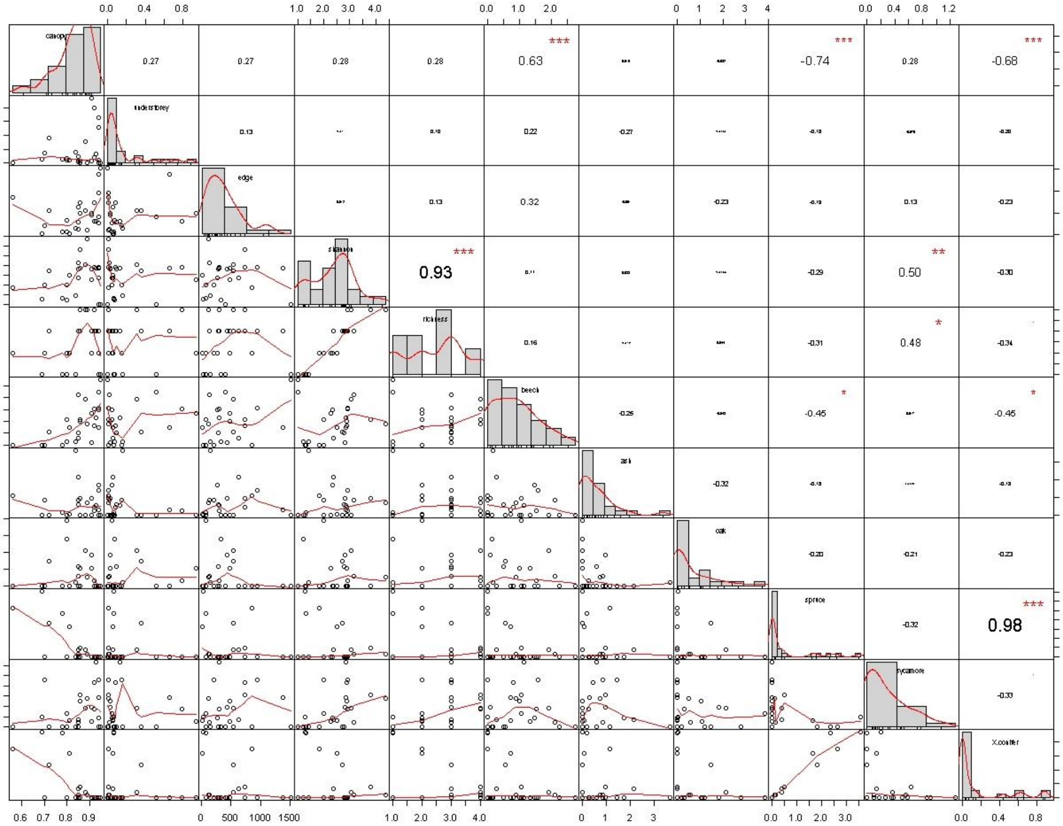


Figure O1. Correlation chart of explanatory variables used in acoustic index models, from left to right: canopy cover (%), understorey cover (%), distance to forest edge (m), tree species true Shannon diversity, tree species richness, the total basal areas (m^2) of beech, ash, oak, spruce and sycamore within each plot, and the amount of conifer in each plot (%).

Appendix P: Acoustic Indices GLMM Results for Hainich

Table P1. Results of GLMMs examining the effects of true Shannon diversity and tree species composition on ACI scores for dawn, daytime and dusk periods. Effect sizes are directly comparable as input variables were centred and standardised to one standard deviation. Significant results are presented in bold.

Characteristic	Estimate	Std err	Z value	95% CI		*Pr(>|z|)*
				Lower	Upper	
ACI (Dawn)						
Intercept	**7.004**	**0.003**	**2234.7**	**6.998**	**7.011**	**<0.001**
True Shannon diversity	**0.010**	**0.003**	**3.1**	**0.004**	**0.017**	**0.002**
Understorey cover	-0.002	0.003	-0.7	-0.008	0.004	0.507
Distance to edge	-0.002	0.003	-0.7	-0.008	0.004	0.461
Ash	0.000	0.004	0.1	-0.007	0.008	0.957
Beech	-0.006	0.004	-1.6	-0.014	0.001	0.108
Oak	-0.002	0.004	-0.6	-0.010	0.005	0.578
Norway spruce	0.001	0.004	0.2	-0.008	0.010	0.845
Sycamore	**-0.012**	**0.004**	**-3.0**	**-0.019**	**-0.004**	**0.002**
ACI (Daytime)						
Intercept	**6.991**	**0.003**	**2627.4**	**6.986**	**7.000**	**<0.001**
True Shannon diversity	**0.009**	**0.002**	**3.9**	**0.004**	**0.013**	**<0.001**
Understorey cover	-0.001	0.002	-0.6	-0.005	0.003	0.553
Distance to edge	-0.002	0.002	-1	-0.006	0.002	0.298
Ash	-0.001	0.003	-0.2	-0.006	0.005	0.806
Beech	-0.003	0.003	-1.3	-0.009	0.002	0.193
Oak	0.003	0.003	1	-0.003	0.008	0.333
Norway spruce	-0.000	0.003	-0.1	-0.006	0.006	0.915
Sycamore	**-0.008**	**0.003**	**-3.2**	**-0.014**	**-0.003**	**0.002**
ACI (Dusk)						
Intercept	**6.977**	**0.002**	**3031.8**	**6.972**	**6.981**	**<0.001**
True Shannon diversity	**0.007**	**0.002**	**3.7**	**0.003**	**0.011**	**<0.001**
Understorey cover	0.002	0.002	0.9	-0.002	0.005	0.370
Distance to edge	-0.002	0.002	-1	-0.006	0.001	0.304
Ash	-0.001	0.002	-0.3	-0.005	0.004	0.756
Beech	**-0.007**	**0.002**	**-2.9**	**-0.011**	**-0.002**	**0.004**
Oak	0.001	0.002	0.4	-0.004	0.006	0.672
Norway spruce	-0.002	0.003	-0.9	-0.008	0.003	0.382
Sycamore	**-0.007**	**0.002**	**-2.9**	**-0.011**	**-0.002**	**0.004**

Table P2. Results of GLMMs examining the effects of true Shannon diversity and tree species composition on BI scores for dawn, daytime and dusk periods. Effect sizes are directly comparable as input variables were centred and standardised to one standard deviation. Significant results are presented in bold.

Characteristic	Estimate	Std err	Z value	95% CI		*Pr(>|z|)*
				Lower	Upper	
BI (Dawn)						
Intercept	**3.892**	**0.021**	**186.4**	**3.851**	**3.933**	**<0.001**
True Shannon diversity	**0.088**	**0.022**	**3.96**	**0.045**	**0.132**	**<0.001**
Understorey cover	0.011	0.021	0.52	-0.030	0.052	0.606
Distance to edge	-0.017	0.021	-0.83	-0.058	0.023	0.408
Ash	0.040	0.027	1.5	-0.012	0.092	0.133
Beech	-0.008	0.026	-0.29	-0.059	0.044	0.773
Oak	0.006	0.026	0.23	-0.045	0.057	0.818
Norway spruce	0.013	0.030	0.41	-0.047	0.072	0.680
Sycamore	**-0.081**	**0.026**	**-3.09**	**-0.133**	**-0.030**	**0.002**
BI (Daytime)						
Intercept	**3.659**	**0.027**	**135.94**	**3.606**	**3.712**	**<0.001**
True Shannon diversity	**0.093**	**0.024**	**3.93**	**0.047**	**0.140**	**<0.001**
Understorey cover	0.011	0.023	0.51	-0.033	0.056	0.612
Distance to edge	-0.027	0.022	-1.22	-0.070	0.016	0.224
Ash	0.024	0.029	0.84	-0.032	0.080	0.398
Beech	-0.008	0.028	-0.28	-0.063	0.047	0.776
Oak	0.016	0.028	0.58	-0.038	0.071	0.561
Norway spruce	0.008	0.032	0.25	-0.056	0.072	0.805
Sycamore	**-0.083**	**0.028**	**-2.97**	**-0.139**	**-0.028**	**0.003**
BI (Dusk)						
Intercept	**3.594**	**0.028**	**129.37**	**3.540**	**3.649**	**<0.001**
True Shannon diversity	**0.100**	**0.025**	**4.04**	**0.052**	**0.149**	**<0.001**
Understorey cover	0.035	0.024	1.5	-0.011	0.081	0.134
Distance to edge	-0.038	0.023	-1.65	-0.084	0.007	**0.098**
Ash	0.014	0.030	0.47	-0.044	0.072	0.638
Beech	-0.044	0.029	-1.52	-0.102	0.013	0.130
Oak	0.003	0.029	0.09	-0.054	0.060	0.929
Norway spruce	0.005	0.034	0.16	-0.061	0.072	0.876
Sycamore	**-0.077**	**0.029**	**-2.63**	**-0.135**	**-0.020**	**0.009**

Appendix P

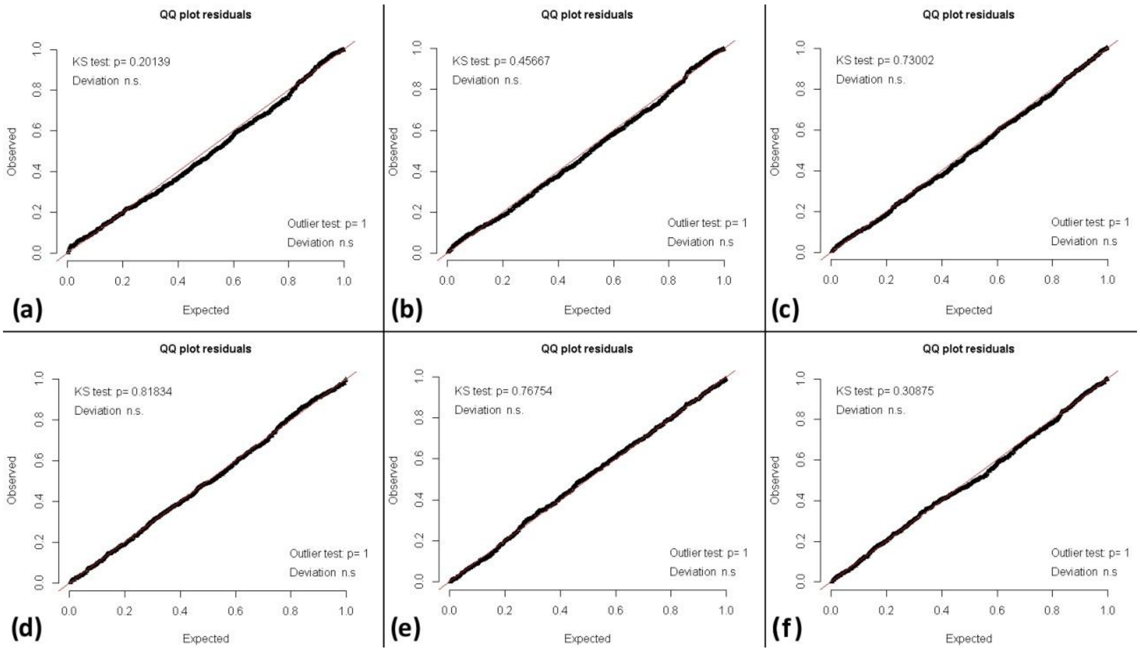


Figure P1. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores of GLMMs assessing tree species true Shannon diversity and tree species composition for ACI at (a) dawn (b) daytime and (c) dusk, and BI at (d) dawn (e) daytime and (e) dusk. Validation tests were generated with *DHARMa* using 10,000 simulations.

Appendix Q: Boxplots of Acoustic Indices Median Values for Hainich

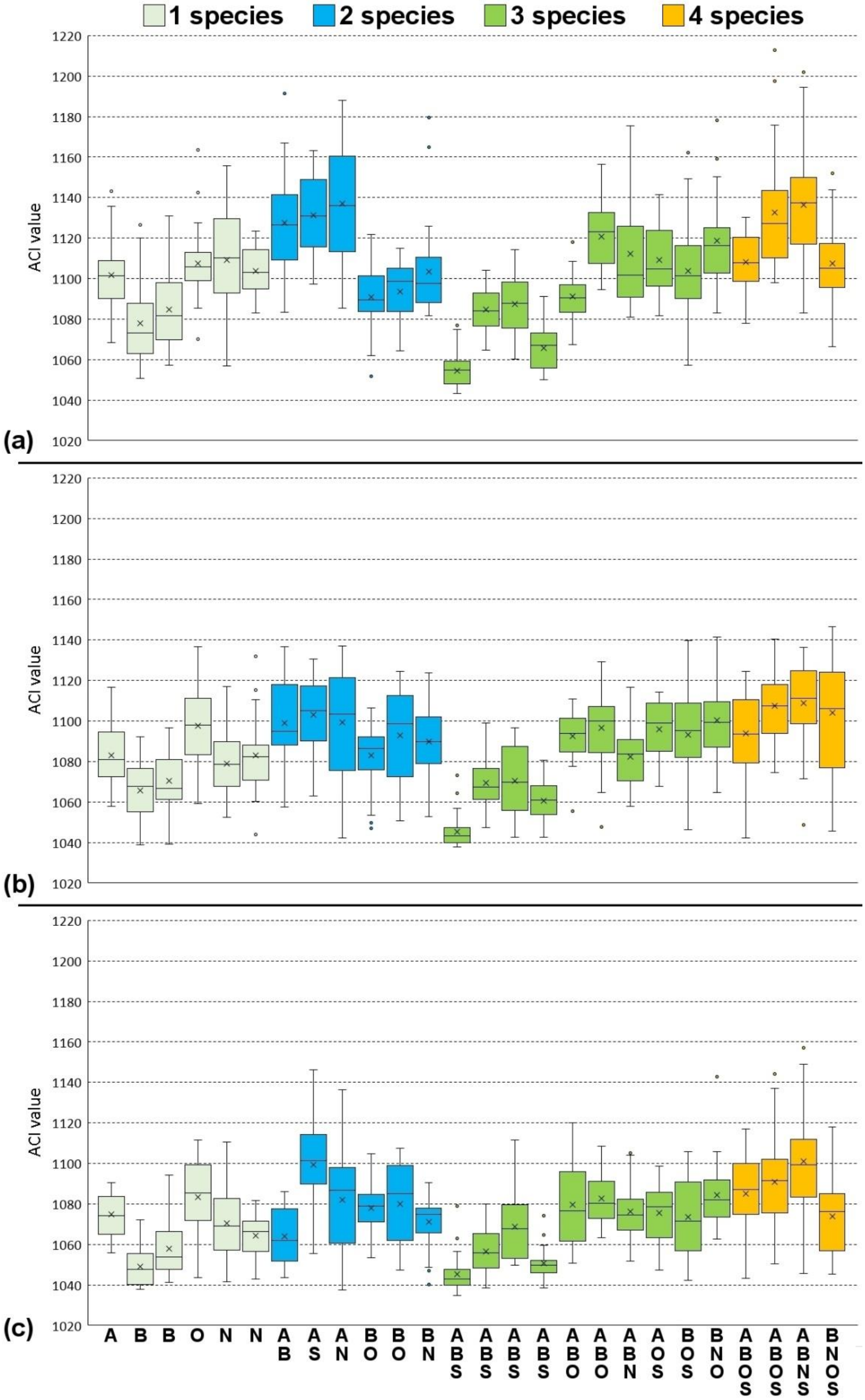


Figure Q1. Median ACI scores at survey locations for 30 days during (a) dawn, (b) daytime, and (c) dusk periods. Means (x), exclusive medians (lines) and interquartile ranges shown with tree species mixes listed below boxplots (A = ash, B = beech, N = Norway spruce, O = oak and S = Sycamore).

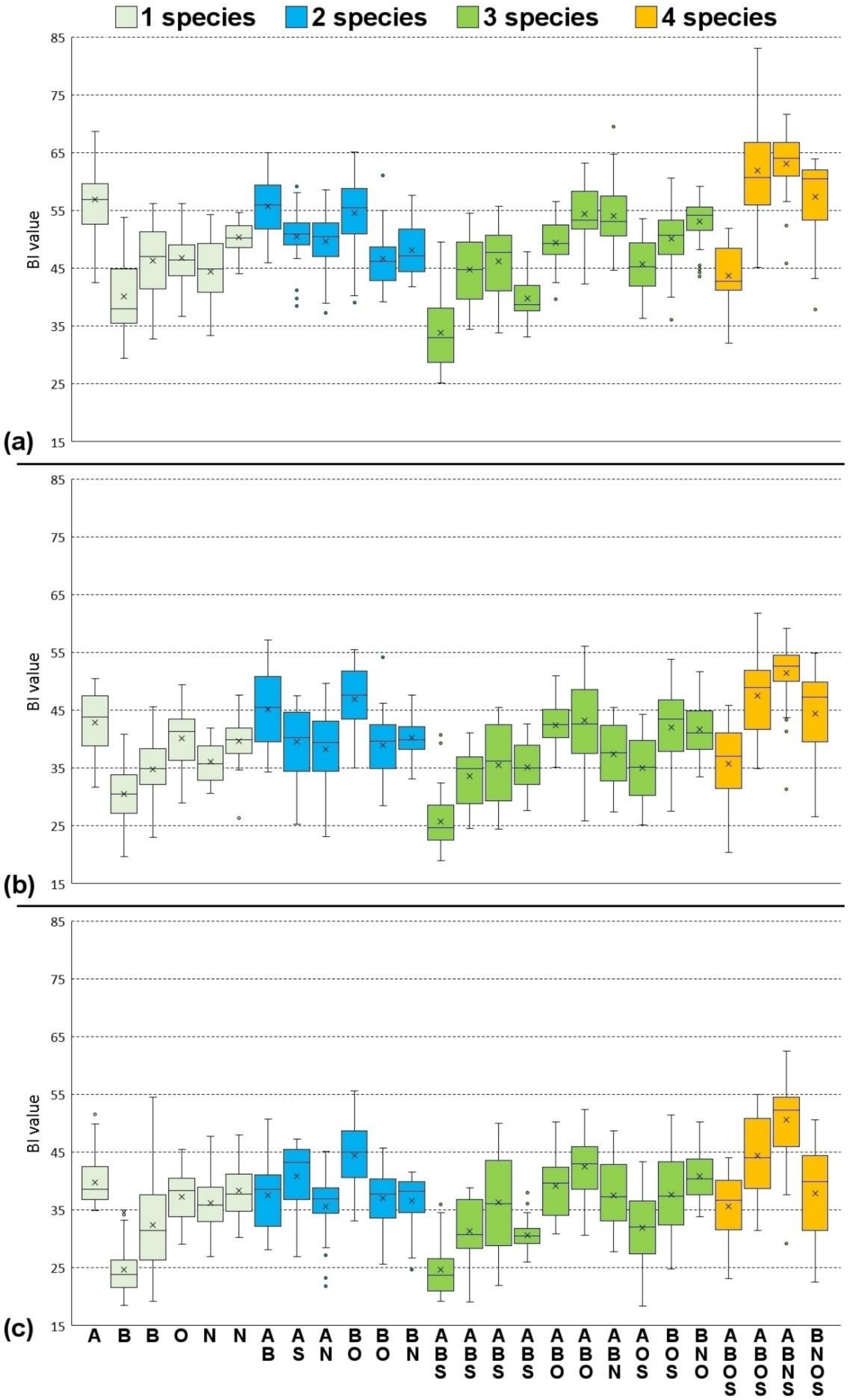


Figure Q2. Median BI scores at survey locations for 30 days during (a) dawn, (b) daytime, and (c) dusk periods. Means (x), exclusive medians (lines) and interquartile ranges shown with tree species mixes listed below boxplots (A = ash, B = beech, N = Norway spruce, O = oak and S = Sycamore).

Appendix R. Acoustic Indices Heatmaps for Knepp, 2018

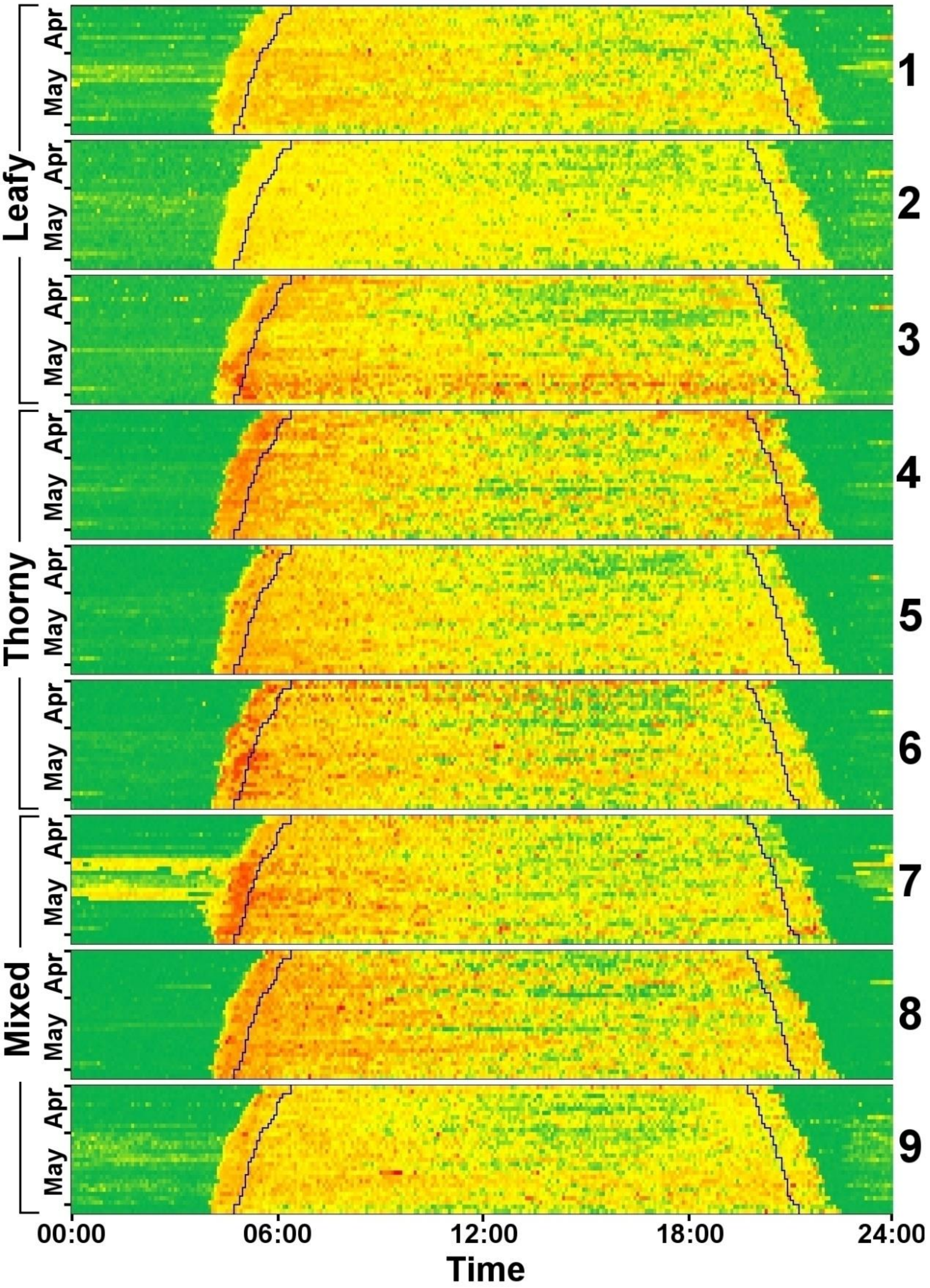


Figure R1. Heatmaps of ACI scores of 1-minute recordings, taken every 5 minutes. Conditional formatting used green as the lowest value, red as the highest and yellow as the 50% percentile with sunrises and sunsets shown as black lines. Note: heatmaps are scaled based on the highest and lowest values recorded within each site and are not directly comparable with each other.

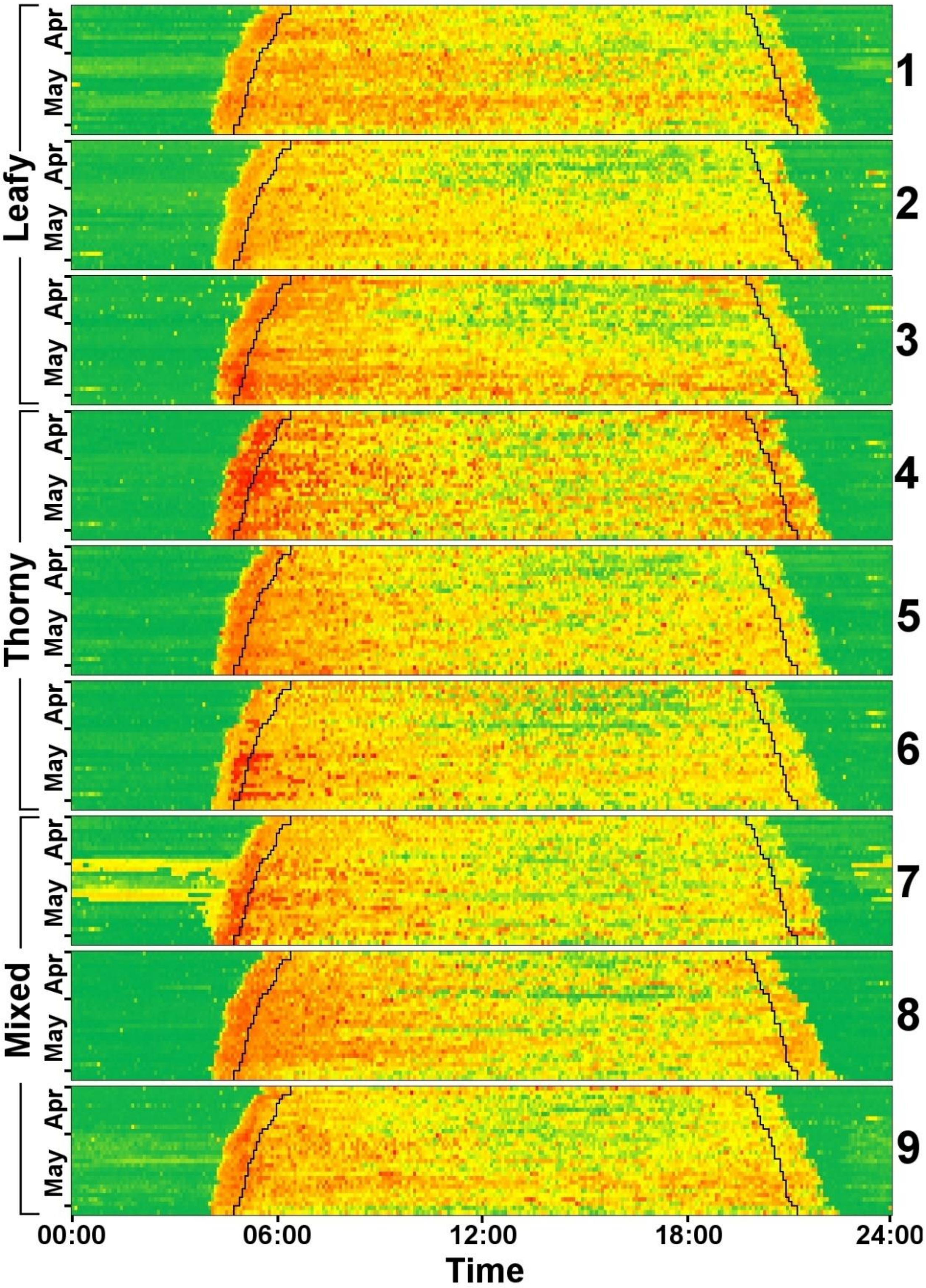


Figure R2. Heatmaps of BI scores of 1-minute recordings, taken every 5 minutes. Conditional formatting used green as the lowest value, red as the highest and yellow as the 50% percentile with sunrises and sunsets shown as black lines. Note: as heatmaps are scaled based on the highest and lowest values recorded within each site, they are not directly comparable with each other.

Appendix S. Results of Site Structural Surveys at Knepp

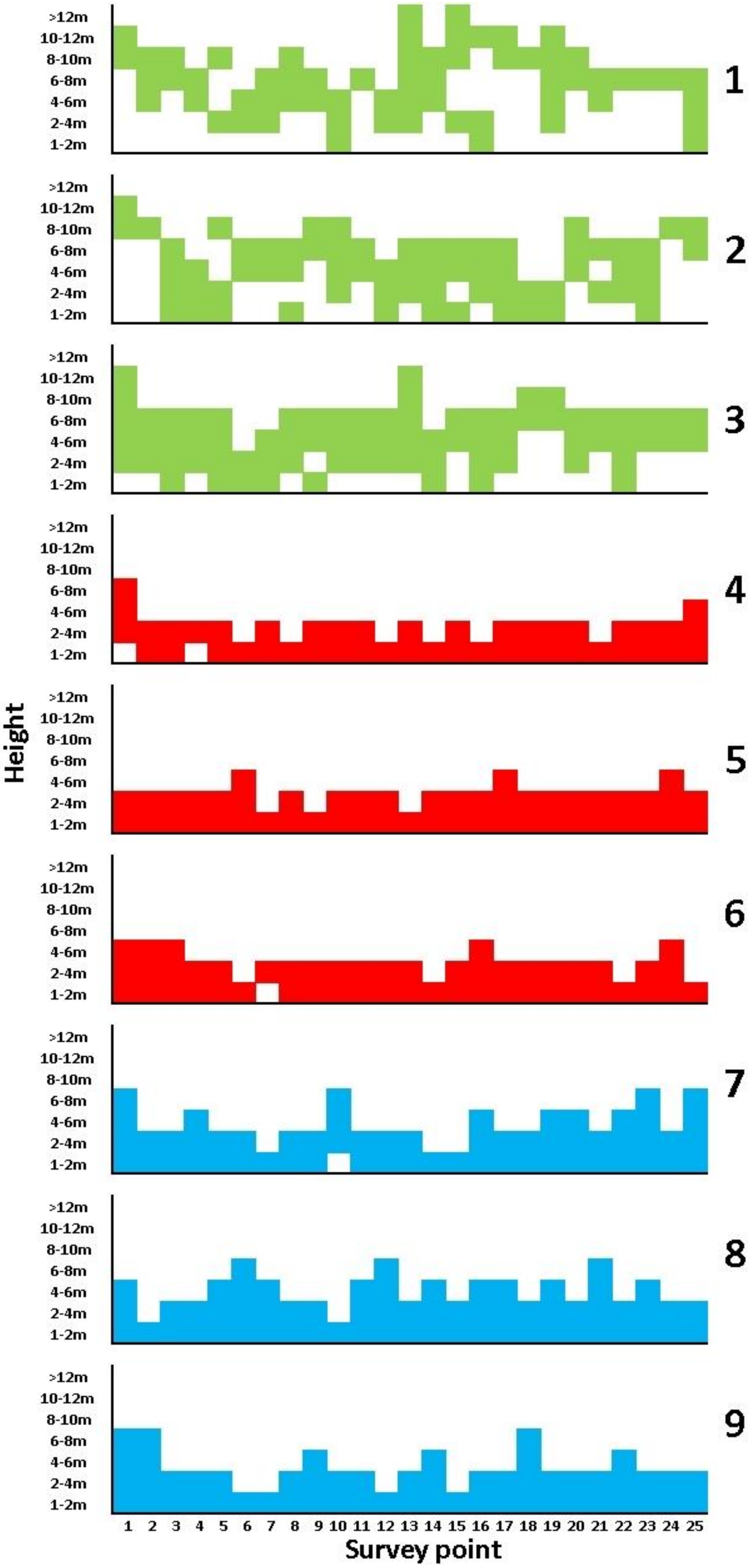


Figure S1. Vegetation structure survey results numbered by site for leafy (green), thorny (red) and mixed (blue) scrub habitats. Images show the 7 height intervals in which vegetation was recorded at each of the 25 survey points.

Appendix T: Correlation Table of Site Variables for Knepp

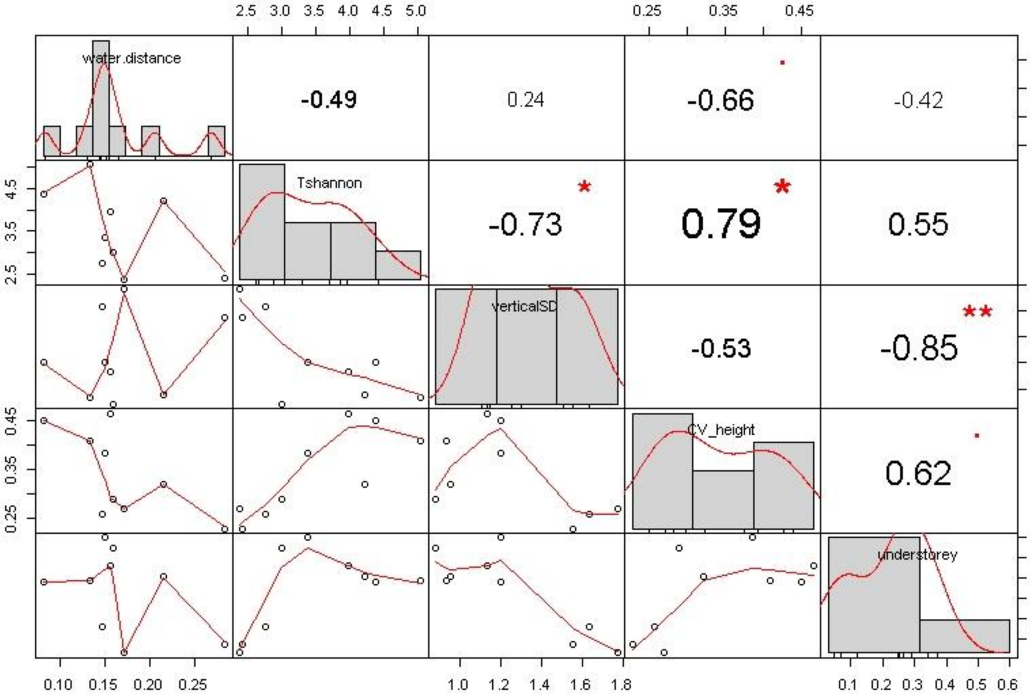


Figure T1. Correlation chart of site characteristic variables used in bat and bird models, from left to right: distance to water (km), true Shannon diversity, vertical structural diversity, CV height and understorey cover (%).

Appendix U. Comparison of Knepp Site Characteristics by Scrub Type

Linear model results indicated significant differences between all scrub types for vertical structural diversity. True Shannon diversity also differed significantly between thorny and leafy sites, and mixed and leafy scrub sites. CV height was significantly different between mixed and leafy, and thorny and mixed sites, and marginally significant between thorny and leafy scrub sites Distance to water, a potential confounding factor for bat activity, did not differ significantly between scrub types (Table U1).

Table U1. Pair-wise comparisons of linear models used to assess variation between site characteristics for different scrub types. Significant results are shown in bold.

Treatments compared	Estimate	Std err	*t* Value	*Pr(>|t|)*
True Shannon diversity				
Mixed - Leafy	**1.393**	**0.551**	**2.531**	**0.045**
Thorny - Leafy	**1.577**	**0.551**	**2.864**	**0.029**
Thorny - Mixed	0.183	0.551	0.333	0.751
Vertical structural diversity				
Mixed - Leafy	**-0.473**	**0.058**	**-8.109**	**<0.001**
Thorny - Leafy	**-0.730**	**0.058**	**-12.506**	**<0.001**
Thorny - Mixed	**-0.257**	**0.058**	**-4.397**	**0.005**
CV Height				
Mixed - Leafy	**0.183**	**0.037**	**4.945**	**0.003**
Thorny - Leafy	0.088	0.037	2.378	0.055
Thorny - Mixed	**-0.095**	**0.037**	**-2.567**	**0.043**
Distance to water				
Mixed - Leafy	-71.00	43.85	-1.619	0.157
Thorny - Leafy	-31.33	43.85	-0.715	0.502
Thorny - Mixed	39.67	43.85	0.905	0.401

Appendix V. Bat Activity GLMMs for Knepp

Analyses revealed that overdispersion was present in all models except NSL, which was modelled with a Poisson distribution. Negative binomial distributions were used for all other models, which greatly improved their AIC and log-likelihood scores (Table V1). Including *day* as a random effect improved the fit of all models except *Myotis* spp., for which log-likelihood tests were identical and the higher AIC score was due to the additional use of *day* in the model as each additional parameter incurs an AIC penalty of 2 for increasing model complexity (Burnham and Anderson, 2002). As both versions of the *Myotis* spp. model produced virtually identical results with no alternation of sign or significances, the most parsimonious model (i.e. *site* only) was selected.

Table V1. AIC scores and overdispersion ratios used to assess possible error distributions and random effects for scrub type models.

Structure[1]	Random[2]	Overdispersion[3]	*P* [3]	loglik	AIC	ΔAIC	weight
			NSL				
P	S D	1.04	0.339	-126.1	262.2	0	0.72
P	S	1.43	<0.001	-128.1	264.1	1.9	0.28
			P. pipistrellus				
NB	S D	0.79	0.993	-276.8	565.6	0	0.928
NB	S	0.81	0.984	-280.4	570.7	5.1	0.072
P	S D	1.21	0.018	-287.5	585	19.4	<0.001
P	S	1.91	<0.001	-328.9	665.9	100.3	<0.001
			P. pygmaeus				
NB	S D	0.89	0.886	-296.4	604.7	0	0.962
NB	S	1.08	0.202	-300.6	611.2	6.5	0.038
P	S D	1.98	<0.001	-362.9	735.7	131	<0.001
P	S	4.36	<0.001	-463.9	935.7	331	<0.001
			Myotis spp.				
NB	S	0.80	0.987	-212.2	434.5	0	0.406
NB	S D	0.81	0.986	-212.2	436.5	2	0.312
P	S D	1.44	<0.001	-240.4	490.8	56.4	<0.001
P	S	1.93	<0.001	-262.8	533.7	99.2	<0.001

[1] Structure key: P = Poisson, NB = Negative binomial.

[2] Random effects key: S = site, D = day.

[3] Overdispersion shown as ratio of residual deviance to residual degrees of freedom, should be ~1 (Crawley, 2007). *P* shows the significance of the overdispersion test.

Validations performed using the *DHARMa* package set for 10,000 simulations (Hartig, 2019) found no significant deviations from uniformity, outliers or spatial autocorrelation for scrub type (Figure V1; Table V2), site characteristic (Figure V2; Table V3) or true Shannon diversity models (Figure V3; Table V4). Spatial autocorrelation tests were performed using the '*re.form = NULL*' setting to remove any correlation already accounted for by random errors (Hartig, 2018). As this function was unavailable for *glmmTMB*, models were also built in *lme4* using *glmer* (Poisson) and *glmer.nb* (negative binomial) in order to perform spatial checks. Results of both *glmmTMB* and *lme4* were compared and, in all cases, found to be virtually identical.

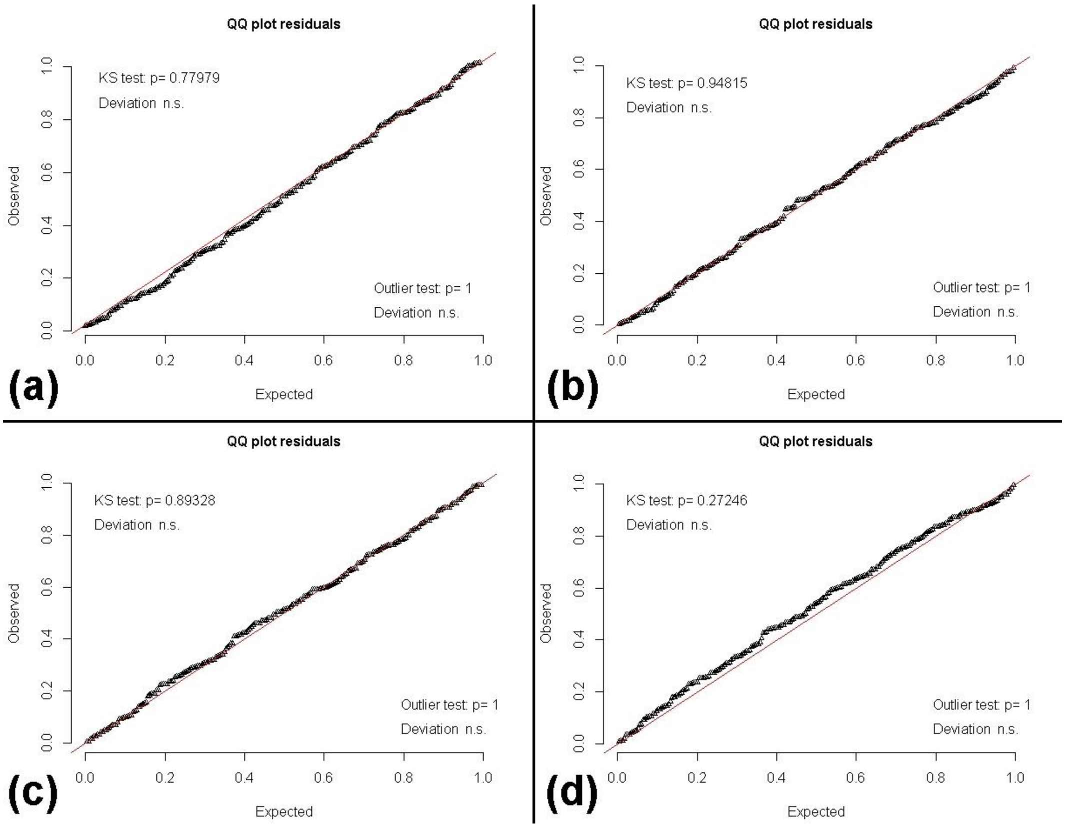


Figure V1. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores for scrub type GLMMs for (a) NSL (b) *P. pipistrellus* (c) *P. pygmaeus* and (d) *Myotis* spp. generated by *DHARMa*.

Table V2. Spatial autocorrelation test results for scrub type GLMMs.

Species model	Observed	Expected	Std. dev.	*P* value
NSL	-0.312	-0.125	0.143	0.190
P. pipistrellus	-0.175	-0.125	0.138	0.717
P. pygmaeus	-0.193	-0.125	0.137	0.618
Myotis spp.	0.079	-0.125	0.141	0.147

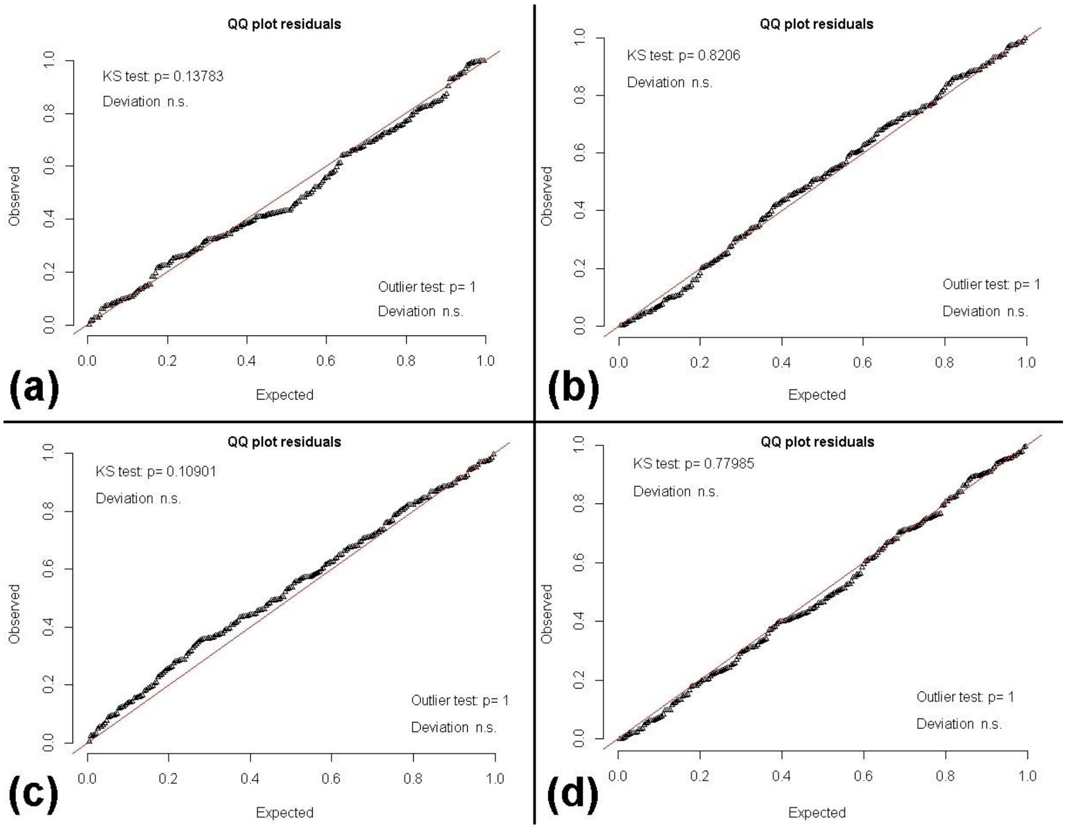


Figure V2. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores for site characteristics GLMMs for (a) NSL (b) *P. pipistrellus* (c) *P. pygmaeus* and (d) *Myotis* spp. generated by *DHARMa*.

Table V3. Spatial autocorrelation test results for site characteristics GLMMs.

Species model	Observed	Expected	Std. dev.	*P* value
NSL	-0.350	-0.125	0.146	0.124
P. pipistrellus	-0.005	-0.125	0.145	0.370
P. pygmaeus	-0.038	-0.125	0.144	0.256
Myotis spp.	-0.201	-0.125	0.143	0.593

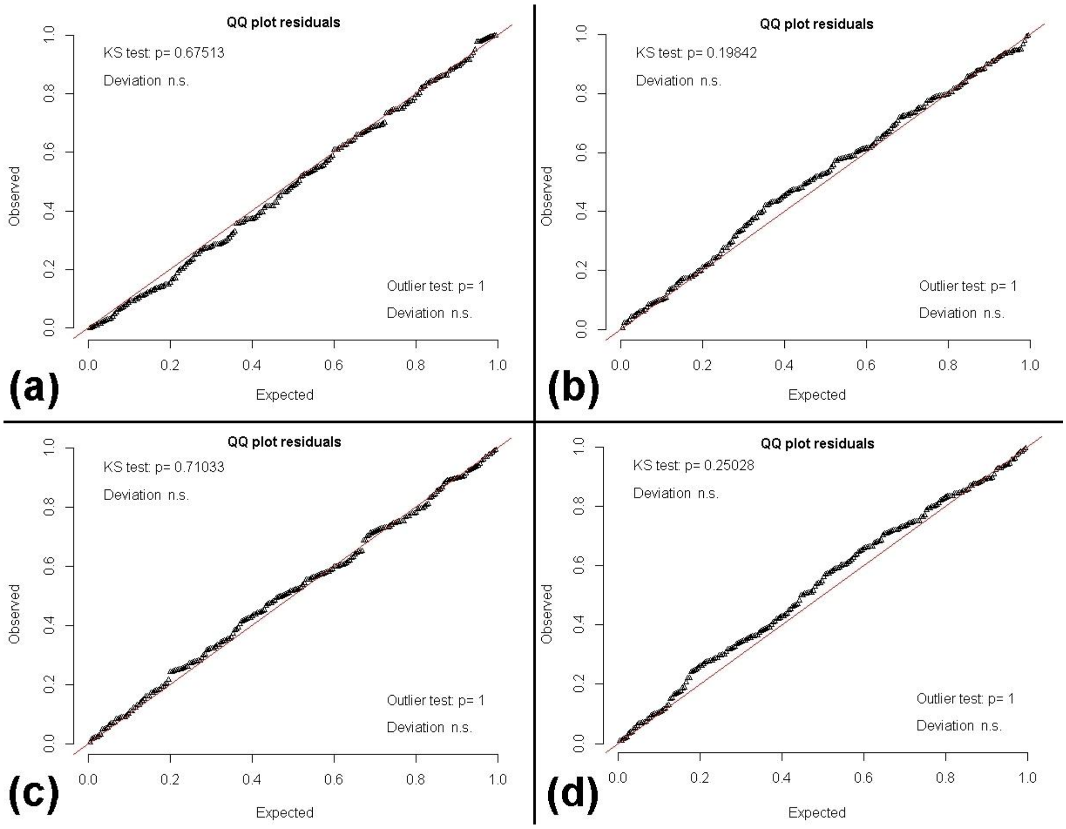


Figure V3. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores for true Shannon diversity GLMMs for (a) NSL (b) *P. pipistrellus* (c) *P. pygmaeus* and (d) *Myotis* spp. generated by *DHARMa*.

Table V4. Spatial autocorrelation test results for true Shannon diversity GLMMs.

Species model	Observed	Expected	Std. dev.	*P* value
NSL	-0.157	-0.125	0.143	0.823
P. pipistrellus	-0.170	-0.125	0.138	0.743
P. pygmaeus	-0.204	-0.125	0.137	0.564
Myotis spp.	0.080	-0.125	0.134	0.126

Appendix W. Acoustic Indices GLMMs for Knepp

Validation checks performed for acoustic index GLMMs with the *DHARMa* package using 10,000 simulations (Hartig, 2019) found no significant deviations from uniformity, outliers or spatial autocorrelation for scrub type (Figure W1; Table W1), site characteristic (Figure W2; Table W2) or true Shannon diversity models (Figure W3; Table W3).

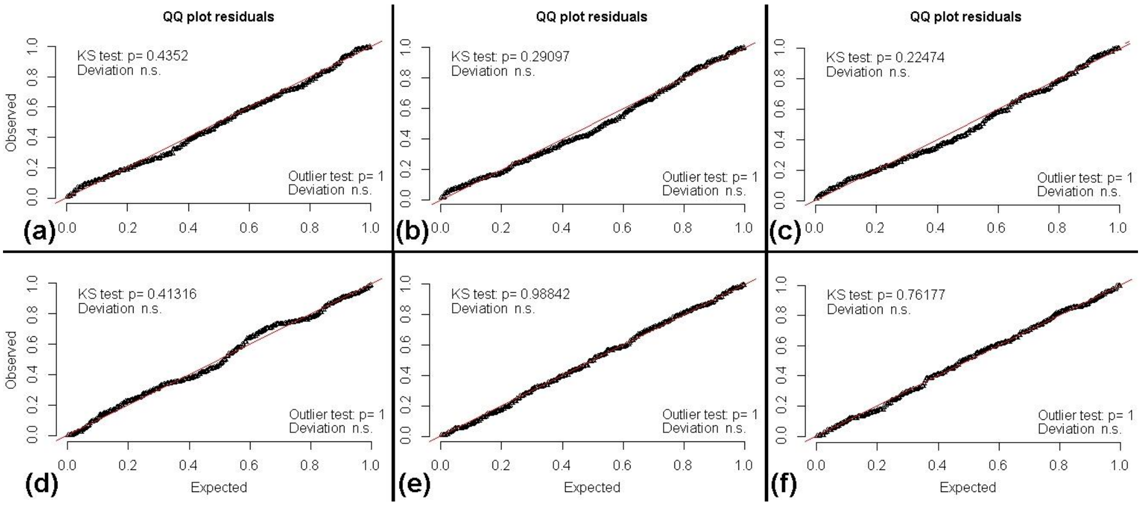


Figure W1. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores for scrub type GLMMs for ACI values at (a) dawn, (b) daytime and (c) dusk, and BI values at (d) dawn, (e) daytime and (f) dusk. All plots were generated by *DHARMa*.

Table W1. Spatial autocorrelation test results for scrub type GLMMs for ACI and BI index scores, obtained using *DHARMa*.

Species model	Observed	Expected	Std. dev.	*P* value
		ACI		
Dawn	-0.133	-0.125	0.145	0.956
Daytime	-0.180	-0.125	0.146	0.708
Dusk	-0.088	-0.125	0.146	0.802
		BI		
Dawn	-0.147	-0.125	0.144	0.880
Daytime	-0.131	-0.125	0.136	0.967
Dusk	-0.089	-0.125	0.143	0.800

Appendix W

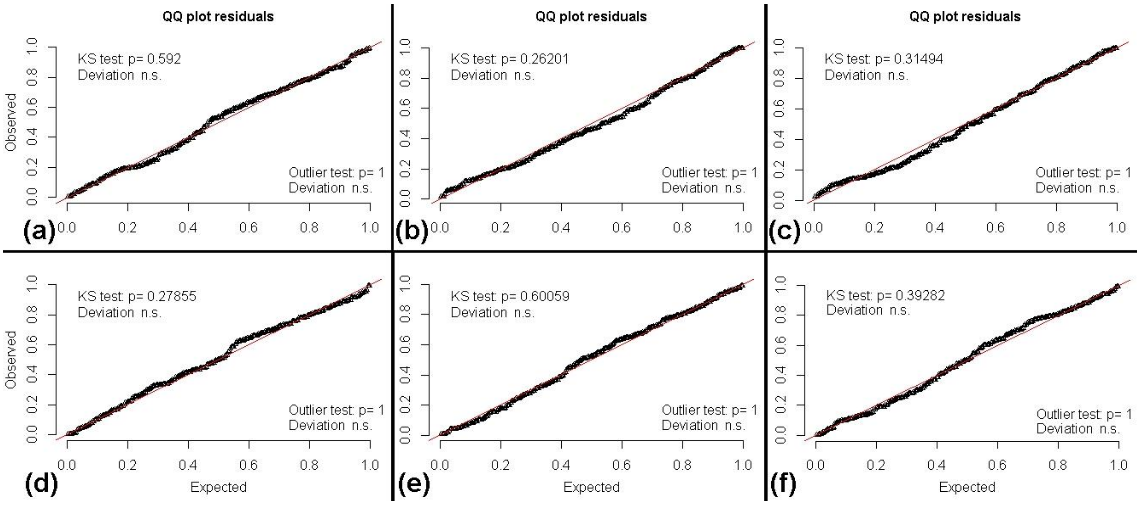


Figure W2. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores for habitat structure (vertical diversity and CV height) GLMMs for ACI values at (a) dawn, (b) daytime and (c) dusk, and BI values at (d) dawn, (e) daytime and (f) dusk. All plots were generated by *DHARMa*.

Table W2. Spatial autocorrelation test results for habitat structure GLMMs for ACI and BI index values.

Species model	Observed	Expected	Std. dev.	*P* value
		ACI		
Dawn	-0.240	-0.125	0.142	0.418
Daytime	-0.267	-0.125	0.142	0.318
Dusk	-0.323	-0.125	0.142	0.164
		BI		
Dawn	-0.240	-0.125	0.141	0.415
Daytime	-0.216	-0.125	0.138	0.508
Dusk	-0.293	-0.125	0.141	0.236

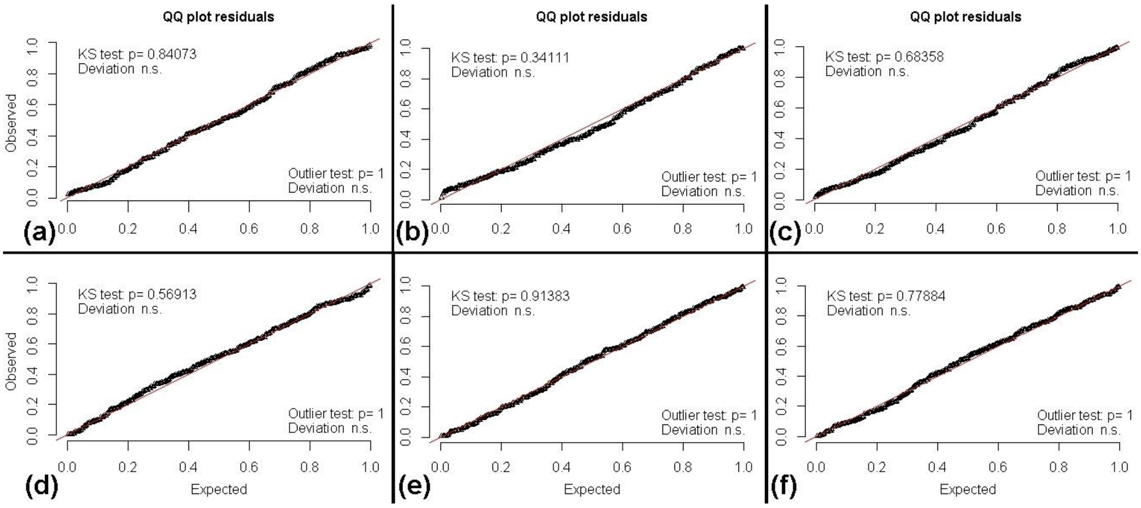


Figure W3. QQ residual plots, one-sample Kolmogorov-Smirnov and outlier test scores for true Shannon diversity GLMMs for ACI values at (a) dawn, (b) daytime and (c) dusk, and BI values at (d) dawn, (e) daytime and (f) dusk. All plots were generated by *DHARMa*.

Table W3. Spatial autocorrelation test results obtained for true Shannon diversity GLMMs for ACI and BI values.

Species model	Observed	Expected	Std. dev.	*P* value
		ACI		
Dawn	-0.273	-0.125	0.140	0.289
Daytime	-0.146	-0.125	0.140	0.880
Dusk	-0.148	-0.125	0.142	0.870
		BI		
Dawn	-0.162	-0.125	0.135	0.784
Daytime	-0.087	-0.125	0.138	0.786
Dusk	-0.052	-0.125	0.140	0.603

Appendix X. Bat Pass Totals for Knepp

Table X1. Total bat pass counts recorded over 26 nights during April, May and June in the Knepp Estate Southern Block, 2016. NSL represents *N. noctula*, *E. serotinus* and *N. leisleri,* and *Myotis* spp. represents *M. brandtii/M. mystacinus*, *M. daubentonii* and *M. nattereri*.

Site	NSL	*P. pipistrellus*	*P. pygmaeus*	*Myotis* spp.
Leafy scrub				
1	2	2	1	13
2	4	0	0	12
3	4	6	2	76
Thorny scrub				
4	5	17	21	11
5	7	49	34	3
6	2	56	2	1
Mixed scrub				
7	8	108	70	10
8	4	11	89	10
9	10	16	174	9
Total	46	265	393	145

List of Abbreviations

AAH	Acoustic Adaptation Hypothesis
ACI	Acoustic Complexity Index
ADI	Acoustic Diversity Index
AEI	Acoustic Evenness Index
AIC	Akaike Information Criterion
AIC_C	Akaike Information Criterion (small sample size)
ANH	Acoustic Niche Hypothesis
ARU	Autonomous Recording Unit
BCT	Bat Conservation Trust
BI	Bioacoustic Index
BTO	British Trust for Ornithology
CD	Compact Disc
CLAC	Cirrus Logic Audio Card
CSV	Comma Separated Values
CV	Coefficient of Variation
DC	Direct Current
dB	Decibel
dBFS	Decibels relative to Full Scale
DBH	Diameter at Breast Height
DIY	Do It Yourself
FFT	Fast Fourier Transform
FLAC	Free Lossless Audio Codec
FS	Full Spectrum
GB	Gigabyte (1,000,000,000 bytes)
GLMM	Generalised Linear Mixed Effect Model
GPS	Global Positioning System
H	Acoustic Entropy Index
H_t	Temporal Entropy Index
KS	Kolmogorov-Smirnov
MB	Megabyte (1,000,000 bytes)
MEMS	Micro-electro-mechanical Systems
MP3	Moving Picture Experts Group Layer-3 Audio
NDSI	Normalized Difference Soundscape Index
NNR	National Nature Reserve
NSL	Noctule (*N. noctula*), Serotine (*E. serotinus*) and Leisler's (*N. leisleri*) bats

Abbreviations

PAM	Passive Acoustic Monitoring
PC	Principal Component
PCA	Principal Components Analysis
QQ	Quantile-Quantile
RMS	Root Mean Square
RSPB	Royal Society for the Protection of Birds
SAC	Special Area of Conservation
SD	Secure Digital
SDHC	Secure Digital High Capacity
SDXC	Secure Digital eXtended Capacity
SNR	Signal-to-Noise Ratio
SPL	Sound Pressure Level
SSSI	Site of Special Scientific Interest
TB	Terabyte (1,000,000,000,000 bytes)
TPP	Temporal Pass Plot
UNESCO	United Nations Educational, Scientific and Cultural Organization
USB	Universal Serial Bus
W4V	Wildlife Acoustics Proprietary Waveform Audio File Format
WAC	Wildlife Acoustics Proprietary Waveform Audio File Format
WAV	Waveform Audio File Format
WWF	World Wide Fund for Nature

References

Abrahams, C. and Denny, M.J. (2018) A first test of unattended, acoustic recorders for monitoring Capercaillie *Tetrao urogallus* lekking activity. *Bird Study*, 65, 197-207.

Acevedo, M.A. Corrada-Bravo, C.J. Corrada-Bravo, H. Villanueva-Rivera, L.J. and Aide, T.M. (2009) Automated classification of bird and amphibian calls using machine learning: A comparison of methods. *Ecological Informatics*, 4, 206-214.

Adamík, P. and Kornan, M. (2004) Foraging ecology of two bark foraging passerine birds in an old-growth temperate forest. *Ornis Fennica*, 81, 13-22.

Adams, A.M. Jantzen, M.K. Hamilton, R.M. and Fenton, M.B. (2012) Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution*, 3, 992-998.

Aide, T.M. Corrada-Bravo, C. Campos-Cerqueira, M. Milan, C. Vega, G. and Alvarez, R. (2013) Real-time bioacoustics monitoring and automated species identification. *PeerJ*, 1, e103.

Aldridge, H.D.J.N. and Rautenbach, I.L. (1987) Morphology, echolocation and resource partitioning in insectivorous bats. *The Journal of Animal Ecology*, 56, 763-778.

Alldredge, M.W. Simons, T.R. and Pollock, K.H. (2007) Factors affecting aural detections of songbirds. *Ecological Applications*, 17, 948-955.

Allouche, O. Kalyuzhny, M. Moreno-Rueda, G. Pizarro, M. and Kadmon, R. (2012) Area–heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences of the USA*, 109, 17495-17500.

Altringham, J.D. (2014) *British Bats (Collins New Naturalist Library, Book 93)*. London, UK: HarperCollins.

Alvarez-Berríos, N. Campos-Cerqueira, M. Hernández-Serna, A. Amanda Delgado, C.J. Román-Dañobeytia, F. and Aide, T.M. (2016) Impacts of small-scale gold mining on birds and anurans near the Tambopata Natural Reserve, Peru, assessed using passive acoustic monitoring. *Tropical Conservation Science*, 9, 832-851.

Amézquita, A. Flechas, S.V. Lima, A.P. Gasser, H. and Hödl, W. (2011) Acoustic interference and recognition space within a complex assemblage of dendrobatid frogs. *Proceedings of the National Academy of Sciences of the USA*, 108, 17058-17063.

Andreassen, T. Surlykke, A. and Hallam, J. (2014) Semi-automatic long-term acoustic surveying: A case study with bats. *Ecological Informatics*, 21, 13-24.

Astaras, C. Linder, J.M. Wrege, P. Orume, R.D. and Macdonald, D.W. (2017) Passive acoustic monitoring as a law enforcement tool for Afrotropical rainforests. *Frontiers in Ecology and the Environment*, 15, 233-234.

Aubin, T. and Jouventin, P. (1998) Cocktail–party effect in king penguin colonies. *Proceedings of the Royal Society of London B*, 265, 1665-1673.

Baeten, L. Verheyen, K. Wirth, C. Bruelheide, H. Bussotti, F. Finér, L. Jaroszewicz, B. Selvi, F. Valladares, F. Allan, E. Ampoorter, E. *et al*. (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics*, 15, 281-291.

Bakker, E.S. Gill, J.L. Johnson, C.N. Vera, F.W. Sandom, C.J. Asner, G.P. and Svenning, J.C. (2016) Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences of the USA*, 113, 847-855.

Bakker, E.S. and Svenning, J.C. (2018) Trophic rewilding: impact on ecosystems under global change. *Proceedings of the Royal Society of London B*, 373, 20170432.

Balenger, S.L. (2015) Stridulated soft song by singing insects. *Animal Behaviour*, 105, 275-280.

Barbaro, L. Allan, E. Ampoorter, E. Castagneyrol, B. Charbonnier, Y. De Wandeler, H. Kerbiriou, C. Milligan, H.T. Vialatte, A. Carnol, M. and Deconchat, M. (2019) Biotic predictors complement models of bat and bird responses to climate and tree diversity in European forests. *Proceedings of the Royal Society of London B*, 286, 20182193.

Barlow, K.E. and Jones, G. (1999) Roosts, echolocation calls and wing morphology of two phonic types of *Pipistrellus pipistrellus*. *Zeitschrift fur Saugetierkunde*, 64, 257-268.

Barron, C. and Little, D. (2009) The control of rhododendron in native woodlands. *Native Woodland Scheme Information Note No. 3*. The Forest Service and Woodlands of Ireland.

Barton, K. (2018) *MuMIn: Multi-Model Inference. R package version 1.42.1* [Online]. Available at: https://CRAN.R-project.org/package=MuMIn [Accessed 10 January 2019].

Bartonička, T. Bielik, A. and Řehák, Z. (2008) Roost switching and activity patterns in the soprano pipistrelle, *Pipistrellus pygmaeus*, during lactation. *Annales Zoologici Fennici*, 45, 503-512.

Bas, Y. Bas, D. and Julien, J.F. (2017) Tadarida: A toolbox for animal detection on acoustic recordings. *Journal of Open Research Software*, 5, 6, DOI: https://doi.org/10.5334/jors.154

Batáry, P. Fronczek, S. Normann, C. Scherber, C. and Tscharntke, T. (2014) How do edge effect and tree species diversity change bird diversity and avian nest survival in Germany's largest deciduous forest? *Forest Ecology and Management*, 319, 44-50.

Bates, D. Maechler, M. Bolker, B. and Walker, S. (2015) Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, 67, 1-48.

BCT (2018) *The National Bat Monitoring Programme. Annual Report 2017* [Online]. Available at: http://www.bats.org.uk/pages/nbmp_annual_report.html [Accessed 18 October 2018].

Beason, R.D. Riesch, R. and Koricheva, J. (2019) AURITA: an affordable, autonomous recording device for acoustic monitoring of audible and ultrasonic frequencies. *Bioacoustics*, 28, 381-396.

Beebee, T.J.C. (1996) *Ecology and Conservation of Amphibians*. London, UK: Chapman & Hall.

Bellamy, C. Scott, C. and Altringham, J. (2013) Multiscale, presence-only habitat suitability models: fine-resolution maps for eight bat species. *Journal of Applied Ecology*, 50, 892-901.

Berthinussen, A. and Altringham, J. (2015) Development of a cost-effective method for monitoring the effectiveness of mitigation for bats crossing linear transport infrastructure. *Defra Research Project WC1060* [Online]. Available at: http://sciencesearch.defra.gov.uk/Document.aspx?Document=12712_WC1060MAINReport.pdf [Accessed 21 December 2017].

Bibby, C. Jones, M. and Marsden, S. (2000) *Expedition Field Techniques: Bird surveys*. Cambridge, UK: Birdlife International.

Biodiversity Exploratories (2017) *The relationships between land use intensity, organismic diversity and acoustic complexity* [Online]. Available at: http://www.biodiversity-exploratories.de/1/projects/vormals-gefoerdert/aboveground-vertebrates-invertebrates-related-studies/besound/ [Accessed 5 January 2018].

Blakey, R.V. Law, B.S. Kingsford, R.T. Stoklosa, J. Tap, P. and Williamson, K. (2016) Bat communities respond positively to large-scale thinning of forest regrowth. *Journal of Applied Ecology*, 53, 1694-1703.

Blumenrath, S. and Dabelsteen, T. (2004) Degradation of great tit (*Parus major*) song before and after foliation: implications for vocal communication in a deciduous forest. *Behaviour*, 141, 935-958.

Blumstein, D.T. Mennill, D.J. Clemins, P. Girod, L. Yao, K. Patricelli, G. Deppe, J.L. Krakauer, A.H. Clark, C. Cortopassi, K.A. and Hanser, S.F. (2011) Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *Journal of Applied Ecology*, 48, 758-767.

Boelman, N.T. Asner, G.P. Hart, P.J. and Martin, R.E. (2007) Multi-trophic invasion resistance in Hawaii: bioacoustics, field surveys, and airborne remote sensing. *Ecological Applications*, 17, 2137-2144.

Böhm, S.M. and Kalko, E.K. (2009) Patterns of resource use in an assemblage of birds in the canopy of a temperate alluvial forest. *Journal of Ornithology*, 150, 799-814.

Bolker, B. (2015) Linear and Generalized Linear Mixed Models. *In:* G.A. Fox, S. Negrete-Yankelevich & V.J. Sosa, eds. *Ecological Statistics*. Oxford, UK: Oxford University Press, 309-333.

Bolker, B. Brooks, M.E. Clark, C.J. Geange, S.W. Poulsen, J.R. Stevens, M.H.H. and White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127-135.

Börk, K.S. (2006) Lunar phobia in the greater fishing bat *Noctilio leporinus* (Chiroptera: Noctilionidae). *Revista de Biología Tropical*, 54, 1117-1123.

Boughey, K.L. Lake, I.R. Haysom, K.A. and Dolman, P.M. (2011) Improving the biodiversity benefits of hedgerows: how physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biological Conservation*, 144, 1790-1798.

Brackenbury, J.H. (1979) Power capabilities of the avian sound-producing system. *Journal of Experimental Biology*, 78, 163-166.

Bradbury, R.B. Hill, R.A. Mason, D.C. Hinsley, S.A. Wilson, J.D. Balzter, H. Anderson, G.Q. Whittingham, M.J. Davenport, I.J. and Bellamy, P.E. (2005) Modelling relationships between birds and vegetation structure using airborne LiDAR data: a review with case studies from agricultural and woodland environments. *Ibis*, 147, 443-452.

Bradbury, J.W. and Vehrencamp, S.L. (2011) *Principles of Animal communication*, Second ed. Massachusetts, USA: Sinauer.

Bradfer-Lawrence, T. Gardner, N. Bunnefeld, L. Bunnefeld, N. Willis, S.G. and Dent, D.H. (2019) Guidelines for the use of acoustic indices in environmental research. *Methods in Ecology and Evolution*, 10, 1796-1807.

Brändle, M. and Brandl, R. (2001) Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology*, 70, 491-504.

Breheny, P. and Burchett, W. (2017) Visualization of Regression Models Using visreg. *The R Journal*, 9, 56-71.

Brooks, M.E. Kristensen, K. van Benthem, K.J. Magnusson, A. Berg, C.W. Nielsen, A. Skaug, H.J. Machler, M. and Bolker, B.M. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378-400.

Broome, A. Summers, R.W. and Vanhala, T. (2016) Understanding the provision of conifer seed for woodland species. *Forestry Commission research Note 23*. Edinburgh, UK: Forestry Comission.

Browning, E. Gibb, R. Glover-Kapfer, P. and Jones, K.E. (2017) Passive acoustic monitoring in ecology and conservation. *WWF Conservation Technology Series*, 1, 1-75.

Brumm, H. (2006) Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A.* 192, 1279-1285.

Brunoldi, M. Bozzini, G. Casale, A. Corvisiero, P. Grosso, D. Magnoli, N. Alessi, J. Bianchi, C.N. Mandich, A. Morri, C. and Povero, P. (2016) A permanent automated real-time passive acoustic monitoring system for bottlenose dolphin conservation in the Mediterranean Sea. *PLOS One*, 11, e0145362.

Buckland, S.T. Marsden, S.J. and Green, R.E. (2008) Estimating bird abundance: making methods work. *Bird Conservation International*, 18, S91-S108.

Bucur, V. (2007) *Urban forest acoustics*. Springer Science & Business Media.

Burnham, K.P. and Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Second ed. New York, USA: Springer-Verlag.

Burns, L.E. and Broders, H.G. (2015) Who swarms with whom? Group dynamics of Myotis bats during autumn swarming. *Behavioral Ecology*, 26, 866-876.

Buxton, R.T. Agnihotri, S. Robin, V.V. Goel, A. and Balakrishnan, R. (2018c) Acoustic indices as rapid indicators of avian diversity in different land-use types in an Indian biodiversity hotspot. *Journal of Ecoacoustics*, 2: #GWPZVD.

Buxton, R.T. Brown, E. Sharman, L. Gabriele, C.M. and McKenna, M.F. (2016) Using bioacoustics to examine shifts in songbird phenology. *Ecology and Evolution*, 6, 4697-4710.

Buxton, R.T. and Jones, I.L. (2012) Measuring nocturnal seabird activity and status using acoustic recording devices: applications for island restoration. *Journal of Field Ornithology*, 83, 47-60.

Buxton, R. Lendrum, P. Crooks, K.R. and Wittemyer, G. (2018a) Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. *Global Ecology and Conservation*, e00493.

Buxton, R. McKenna, M.F. Clapp, M. Meyer, E. Stabenau, E. Angeloni, L.M. Crooks, K. and Wittemyer, G. (2018b) Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. *Conservation Biology*, 32, 1174-1184.

Calladine, J. Bielinski, A. and Shaw, G. (2013) Effects on bird abundance and species richness of edge restructuring to include shrubs at the interface between conifer plantations and moorland. *Bird Study*, 60, 345-356.

Carrasco, L. Giam, X. Papeş, M. and Sheldon, K.S. (2019) Metrics of Lidar-Derived 3D Vegetation Structure Reveal Contrasting Effects of Horizontal and Vertical Forest Heterogeneity on Bird Species Richness. *Remote Sensing*, 11, 743.

Carver, S. (2014) Making real space for nature: a continuum approach to UK conservation. *ECOS*, 35, 4-14.

Carver, S. (2019) Rewilding through land abandonment. *In*: N. Pettorelli, S. Durant & J. Du Toit, eds. *Rewilding (Ecological Reviews)*. Cambridge, UK: Cambridge University Press, 99-122.

Castagneyrol, B. and Jactel, H. (2012) Unraveling plant–animal diversity relationships: a meta-regression analysis. *Ecology*, 93, 2115-2124.

Castaño-Villa, G.J. Estevez, J.V. Guevara, G. Bohada-Murillo, M. and Fonturbel, F.E. (2019) Differential effects of forestry plantations on bird diversity: A global assessment. *Forest Ecology and Management*, 440, 202-207.

Catchpole, C.K. and Slater, P.J. (2008) *Bird song: biological themes and variations*. Second ed. Cambridge, UK: Cambridge University Press.

Catto, C.M.C. Racey, P.A. and Stephenson, P.J. (1995) Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology*, 235, 635-644.

Ceballos, G. Ehrlich, P.R. Barnosky, A.D. García, A. Pringle, R.M. and Palmer, T.M. (2015) Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, 1, e1400253.

Celis-Murillo, A. Deppe, J.L. and Allen, M.F. (2009) Using soundscape recordings to estimate bird species abundance, richness, and composition. *Journal of Field Ornithology*, 80, 64-78.

Charbonnier, Y.M. Barbaro, L. Barnagaud, J.Y. Ampoorter, E. Nezan, J. Verheyen, K. and Jactel, H. (2016) Bat and bird diversity along independent gradients of latitude and tree composition in European forests. *Oecologia*, 182, 529-537.

Charif, R.A. Strickman, L.M. and Waack, A.M. (2010) *Raven Pro 1.4 User's Manual*. The Cornell Lab of Ornithology, Ithaca, NY.

Ciechanowski, M. Zając, T. Zielińska, A. and Dunajski, R. (2010) Seasonal activity patterns of seven vespertilionid bat species in Polish lowlands. *Acta Theriologica*, 55, 301-314.

Colak, A.H. Cross, J.R. and Rotherham, I.D. (1998) *Rhododendron ponticum* in native and exotic environments, with particular reference to Turkey and the British Isles. *Practical Ecology and Conservation*, 2, 34-41.

Cole, E.F. and Sheldon, B.C. (2017) The shifting phenological landscape: Within-and between-species variation in leaf emergence in a mixed-deciduous woodland. *Ecology and Evolution*, 7, 1135-1147.

Collins, J. (2016) *Bat surveys for professional ecologists: good practice guidelines*, Third ed. London: Bat Conservation Trust.

Collins, S. (2004) Vocal fighting and flirting: the functions of birdsong. *In:* P. Marler & H. Slabbekoorn H, eds. *Nature's Music: The Science of Birdsong*. San Diego, USA: Elsevier Academic Press, 39-79.

Collins, J. and Jones, G. (2009) Differences in bat activity in relation to bat detector height: implications for bat surveys at proposed windfarm sites. *Acta Chiropterologica*, 11, 343-350.

Comrey, A.L. and Lee, H.B. (1992) *A first course in factor analysis*, Second ed. Hillsdale, USA: Lawrence Erlbaum Associates.

Connor, E.F. Li, S. and Li, S. (2012) Automating identification of avian vocalizations using time–frequency information extracted from the Gabor transform. *The Journal of the Acoustical Society of America*, 132, 507-517.

Côté, S.D. Rooney, T.P. Tremblay, J.P. Dussault, C. and Waller, D.M. (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35, 113-147.

Cragg, J.L. Burger, A.E. and Piatt, J.F. (2015) Testing the effectiveness of automated acoustic sensors for monitoring vocal activity of Marbled Murrelets *Brachyramphus marmoratus*. *Marine Ornithology*, 43, 151-160.

Crawley, M.J. (2007) *The R book*. Hoboken, USA: John Wiley & Sons.

Critchley, C.N.R. Wilson, L.A. Mole, A.C. Astbury, S.S. and Bhogal, A. (2010) Restoration of Herbaceous Hedgerow Flora: Review and Analysis of Ecological

Factors and Restoration Techniques. Phase 1. *DEFRA Project BD5301 Final Report*. Abingdon, UK: ADAS.

Cross, J.R. (1975) Biological flora of the British Isles *Rhododendron ponticum*. *Journal of Ecology*, 63, 345-364.

Darras, K. Batáry, P. Furnas, B. Celis-Murillo, A. Van Wilgenburg, S.L. Mulyani, Y.A. and Tscharntke, T. (2018) Comparing the sampling performance of sound recorders versus point counts in bird surveys: A meta-analysis. *Journal of Applied Ecology*, 55, 2575-2586.

Davidson-Watts, I. Walls, S. and Jones, G. (2006) Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. *Biological Conservation*, 133, 118-127.

Day, J. Robertson, P. and Symes, N. (2003) *The scrub management handbook: guidance on the management of scrub on nature conservation sites*. Wetherby, UK: English Nature.

Debano, S.J. (2006) Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona. *Biodiversity and Conservation*, 15, 2547-2564.

DEFRA (2007) *Hedgerow Survey Handbook. A standard procedure for local surveys in the UK* [Online]. Available at: https://www.gov.uk/government/publications/hedgerow-survey-handbook [Accessed 21 July 2019].

DEFRA (2015) *Bats: protection and licences* [Online]. Available at: https://www.gov.uk/guidance/bats-protection-surveys-and-licences [Accessed 18 October 2018].

DEFRA (2018) *A green future: our 25 year plan to improve the environment*. DEFRA Policy Paper, 11 Jan 2018. Crown Copyright.

Dehnen-Schmutz, K. Perrings, C. and Williamson, M. (2004) Controlling *Rhododendron ponticum* in the British Isles: an economic analysis. *Journal of Environmental Management*, 70, 323-332.

Dehnen-Schmutz, K. and Williamson, M. (2006) *Rhododendron ponticum* in Britain and Ireland: social, economic and ecological factors in its successful invasion. *Environment and History*, 12, 325-350.

Deichmann, J.L. Acevedo-Charry, O. Barclay, L. Burivalova, Z. Campos-Cerqueira, M. d'Horta, F. Game, E.T. Gottesman, B.L. Hart, P.J. Kalan, A.K. and Linke, S. (2018) It's time to listen: there is much to be learned from the sounds of tropical ecosystems. *Biotropica*, 50, 713-718.

Deinet, S. Ieronymidou, C. McRae, L. Burfield, I.J. Foppen, R.P. Collen, B. and Böhm, M. (2013) *Wildlife comeback in Europe: The recovery of selected mammal and bird species.* Final report to Rewilding Europe by ZSL, BirdLife International and the European Bird Census Council. London, UK: ZSL.

Dekeukeleire, D. van Schrojenstein Lantman, I.M. Hertzog, L.R. Vandegehuchte, M.L. Strubbe, D. Vantieghem, P. Martel, A. Verheyen, K. Bonte, D. and Lens, L. (2019) Avian top-down control affects invertebrate herbivory and sapling growth more strongly than overstorey species composition in temperate forest fragments. *Forest Ecology and Management*, 442, 1-9.

Delibes-Mateos, M. Barrio, I. Barbosa, A. Martínez-Solano, Í, Fa, J. and Ferreira, C. (2019) Rewilding and the risk of creating new, unwanted ecological interactions. *In*: N. Pettorelli, S. Durant & J. Du Toit, eds. *Rewilding (Ecological Reviews)*. Cambridge, UK: Cambridge University Press, 355-374.

Denzinger, A. and Schnitzler, H.U. (2013) Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4, 164.

Depraetere, M. Pavoine, S. Jiguet, F. Gasc, A. Duvail, S. and Sueur, J. (2012) Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. *Ecological Indicators*, 13, 46-54.

Díaz, L. (2006) Influences of forest type and forest structure on bird communities in oak and pine woodlands in Spain. *Forest Ecology and Management*, 223, 54-65.

Díaz, S. Settele, J. Brondízio, E. Ngo, H. Guèze, M. Agard, J. Arneth, A. Balvanera, P. Brauman, K. Butchart, S. Chan, K. *et. al*. (2019) *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn, Germany; IPBES secretariat.

Dietz, C. Dietz, I. and Siemers, B.M. (2006) Wing measurement variations in the five European horseshoe bat species (Chiroptera: Rhinolophidae). *Journal of Mammalogy*, 87, 1241-1251.

Dietz, C. and Kiefer, A. (2016) *Bats of Britain and Europe*. London, UK: Bloomsbury Publishing.

Digby, A. Towsey, M. Bell, B.D. and Teal, P.D. (2013) A practical comparison of manual and autonomous methods for acoustic monitoring. *Methods in Ecology and Evolution*, 4, 675-683.

Dolman, P. Fuller, R.J. Gill, R. Hooton, D. and Tabor, R. (2010) Escalating ecological impacts of deer in lowland woodland. *British Wildlife*, 21, 242-254.

Donald, P.F. Fuller, R.J. Evans, A.D. and Gough, S.J. (1998) Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. *Biological Conservation*, 85, 183-197.

Doohan, B. Fuller, S. Parsons, S. and Peterson, E.E. (2019) The sound of management: Acoustic monitoring for agricultural industries. *Ecological Indicators*, 96, 739-746.

Dormann, C.F. Elith, J. Bacher, S. Buchmann, C. Carl, G. Carré, G. Marquéz, J.R.G. Gruber, B. Lafourcade, B. Leitão, P.J. and Münkemüller, T. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27-46.

Doughty, C.E. Roman, J. Faurby, S. Wolf, A. Haque, A. Bakker, E.S. Malhi, Y. Dunning, J.B. and Svenning, J.C. (2016) Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences of the USA*, 113, 868-873.

Dyulgerova, S. Gramatikov, M. Pedashenko, H. Vassilev, K. Kati, V. and Nikolov, S.C. (2015) Farmland birds and agricultural land abandonment: evidences from Bulgaria. *Acta Zoologica Bulgarica*, 67, 223-234.

Early, R. Bradley, B.A. Dukes, J.S. Lawler, J.J. Olden, J.D. Blumenthal, D.M. Gonzalez, P. Grosholz, E.D. Ibañez, I., Miller, L.P. and Sorte, C.J. (2016) Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications*, 7: 12485.

Edwards, C. (2006) *Practice Guide: Managing and controlling invasive rhododendron*. Edinburgh, UK: Forestry Commission.

Eernisse, N. (2017) *Knepp Castle Estate Scrub and hedgerow changes 2001 – 2015 Southern Block* [Online]. Available at: https://knepp.co.uk/s/Scrub-and-Hedgerow-Changes-2001-2015-Knepp-Southern-Block-Nienke-Eernisse.pdf [Accessed 4 August 2019].

Eichhorn, M.P. Ryding, J. Smith, M.J. Gill, R.M. Siriwardena, G.M. and Fuller, R.J. (2017) Effects of deer on woodland structure revealed through terrestrial laser scanning. *Journal of Applied Ecology*, 54, 1615-1626.

Eldridge, A. Guyot, P. Moscoso, P. Johnston, A. Eyre-Walker, Y. and Peck, M. (2018) Sounding out ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats. *Ecological Indicators*, 95, 939-952.

Entwistle, A.C. Harris, S. Hutson, A.M. Racey, P.A. Walsh, A. Gibson, S.D. Hepburn, I. Johnson, J. and Varela, N. (2001) *Habitat management for bats. A guide for land managers, land owners and their advisors*. Peterborough, UK: JNCC.

Erbe, C. Verma, A. McCauley, R. Gavrilov, A. and Parnum, I. (2015) The marine soundscape of the Perth Canyon. *Progress in Oceanography*, 137, 38-51.

Erdelen, M. (1984) Bird communities and vegetation structure: I. Correlations and comparisons of simple and diversity indices. *Oecologia*, 61, 277-284.

Everest, F.A. and Pohlmann, K.C. (2015) *Master handbook of acoustics*, Fifth ed. New York, USA: McGraw Hill.

Fairbrass, A.J. Rennett, P. Williams, C. Titheridge, H. and Jones, K.E. (2017) Biases of acoustic indices measuring biodiversity in urban areas. *Ecological Indicators*, 83, 169-177.

FAO (2010) *Global Forest Resources Assessment 2010. FAO Forestry Paper 163*. Food and Agriculture Organization of the United Nations, Rome, Italy.

Farina, A. (2014) *Soundscape Ecology: Principles, Patterns, Methods and Applications*. Dordrecht, Netherlands: Springer.

Farina, A. (2018) Perspectives in ecoacoustics: A contribution to defining a discipline. *Journal of Ecoacoustics*, 2, TRZD5I.

Farina, A. Ceraulo, M. Bobryk, C. Pieretti, N. Quinci, E. and Lattanzi, E. (2015) Spatial and temporal variation of bird dawn chorus and successive acoustic morning activity in a Mediterranean landscape. *Bioacoustics*, 24, 269-288.

Farina, A. and Gage, S.H. (2017) Ecoacoustics: a new science. *In*: A. Farina & S. Gage, eds. *Ecoacoustics: The Ecological Role of Sounds*. New Jersey, USA: John Wiley and Sons Ltd, 1-11.

Farina, A. Lattanzi, E. Malavasi, R. Pieretti, N. and Piccioli, L. (2011b) Avian soundscapes and cognitive landscapes: theory, application and ecological perspectives. *Landscape Ecology*, 26, 1257-1267.

Farina, A. Pieretti, N. and Morganti, N. (2013) Acoustic patterns of an invasive species: the Red-billed Leiothrix (*Leiothrix lutea* Scopoli 1786) in a Mediterranean shrubland. *Bioacoustics*, 22, 175-194.

Farina, A. Pieretti, N. and Piccioli, L. (2011a) The soundscape methodology for long-term bird monitoring: A Mediterranean Europe case-study. *Ecological Informatics*, 6, 354-363.

Felton, A. Lindbladh, M. Brunet, J. and Fritz, Ö. (2010) Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. *Forest Ecology and Management*, 260, 939-947.

Ferger, S.W. Schleuning, M. Hemp, A. Howell, K.M. and Böhning-Gaese, K. (2014) Food resources and vegetation structure mediate climatic effects on species richness of birds. *Global Ecology and Biogeography*, 23, 541-549.

Fernández, N. Navarro, L.M. and Pereira, H.M. (2017) Rewilding: a call for boosting ecological complexity in conservation. *Conservation Letters*, 10, 276-278.

Fisher, R. (1925) Theory of Statistical Estimation. *Mathematical Proceedings of the Cambridge Philosophical Society*, 22, 700-725.

Flaspohler, D.J. Giardina, C.P. Asner, G.P. Hart, P. Price, J. Lyons, C.K.A. and Castaneda, X. (2010) Long-term effects of fragmentation and fragment properties on bird species richness in Hawaiian forests. *Biological Conservation*, 143, 280-288.

Foss, R.N. (1979) Effects of wind and ground plane attenuation on sound propagation near the ground. *The Journal of the Acoustical Society of America*, 66, 1088-1092.

Fox, J. and Weisberg, S. (2018) Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. *Journal of Statistical Software*, 87, 1-27.

Fox, J. and Weisberg, S. (2019) *An {R} Companion to Applied Regression*, Third ed. Thousand Oaks, USA: Sage.

Francis, C.D. Ortega, C.P. and Cruz, A. (2011) Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings of the Royal Society of London B,* 278, 2025-2031.

Freeman, S.N. Noble, D.G. Newson, S.E. and Baillie, S.R. (2007) Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. *Bird Study*, 54, 61-72.

Froidevaux, J.S. Boughey, K.L. Hawkins, C.L. Broyles, M. and Jones, G. (2019) Managing hedgerows for nocturnal wildlife: Do bats and their insect prey benefit from targeted agri-environment schemes? *Journal of Applied Ecology*, 56, 1610-1623.

Froidevaux, J.S. Zellweger, F. Bollmann, K. Jones, G. and Obrist, M.K. (2016) From field surveys to LiDAR: shining a light on how bats respond to forest structure. *Remote Sensing of Environment*, 175, 242-250.

Froidevaux, J.S. Zellweger, F. Bollmann, K. and Obrist, M.K. (2014) Optimizing passive acoustic sampling of bats in forests. *Ecology and Evolution*, 4, 4690-4700.

Frommolt, K.H. and Tauchert, K.H. (2014) Applying bioacoustic methods for long-term monitoring of a nocturnal wetland bird. *Ecological Informatics*, 21, 4-12.

Fuentes-Montemayor, E. Goulson, D. Cavin, L. Wallace, J.M. and Park, K.J. (2012) Factors influencing moth assemblages in woodland fragments on farmland: implications for woodland management and creation schemes. *Biological Conservation*, 153, 265-275.

Fuentes-Montemayor, E. Goulson, D. Cavin, L. Wallace, J.M. and Park, K.J. (2013) Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment*, 172, 6-15.

Fuentes-Montemayor, E. Watts, K. Macgregor, N.A. Lopez-Gallego, Z. and Park, K. (2017) Species mobility and landscape context determine the importance of local and landscape-level attributes. *Ecological Applications,* 27, 1541-1554.

Fullard, J.H. Jackson, M.E. Jacobs, D.S. Pavey, C.R. and Burwell, C.J. (2008) Surviving cave bats: auditory and behavioural defences in the Australian noctuid moth, *Speiredonia spectans*. *Journal of Experimental Biology*, 211, 3808-3815.

Fuller, R.J. (2000) Influence of treefall gaps on distributions of breeding birds within interior old-growth stands in Białowieża Forest, Poland. *The Condor*, 102, 267-274.

Fuller, S. Axel, A.C. Tucker, D. and Gage, S.H. (2015) Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? *Ecological Indicators*, 58, 207-215.

Gage, S.H. and Farina, A. (2017) The role of sound in terrestrial ecosystems: Three case examples from Michigan, USA. *In*: A. Farina & S. Gage, eds. *Ecoacoustics: The Ecological Role of Sounds.* New Jersey, USA: John Wiley and Sons Ltd, 31-60.

Gage, S.H. Towsey, M. and Kasten, E.P. (2017) Analytical methods in ecoacoustics. *In*: A. Farina & S. Gage, eds. *Ecoacoustics: The Ecological Role of Sounds*. New Jersey, USA: John Wiley and Sons Ltd, 273-296.

Gasc, A. Francomano, D. Dunning, J.B. and Pijanowski, B.C. (2016) Future directions for soundscape ecology: The importance of ornithological contributions. *The Auk: Ornithological Advances*, 134, 215-228.

Gasc, A. Sueur, J. Jiguet, F. Devictor, V. Grandcolas, P. Burrow, C. Depraetere, M. and Pavoine, S. (2013) Assessing biodiversity with sound: Do acoustic diversity indices reflect phylogenetic and functional diversities of bird communities? *Ecological Indicators*, 25, 279-287.

Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, 27, 2865-2873.

Gentry, K.E. and Luther, D.A. (2017) Spatiotemporal patterns of avian vocal activity in relation to urban and rural background noise. *Journal of Ecoacoustics*, 1, Z9TQHU.

Gerhardt, H.C. (1994) The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics*, 25, 293-324.

Gerlach, J. (2009) Conservation of the Seychelles sheath-tailed bat *Coleura seychellensis* on Silhouette Island, Seychelles. *Endangered Species Research*, 8, 5-13.

Gerlach, J. (2011) Conservation of the Seychelles sheath-tailed bat *Coleura seychellensis* from 1997-2011 and future prospects. *Phelsuma*, 19, 56-68.

Gil, D. Honarmand, M. Pascual, J. Pérez-Mena, E. and Macías Garcia, C. (2014) Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behavioral Ecology*, 26, 435-443.

Gill, R.M.A. (1992) A review of damage by mammals in north temperate forests: 1. Deer. *Forestry: An International Journal of Forest Research*, 65, 145-169.

Gill, R.M.A. and Beardall, V. (2001) The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry: An International Journal of Forest Research*, 74, 209-218.

Gillson, L. Ladle, R.J. and Araújo, M.B. (2011) Baselines, patterns and process. *In*: R.J. Ladle & R.J. Whittaker, eds. *Conservation Biogeography*. New Jersey, USA: Blackwell Publishing Ltd, 31-44.

Gini, C.W. (1971) Variability and mutability, contribution to the study of statistical distributions and relations. Studi cconomico-giuridici della r. universita de cagliari (1912). *Reviewed in*: Light, R.J, Margolin, B.H.: An analysis of variance for categorical data. *Journal of American Statistical Association*, 66, 534-544.

Goerg, G.M. (2011) Lambert W random variables—a new family of generalized skewed distributions with applications to risk estimation. *The Annals of Applied Statistics*, 5, 2197-2230.

Greenaway, T. (2011) *Knepp Wildland Project: Year 10 for the re-wilding project* [Online]. Available at: https://knepp.co.uk/s/Paper-for-the-sheffield-uni-lecture.pdf [Accessed 5 February 2019].

Grueber, C.E. Nakagawa, S. Laws, R.J. and Jamieson, I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, 24, 699-711.

Hagens, S.V. Rendall, A.R. and Whisson, D.A. (2018) Passive acoustic surveys for predicting species' distributions: Optimising detection probability. *PLOS One*, 13, e0199396.

Hanák, V. (1970) Notes on the distribution and systematics of *Myotis mystacinus* Kuhl, 1819. *Bijdragen tot de Dierkunde*, 40, 56-58.

Harrison, X.A. Donaldson, L. Correa-Cano, M.E. Evans, J. Fisher, D.N. Goodwin, C.E. Robinson, B.S. Hodgson, D.J. and Inger, R. (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794.

Hartbauer, M. and Römer, H. (2016) Rhythm generation and rhythm perception in insects: the evolution of synchronous choruses. *Frontiers in Neuroscience*, 10, 223.

Hartig, F. (2018) *Spatial autocorrelation with nbinom1 and nbinom2 #81* [Online]. Available at: https://github.com/florianhartig/DHARMa/issues/81 [Accessed 14 August 2019].

Hartig, F. (2019) *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.4.* [Online]. Available at: https://CRAN.R-project.org/package=DHARMa [Accessed 5 March 2019].

Haselmayer, J. and Quinn, J.S. (2000) A comparison of point counts and sound recording as bird survey methods in Amazonian Southeast Peru. *The Condor*, 102, 887–893.

Heinicke, S. Kalan, A.K. Wagner, O.J. Mundry, R. Lukashevich, H. and Kühl, H.S. (2015) Assessing the performance of a semi-automated acoustic monitoring system for primates. *Methods in Ecology and Evolution*, 6, 753-763.

Hewson, C.M. Austin, G.E. Gough, S.J. and Fuller, R.J. (2011) Species-specific responses of woodland birds to stand-level habitat characteristics: the dual importance of forest structure and floristics. *Forest Ecology and Management*, 261, 1224-1240.

Hilje, B. Stack, S. and Sánchez-Azofeifa, A. (2017) Lianas Abundance is Positively Related with the Avian Acoustic Community in Tropical Dry Forests. *Forests*, 8, 311.

Hill, A.P. Prince, P. Piña Covarrubias, E. Doncaster, C.P. Snaddon, J.L. and Rogers, A. (2018) AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods in Ecology and Evolution*, 9, 1199-1211.

HM Nautical Almanac Office (2017) *Rising and setting times of Sun, Moon or planet* [Online]. Available at: http://astro.ukho.gov.uk/surfbin/placefinder.cgi?program=Rise_Set [Accessed 25 January 2018].

Holmes, R.T. and Robinson, S.K. (1981) Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. *Oecologia*, 48, 31-35.

Hu, W. Bulusu, N. Chou, C.T. Jha, S. Taylor, A. and Tran, V.N. (2009) Design and evaluation of a hybrid sensor network for cane toad monitoring. *ACM Transactions on Sensor Networks (TOSN)*, 5, 4.

Huang, Q. Swatantran, A. Dubayah, R. and Goetz, S.J. (2014) The influence of vegetation height heterogeneity on forest and woodland bird species richness across the United States. *PLOS One*, 9, p.e103236.

Hutto, R.L. and Stutzman, R.J. (2009) Humans versus autonomous recording units: a comparison of point-count results. *Journal of Field Ornithology*, 80, 387-398.

IInstEco (International Institute of Ecoacoustics) (2018) *Soundscape Explorer* [Online]. Available at: http://www.iinsteco.org/soundscape_explorer/ [Accessed 2 January 2018].

Irwin, S. Pedley, S.M. Coote, L. Dietzsch, A.C. Wilson, M.W. Oxbrough, A. Sweeney, O. Moore, K.M. Martin, R. Kelly, D.L. and Mitchell, F.J. (2014) The value of plantation forests for plant, invertebrate and bird diversity and the potential for cross-taxon surrogacy. *Biodiversity and Conservation*, 23, 697-714.

Jan, C.M. Frith, K. Glover, A.M. Butlin, R.K. Scott, C.D. Greenaway, F. Ruedi, M. Frantz, A.C. Dawson, D.A. and Altringham, J.D. (2010) *Myotis alcathoe* confirmed in the UK from mitochondrial and microsatellite DNA. *Acta Chiropterologica*, 12, 471-483.

Jenkins, E.V. Laine, T. Morgan, S.E. Cole, K.R. and Speakman, J.R. (1998) Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. *Animal Behaviour*, 56, 909-917.

Jenkins, T.A.R. Mackie, E.D. Matthews, R.W. Miller, G. Randle, T.J. and White, M.E. (2018) *FC Woodland Carbon Code: Carbon Assessment Protocol (v2.0)*. Crown copyright, courtesy of the Forestry Commission.

Johnston, A. Newson, S.E. Risely, K. Musgrove, A.J. Massimino, D. Baillie, S.R. and Pearce-Higgins, J.W. (2014) Species traits explain variation in detectability of UK birds. *Bird Study*, 61, 340-350.

Jolliffe, I.T. (2002) *Principal Component Analysis*, Second ed. New York: Springer-Verlag.

Jones, G. and Barratt, E.M. (1999) *Vespertilio pipistrellus* Schreber, 1774 and *V. pygmaeus* Leach, 1825 (currently *Pipistrellus pipistrellus* and *P. pygmaeus*; Mammalia, Chiroptera): proposed designation of neotypes. *Bulletin of Zoological Nomenclature*, 56, 182-186.

Jones, G. Jacobs, D.S. Kunz, T.H. Willig, M.R. and Racey, P.A. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, 8, 93-115.

Joo, W. Gage, S.H. and Kasten, E.P. (2011) Analysis and interpretation of variability in soundscapes along an urban–rural gradient. *Landscape and Urban Planning*, 103, 259-276.

Jorge, F.C. Machado, C.G. da Cunha Nogueira, S.S. and Nogueira-Filho, S.L.G. (2018) The effectiveness of acoustic indices for forest monitoring in Atlantic rainforest fragments. *Ecological Indicators*, 91, 71-76.

Jost, L. (2006) Entropy and diversity. *Oikos*, 113, 363-375.

Jung, K. Kaiser, S. Böhm, S. Nieschulze, J. and Kalko, E.K. (2012) Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *Journal of Applied Ecology*, 49, 523-531.

Kalko, E.K. and Schnitzler, H.U. (1993) Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. *Behavioral Ecology and Sociobiology*, 33, 415-428.

Kasten, E.P. Gage, S.H. Fox, J. and Joo, W. (2012) The remote environmental assessment laboratory's acoustic library: An archive for studying soundscape ecology. *Ecological Informatics*, 12, 50-67.

Katz, J. Hafner, S.D. and Donovan, T. (2016) Tools for automated acoustic monitoring within the R package monitoR. *Bioacoustics*, 25, 197-210.

Kelty, M.J. (2006) The role of species mixtures in plantation forestry. *Forest Ecology and Management*, 233, 195-204.

Kennedy, C.E.J. and Southwood, T.R.E. (1984) The number of species of insects associated with British trees: a re-analysis. *The Journal of Animal Ecology*, 53, 455-478.

Kerbiriou, C. Bas, Y. Le Viol, I. Lorrilliere, R. Mougnot, J. and Julien, J.F. (2019) Potential of bat pass duration measures for studies of bat activity. *Bioacoustics*, 28, 177-192.

Kernon Countryside Consultants (2007) *Knepp Feasibility Assessment Final 2.3.07 - Knepp Wildland* [Online]. Available at: https://knepp.co.uk/s/Knepp-Feasibility-Assessment-Final-2307-compressed3.pdf [Accessed 5 August 2019].

Kleindorfer, S. Evans, C. and Mahr, K. (2016) Female in-nest chatter song increases predation. *Biology Letters*, 12, 20150513.

Klingbeil, B.T. and Willig, M.R. (2015) Bird biodiversity assessments in temperate forest: the value of point count versus acoustic monitoring protocols. *PeerJ, 3, e973*.

Knepp Estate (2018a) *Wildlife Successes* [Online]. Available at: https://knepp.co.uk/the-results/ [Accessed 8 January 2018].

Knepp Estate (2018b) *Free-roaming Herbivores* [Online]. Available at: https://knepp.co.uk/the-drivers/ [Accessed 31 July 2019].

Knepp Estate (2019a) *Farming at Knepp* [Online]. Available at: https://www.kneppestate.co.uk/farming-at-knepp [Accessed 3 September 2019].

Knepp Estate (2019b) *Bats* [Online]. Available at: https://knepp.co.uk/bats [Accessed 19 September 2019].

Koch, R. (2016) *Swift Recorder Users Guide v2.1* [Online]. Available at: http://www.birds.cornell.edu/brp/wp-content/uploads/2017/07/Swift-Recorder-Users-Guide-Ver-2_1.pdf [Accessed 9 May 2019].

Kogan, J.A. and Margoliash, D. (1998) Automated recognition of bird song elements from continuous recordings using dynamic time warping and hidden Markov models: A comparative study. *The Journal of the Acoustical Society of America*, 103, 2185-2196.

Korňan, M. and Adamík, P. (2017) Tree species preferences of foraging insectivorous birds in a primeval mountain mixed forest: implications for management. *Scandinavian Journal of Forest Research*, 32, 671-678.

Krause, B.L. (1987) Bioacoustics, habitat ambience in ecological balance. *Whole Earth Review*, 57, 14-18.

Kuehn, J. (2009) Chapter 32 - Noise Measurement. *In:* W. Boyes, ed. *Instrumentation Reference Book*. Fourth ed. Boston, USA: Butterworth-Heinemann, 593-614.

Kułaga, K. and Budka, M. (2019) Bird species detection by an observer and an autonomous sound recorder in two different environments: Forest and farmland. *PLOS one*, 14, e0211970.

La, V.T. and Nudds, T.D. (2016) Effect of revisitation surveys on detection of wetland birds with different diel vocalization patterns. *Journal of Fish and Wildlife Management*, 7, 509-519.

Lacoeuilhe, A. Machon, N. Julien, J.F. and Kerbiriou, C. (2016) Effects of hedgerows on bats and bush crickets at different spatial scales. *Acta Oecologica*, 71, 61-72.

Lacoeuilhe, A. Machon, N. Julien, J.F. and Kerbiriou, C. (2018) The relative effects of local and landscape characteristics of hedgerows on bats. *Diversity*, 10, 72.

Lellouch, L. Pavoine, S. Jiguet, F. Glotin, H. and Sueur, J. (2014) Monitoring temporal change of bird communities with dissimilarity acoustic indices. *Methods in Ecology and Evolution*, 5, 495-505.

Lengagne, T. and Slater, P.J. (2002) The effects of rain on acoustic communication: Tawny Owls have good reason for calling less in wet weather. *Proceedings of the Royal Society of London B*, 269, 2121-2125.

Ligges, U. Krey, S. Mersmann, O. and Schnackenberg, S. (2016) *tuneR: Analysis of music* [Online]. Available at: http://r-forge.r-project.org/projects/tuner/ [Accessed 20 December 2017].

Littlewood, N.A. (2008) Grazing impacts on moth diversity and abundance on a Scottish upland estate. *Insect Conservation and Diversity*, 1, 151-160.

Liu, C.M. Hsu, H.W. and Lee, W.C. (2008) Compression artifacts in perceptual audio coding. *IEEE Transactions on Audio, Speech, and Language Processing*, 16, 681-695.

Lomolino, M.V. Pijanowski, B.C. and Gasc, A. (2015) The silence of biogeography. *Journal of Biogeography*, 42, 1187-1196.

London Metropolitan Police (2016) *Photography advice* [Online]. Available at: http://content.met.police.uk/Site/photographyadvice [Accessed 28 February 2016].

Lorimer, J. Sandom, C. Jepson, P. Doughty, C. Barua, M. and Kirby, K.J. (2015) Rewilding: Science, practice, and politics. *Annual Review of Environment and Resources*, 40, 39-62.

Lučan, R.K. Andreas, M. Benda, P. Bartonička, T. Březinová, T. Hoffmannová, A. Hulová, Š. Hulva, P. Neckářová, J. Reiter, A. and Svačina, T. (2009) Alcathoe bat (*Myotis alcathoe*) in the Czech Republic: distributional status, roosting and feeding ecology. *Acta Chiropterologica*, 11, 61-69.

MacArthur, R.H. and MacArthur, J.W. (1961) On bird species diversity. *Ecology*, 42, 594-598.

Machado, R.B. Aguiar, L. and Jones, G. (2017) Do acoustic indices reflect the characteristics of bird communities in the savannas of Central Brazil? *Landscape and Urban Planning*, 162, 36-43.

Maier, C. (1992) Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. *Journal of Zoology*, 228, 69-80.

Malavasi, R. and Farina, A. (2013) Neighbours' talk: interspecific choruses among songbirds. *Bioacoustics*, 22, 33-48.

Malo, A.F. Godsall, B. Prebble, C. Grange, Z. McCandless, S. Taylor, A. and Coulson, T. (2013) Positive effects of an invasive shrub on aggregation and abundance of a native small rodent. *Behavioral Ecology,* 24, 759-767.

Mammides, C. Goodale, E. Dayananda, S.K. Kang, L. and Chen, J. (2017) Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. *Ecological Indicators*, 82, 470-477.

Marques, T.A. Thomas, L. Martin, S.W. Mellinger, D.K. Ward, J.A. Moretti, D.J. Harris, D. and Tvack, P. (2013) Estimating animal population density using passive acoustics. *Biological Reviews*, 88, 287-309.

Marris, E. (2009) Conservation biology: reflecting the past. *Nature News*, 462, 30-32.

Mason, R. Roe, P. Towsey, M. Jinglan, Z. Gibson, J. and Gage, S. (2008) Towards an Acoustic Environmental Observatory. *In:* P. Kellenburger, ed. *Fourth IEEE International Conference on eScience, Indianapolis 7-12 December 2008*. IEEE Publishing, 135-142.

Maudsley, M.J. (2000) A review of the ecology and conservation of hedgerow invertebrates in Britain. *Journal of Environmental Management*, 60, 65-76.

McCauley, S.J. Bouchard, S.S. Farina, B.J. Isvaran, K. Quader, S. Wood, D.W. and St. Mary, C.M. (2000) Energetic dynamics and anuran breeding phenology: insights from a dynamic game. *Behavioral Ecology*, 11, 429-436.

McCracken, D.I. Foster, G.N. and Kelly, A. (1995) Factors affecting the size of leatherjacket (Diptera: Tipulidae) populations in pastures in the west of Scotland. *Applied Soil Ecology*, 2, 203-213.

Mejías, J.A. Arroyo, J. and Ojeda, F. (2002) Reproductive ecology of *Rhododendron ponticum* (Ericaceae) in relict Mediterranean populations. *Botanical Journal of the Linnean Society*, 140, 297-311.

Melin, M. Hinsley, S.A. Broughton, R.K. Bellamy, P. and Hill, R.A. (2018) Living on the edge: utilising lidar data to assess the importance of vegetation structure for avian diversity in fragmented woodlands and their edges. *Landscape Ecology*, 33, 895-910.

Mennill, D.J. Burt, J.M. Fristrup, K.M. and Vehrencamp, S.L. (2006) Accuracy of an acoustic location system for monitoring the position of duetting songbirds in tropical forest. *The Journal of the Acoustical Society of America*, 119, 2832-2839.

Menzel, J.M. Menzel Jr, M.A. Kilgo, J.C. Ford, W.M. Edwards, J.W. and McCracken, G.F. (2005) Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *The Journal of Wildlife Management*, 69, 235-245.

Merchant, N.D. Fristrup, K.M. Johnson, M.P. Tyack, P.L. Witt, M.J. Blondel, P. and Parks, S.E. (2015) Measuring acoustic habitats. *Methods in Ecology and Evolution*, 6, 257-265.

Merckx, T. and Pereira, H.M. (2015) Reshaping agri-environmental subsidies: From marginal farming to large-scale rewilding. *Basic and Applied Ecology*, 16, 95-103.

Metcalf, O.C. Ewen, J.G. McCready, M. Williams, E.M. and Rowcliffe, J.M. (2019) A novel method for using ecoacoustics to monitor post-translocation behaviour in an endangered passerine. *Methods in Ecology and Evolution*, 10, 626-636.

Miller, B.W. (2001) A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica*, 3, 93-105.

Milne, R.I. and Abbott, R.J. (2000) Origin and evolution of invasive naturalized material of *Rhododendron ponticum* L. in the British Isles. *Molecular Ecology*, 9, 541-556.

Mölder, A. Bernhardt-Römermann, M. and Schmidt, W. (2006) Forest ecosystem research in Hainich National Park (Thuringia): first results on flora and vegetation in stands with contrasting tree species diversity. *Waldökologie*, 3, 83-99.

Moran, P.A.P. (1950) Notes on continuous stochastic phenomena. *Biometrika*, 37, 17-23.

Morton, E.S. (1975) Ecological sources of selection on avian sounds. *American Naturalist*, 109, 17-34.

Müller, J. and Brandl, R. (2009) Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology*, 46, 897-905.

Müller, J. Brandl, R. Buchner, J. Pretzsch, H. Seifert, S. Strätz, C. Veith, M. and Fenton, B. (2013) From ground to above canopy—Bat activity in mature forests is driven by vegetation density and height. *Forest Ecology and Management*, 306, 179-184.

Müller, J. Mehr, M. Bässler, C. Fenton, M.B. Hothorn, T. Pretzsch, H. Klemmt, H.J. and Brandl, R. (2012) Aggregative response in bats: prey abundance versus habitat. *Oecologia*, 169, 673-684.

Müller, J. Stadler, J. and Brandl, R. (2010) Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of lidar. *Remote Sensing of Environment*, 114, 490-495.

Murakami, M. and Nakano, S. (2000) Species-specific bird functions on a forest-canopy food web. *Proceedings of the Royal Society of London B*, 267, 1597-1601.

Myers, D. Berg, H. and Maneas, G. (2019) Comparing the soundscapes of organic and conventional olive groves: A potential method for bird diversity monitoring. *Ecological Indicators*, 103, 642-649.

Nationalpark-Verwaltung (2018) *Primeval woodland in the heart of Germany* [Online]. Available at: www.nationalpark-hainich.de/en/national-park/hainich-national-park.html [Accessed 1 January 2018].

Newson, S.E. Bas, Y. Murray, A. and Gillings, S. (2017) Potential for coupling the monitoring of bush-crickets with established large-scale acoustic monitoring of bats. *Methods in Ecology and Evolution*, 8, 1051-1062.

Newson S.E. and Berthinussen A. (2019) Improving our understanding of the distribution and status of bats within the Ryevitalise Landscape Partnership Scheme area. *BTO Research Report no. 716*. Thetford, UK: British Trust for Ornithology.

Newson, S.E. Evans, H.E. and Gillings, S. (2015) A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation*, 191, 38-49.

Newson, S.E. Johnston, A. Renwick, A.R. Baillie, S.R. and Fuller, R.J. (2012) Modelling large-scale relationships between changes in woodland deer and bird populations. *Journal of Applied Ecology*, 49, 278-286.

Nixon, C.J. and Worrell, R. (1999) The potential for the natural regeneration of conifers in Britain. *Forestry Commission Bulletin 120*. Edinburgh, UK: Forestry Commission.

Nogués-Bravo, D. Simberloff, D. Rahbek, C. and Sanders, N.J. (2016) Rewilding is the new Pandora’s box in conservation. *Current Biology*, 26, R87-R91.

Norberg, U.M. and Rayner, J.M. (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London B*, 316, 335-427.

Nuttle, T. Yerger, E.H. Stoleson, S.H. and Ristau, T.E. (2011) Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere*, 2, 1-11.

Obrist, M.K. Pavan, G. Sueur, J. Riede, K. Llusia, D. and Márquez, R. (2010) Bioacoustics approaches in biodiversity inventories. *In*: J. Eymann, J. Degreef, C. Häuser, J.C. Monje, Y. Samyn & D. VandenSpiegel, eds. *Manual on Field Recording Techniques and Protocols for All Taxa Biodiversity Inventories*. ABC Taxa Vol. 8, 68-99.

Obrist, M.K. Rathey, E. Bontadina, F. Martinoli, A. Conedera, M. Christe, P. and Moretti, M. (2011) Response of bat species to sylvo-pastoral abandonment. *Forest Ecology and Management*, 261, 789-798.

O'Connell, S. Irwin, S. Wilson, M.W. Sweeney, O.F.M. Kelly, T.C. and O'Halloran, J. (2012) How can forest management benefit bird communities? Evidence from eight years of research in Ireland. *Irish Forestry Journal*, 69, 44-57.

Odom, K.J. Hall, M.L. Riebel, K. Omland, K.E. and Langmore, N.E. (2014) Female song is widespread and ancestral in songbirds. *Nature Communications*, 5, 3379

O’Halloran, J. Irwin, S. Kelly, D.L. Kelly, T.C. Mitchell, F.J.G. Coote, L. Oxbrough, A. Wilson, M.W. Martin, R.D. Moore, K. Sweeney, O. Dietzsch, A.C. Walsh, A.

Keady, S. French, V. Fox, H. Kopke, K. Butler, F. and Neville, P. (2011) *Management of biodiversity in a range of Irish forest types*. Dublin, Ireland: Department of Agriculture, Fisheries and Food.

Olff, H. Vera, F.W.M. Bokdam, J. Bakker, E.S. Gleichman, J.M. De Maeyer, K. and Smit, R. (1999) Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biology*, 1, 127-137.

Open University (2007) *TA212/Block 3:1 musical instruments*. 1.1 ed. Milton Keynes, UK: Open University Press.

Palmer, M.S. Krueger, J. and Isbell, F. (2019) Bats join the ranks of oxpeckers and cleaner fish as partners in a pest-reducing mutualism. *Ethology*, 125, 170-175.

Parrott, J. and Mackenzie, N. (2013) *A critical review of work undertaken to control invasive rhododendron in Scotland*: *a report commissioned by Forestry Commission Scotland and Scottish Natural Heritage*. Coille Alba.

Parsons, S. and Jones, G. (2000) Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. *Journal of Experimental Biology*, 203, 2641-2656.

Patriquin, K.J. Hogberg, L.K. Chruszcz, B.J. and Barclay, R.M. (2003) The influence of habitat structure on the ability to detect ultrasound using bat detectors. *Wildlife Society Bulletin*, 31, 475-481.

Payn, T. Carnus, J.M. Freer-Smith, P. Kimberley, M. Kollert, W. Liu, S. Orazio, C. Rodriguez, L. Silva, L.N. and Wingfield, M.J. (2015) Changes in planted forests and future global implications. *Forest Ecology and Management*, 352, 57-67.

Pearce, H. and Walters, C.L. (2012) Do Green Roofs Provide Habitat for Bats in Urban Areas? *Acta Chiropterologica*, 14, 469-478.

Peck, K.M. (1989) Tree species preferences shown by foraging birds in forest plantations in northern England. *Biological Conservation*, 48, 41-57.

Peco, B. Carmona, C.P. de Pablos, I. and Azcarate, F.M. (2012) Effects of grazing abandonment on functional and taxonomic diversity of Mediterranean grasslands. *Agriculture Ecosystems and Environment*, 152, 27-32.

Peersonic (2016) *The Peersonic Ultrasonic recorder and monitor RPA2 Rev 8.0* [Online] www.dropbox.com/s/vd2o6h9j8wr8tdj/The RPA2 User Manual Rev 8.0.pdf?dl=1 [Accessed 15 February 2016].

Pekin, B.K. Jung, J. Villanueva-Rivera, L.J. Pijanowski, B.C. and Ahumada, J.A. (2012) Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. *Landscape Ecology*, 27, 1513-1522.

Penone, C. LeViol, I. Pellissier, V. Julien, J.F. Bas, Y. and Kerbiriou, C. (2013) Use of large-scale acoustic monitoring to assess anthropogenic pressures on Orthoptera communities. *Conservation Biology*, 27, 979-987.

Pereira, H.M. and Cooper, H.D. (2006) Towards the global monitoring of biodiversity change. *Trends in Ecology & Evolution*, 21, 123-129.

Pérez-Granados, C. Bota, G. Giralt, D. Albarracín, J. and Traba, J. (2019) Cost-Effectiveness Assessment of Five Audio Recording Systems for Wildlife Monitoring: Differences between Recording Distances and Singing Direction. *Ardeola*, 66, 311-325.

Peterken, G.F. (2001) Ecological effects of introduced tree species in Britain. *Forest Ecology and Management*, 141, 31-42.

Peterson, B.G. and Carl, P. (2018) *PerformanceAnalytics: Econometric Tools for Performance and Risk Analysis. R package* version 1.5.2. [Online]. Available at: https://CRAN.R-project.org/package=PerformanceAnalytics [Accessed 31 December 2018].

Petty, S.J. and Avery, M. (1990) *Forest bird communities: a review of the ecology and management of forest bird communities in relation to silvicultural practices in the British uplands (Vol. 26).* Edinburgh, UK: Forestry Commission.

Phillips, Y.F. Towsey, M. and Roe, P. (2018) Revealing the ecological content of long-duration audio-recordings of the environment through clustering and visualisation. *PLOS One*, 13, e0193345.

Pieretti, N. Duarte, M.H.L. Sousa-Lima, R.S. Rodrigues, M. Young, R.J. and Farina, A. (2015) Determining Temporal Sampling Schemes for Passive Acoustic Studies in Different Tropical Ecosystems. *Tropical Conservation Science*, 8, 215-234.

Pieretti, N. and Farina, A. (2013) Application of a recently introduced index for acoustic complexity to an avian soundscape with traffic noise. *The Journal of the Acoustical Society of America*, 134, 891-900.

Pieretti, N. Farina, A. and Morri, D. (2011) A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). *Ecological Indicators*, 11, 868-873.

Pijanowski, B.C. Farina, A. Dumyahn, S. Krause, B. and Gage, S. (2011a) What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*, 26, 1213-1232.

Pijanowski, B.C. Villanueva-Rivera, L.J. Dumyahn, S.L. Farina, A. Krause, B. Napoletano, B.M. Gage, S.H. and Pieretti, N. (2011b) Soundscape ecology: the science of sound in the landscape. *BioScience,* 61, 203-216.

Pimm, S.L. Jenkins, C.N. Abell, R. Brooks, T.M. Gittleman, J.L. Joppa, L.N. Raven, P.H. Roberts, C.M. and Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752.

Pitcher, B.J. Briefer, E.F. Vannoni, E. and McElligott, A.G. (2014) Fallow bucks attend to vocal cues of motivation and fatigue. *Behavioral Ecology*, 25, 392-401.

Planitz, B.M. Roe, P. Sumitomo, J. Towsey, M.W. Williamson, I. and Wimmer, J. (2009) Listening to nature: techniques for large-scale monitoring of ecosystems using acoustics. *In*: *3rd eResearch Australasia Conference, Sydney 9-13 November 2009*.

Pohl, N.U. Slabbekoorn, H. Neubauer, H. Heil, P. Klump, G.M. and Langemann, U. (2013) Why longer song elements are easier to detect: threshold level-duration functions in the great tit and comparison with human data. *Journal of Comparative Physiology A*, 199, 239-252.

Potamitis, I. Ntalampiras, S. Jahn, O. and Riede, K. (2014) Automatic bird sound detection in long real-field recordings: Applications and tools. *Applied Acoustics*, 80, 1-9.

Poulsen, B.O. (2002) Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. *Biodiversity & Conservation*, 11, 1551-1566.

Primo (2011) *Electret condenser microphone EM172* [Online]. Available at: http://www.primomic.de/pdf/EM172.pdf [Accessed 1 May 2018].

Prince, P. Hill, A. Piña Covarrubias, E. Doncaster, P. Snaddon, J.L. and Rogers, A. (2019) Deploying acoustic detection algorithms on low-cost, open-source acoustic sensors for environmental monitoring. *Sensors*, 19, 553.

Putland, R.L. Constantine, R. and Radford, C.A. (2017) Exploring spatial and temporal trends in the soundscape of an ecologically significant embayment. *Scientific Reports*, 7, 5713.

Quinn, G.P. and Keough, M.J. (2002) *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.

QUT (2016) *Biosecurity threat, invasive pest starlings, monitoring collaboration for QUT and West Australian government* [Online]. Available at: https://www.qut.edu.au/science-engineering/about/news?id=110896 [Accessed 18 May 2019].

R Core Team (2018) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria [Online]. Available at: http://www.R-project.org/ [Accessed 10 March 2019].

Rachwald, A. Bradford, T. Borowski, Z. and Racey, P.A. (2016) Habitat preferences of soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825) and common pipistrelle *Pipistrellus* (Schreber, 1774) in two different woodlands in North East Scotland. *Zoological Studies*, 55, 1-8.

Rainho, A. Augusto, A.M. and Palmeirim, J.M. (2010) Influence of vegetation clutter on the capacity of ground foraging bats to capture prey. *Journal of Applied Ecology*, 47, 850-858.

Rajan, S.C. Athira, K. Jaishanker, R. Sooraj, N.P. and Sarojkumar, V. (2019) Rapid assessment of biodiversity using acoustic indices. *Biodiversity and Conservation*, 28, 2371-2383.

Ramirez, J.I. Jansen, P.A. and Poorter, L. (2018) Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: A semi-quantitative review. *Forest Ecology and Management*, 424, 406-419.

Rasband, W.S. (2017) *ImageJ (National Institutes of Health, Bethesda)* [Online]. Available at: http://rsb.info.nih.gov/ij/ [Accessed 6 December 2017].

Razgour, O. Hanmer, J. and Jones, G. (2011) Using multi-scale modelling to predict habitat suitability for species of conservation concern: the grey long-eared bat as a case study. *Biological Conservation*, 144, 2922-2930.

Reason, P.F. Newson, S.E. and Jones, K.E. (2016) *Recommendations for using automatic bat identification software with full spectrum recordings* [Online]. Available at: https://cdn.bats.org.uk/pdf/AutomaticID_Recommendations_Version_date_210416.pdf [Accessed 7 June 2019].

Reif, J. Marhoul, P. and Koptík, J. (2013) Bird communities in habitats along a successional gradient: Divergent patterns of species richness, specialization and threat. *Basic and Applied Ecology*, 14, 423-431.

Renner, S.C. Suarez-Rubio, M. Kaiser, S. Nieschulze, J. Kalko, E.K. Tschapka, M. and Jung, K. (2018) Divergent response to forest structure of two mobile vertebrate groups. *Forest Ecology and Management*, 415, 129-138.

Retamosa Izaguirre, M.I. Ramírez-Alán, O. and De la O Castro, J. (2018) Acoustic indices applied to biodiversity monitoring in a Costa Rica dry tropical forest. *Journal of Ecoacoustics*, 2: #TNW2NP.

RHS (2018) *Hedges: selection* [Online]. Available at: https://www.rhs.org.uk/advice/profile?pid=351#section-3 [Accessed 3 November 2018].

Richards, S.A. (2008) Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, 45, 218-227.

Richmond Biodiversity Partnership (2010) *London Borough of Richmond upon Thames: Bats* [Online]. Available at: https://www.richmond.gov.uk/media/6904/bats.pdf [Accessed 22 December 2017].

Riede, K. (1998) Acoustic monitoring of Orthoptera and its potential for conservation. *Journal of Insect Conservation*, 2, 217-223.

Ritchie, M.E. and Olff, H. (1999) Herbivore diversity and plant dynamics: compensatory and additive effects. *In*: H. Olff, V.K. Brown & R.H. Drent, eds. *Herbivores: Between Plants and Predators*. Oxford, UK: Blackwell Science, 175-204.

Rivers, N.M. Butlin, R.K. and Altringham, J.D. (2006) Autumn swarming behaviour of Natterer's bats in the UK: population size, catchment area and dispersal. *Biological Conservation*, 127, 215-226.

Roberge, J. Virkkala, R. and Mönkkönen, M. (2018) Boreal Forest Bird Assemblages and Their Conservation. *In*: G. Mikusiński, J. Roberge & R. Fuller, eds. *Ecology and Conservation of Forest Birds*. Cambridge, UK: Cambridge University Press, 183-230.

Robertson, P.A. (1992) Woodland Management for Pheasants. *Forestry Commission Bulletin 106*, 1-18.

Rodriguez, A. Gasc, A. Pavoine, S. Grandcolas, P. Gaucher, P. and Sueur, J. (2014) Temporal and spatial variability of animal sound within a neotropical forest. *Ecological Informatics*, 21, 133-143.

Rodwell, J.S. (2006) *National vegetation classification: Users' handbook*. Peterborough, UK: Joint Nature Conservation Committee.

Roe, P. and Wimmer, J. (2014) *QUT Acoustic Monitoring Workshop* [Online]. Available at: http://birdlife.org.au/images/uploads/branches/documents/SQ-Acoustics_workshop_ overview.pdf [Accessed 8 May 2019].

Rogowitz, B.E. Treinish, L.A. and Bryson, S. (1996) How not to lie with visualization. *Computers in Physics*, 10, 268-273.

Root-Gutteridge, H. Bencsik, M. Chebli, M. Gentle, L.K. Terrell-Nield, C. Bourit, A. and Yarnell, R.W. (2014) Identifying individual wild Eastern grey wolves (*Canis lupus lycaon*) using fundamental frequency and amplitude of howls. *Bioacoustics*, 23, 55-66.

Ross, J.C. and Allen, P.E. (2014) Random forest for improved analysis efficiency in passive acoustic monitoring. *Ecological Informatics*, 21, 34-39.

RStudio Team (2016) *RStudio: Integrated Development for R. RStudio*, Inc., Boston, MA.

Ruczyński, I. Zahorowicz, P. Borowik, T. and Hałat, Z. (2017) Activity patterns of two syntopic and closely related aerial-hawking bat species during breeding season in Białowieża Primaeval Forest. *Mammal Research*, 62, 65-73.

Ruppé, L. Clément, G. Herrel, A. Ballesta, L. Décamps, T. Kéver, L. and Parmentier, E. (2015) Environmental constraints drive the partitioning of the soundscape in fishes. *Proceedings of the National Academy of Sciences of the USA*, 112, 6092-6097.

Ruskule, A. Nikodemus, O. Kasparinskis, R. Bell, S. and Urtane, I. (2013) The perception of abandoned farmland by local people and experts: Landscape value and perspectives on future land use. *Landscape and Urban Planning*, 115, 49-61.

Rutten, G. Ensslin, A. Hemp, A. and Fischer, M. (2015) Vertical and horizontal vegetation structure across natural and modified habitat types at Mount Kilimanjaro. *PLOS One*, 10, e0138822.

Rydell, J. Nyman, S. Eklöf, J. Jones, G. and Russo, D. (2017) Testing the performances of automated identification of bat echolocation calls: A request for prudence. *Ecological Indicators*, 78, 416-420.

Šálek, M. Svobodová, J. and Zasadil, P. (2010) Edge effect of low-traffic forest roads on bird communities in secondary production forests in central Europe. *Landscape Ecology*, 25, 1113-1124.

Sandom, C.J. Clouttick, D. Manwill, M. and Bull, J.W. (2016) *Rewilding Knowledge Hub: Bibliography - Version 1.0* [Online]. Available at: https://www.rewildingbritain.org.uk/assets/uploads/files/knowledge-hub/Rewilding_Knowledge_Hub_Summary_v1.0LowRes.pdf [Accessed 3 August 2019].

Sandom, C.J. Dempsey, B. Bullock, D. Ely, A. Jepson, P. Jimenez-Wisler, S. Newton, A. Pettorelli, N. and Senior, R.A. (2019) Rewilding in the English uplands: Policy and practice. *Journal of Applied Ecology*, 56, 266-273.

Sandom, C.J. Ejrnæs, R. Hansen, M.D. and Svenning, J.C. (2014) High herbivore density associated with vegetation diversity in interglacial ecosystems. *Proceedings of the National Academy of Sciences of the USA*, 111, 4162-4167.

Sauer, J.R. Peterjohn, B.G. and Link, W.A. (1994) Observer differences in the North American breeding bird survey. *The Auk*, 111, 50-62.

Schieltz, J.M. and Rubenstein, D.I. (2016) Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? *Environmental Research Letters*, 11, 113003.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103-113.

Schirmel, J. Bundschuh, M. Entling, M.H. Kowarik, I. and Buchholz, S. (2016) Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. *Global Change Biology*, 22, 594-603.

Schmidt, A.K. and Balakrishnan, R. (2015) Ecology of acoustic signalling and the problem of masking interference in insects. *Journal of Comparative Physiology A*, 201, 133-142.

Schnitzler, H.U. and Kalko, E.K. (2001) Echolocation by Insect-Eating Bats. *Bioscience*, 51, 557-569.

Schnitzler, H.U. Moss, C.F. and Denzinger, A. (2003) From spatial orientation to food acquisition in echolocating bats. *Trends in Ecology and Evolution*, 18, 386-394.

Schulze, K.A. Rosenthal, G. and Peringer, A. (2018) Intermediate foraging large herbivores maintain semi-open habitats in wilderness landscape simulations. *Ecological Modelling*, 379, 10-21.

Scott, C. (2012) *Automated techniques for bat echolocation call analysis*. Ph.D. thesis, University of Leeds.

Scott, C. (2017) *BatClassify* [Online] Available at: https://bitbucket.org/chrisscott/batclassify [Accessed 21 December 2017].

Scott, C. and Altringham, J. (2014) *Report to DEFRA WC1015 Developing Effective Methods for the Systematic Surveillance of Bats in Woodland Habitats in the UK* [Online]. Available at: http://sciencesearch.defra.gov.uk/Document.aspx?Document=12239_WC1015WoodlandBatsFinalReport.pdf [Accessed 12 May 2019].

Sekercioglu, C.H. (2002) Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biological Conservation*, 107, 229-240.

Servick, K. (2014) Eavesdropping on Ecosystems. *Science*, 343, 834-837.

Sethi, S.S. Ewers, R.M. Jones, N.S. Orme, C.D.L. and Picinali, L. (2018) Robust, real-time and autonomous monitoring of ecosystems with an open, low-cost, networked device. *Methods in Ecology and Evolution*, 9, 2383-2387.

Shannon, C.E. (1948) A mathematical theory of communication. *Bell System Technical Journal*, 27, 379-423.

Sheehan, D.K. Gregory, R.D. Eaton, M.A. Bubb, P.J. and Chenery, A.M. (2010) *The wild bird index–guidance for national and regional use*. UNEP-WCMC, Cambridge, 25.

Shonfield, J. and Bayne, E. (2017) Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*, 12: 14.

Siemers, B.M. and Schnitzler, H.U. (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature*, 429, 657.

Siemers, B.M. and Swift, S.M. (2006) Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). *Behavioral Ecology and Sociobiology*, 59, 373-380.

Sleep, D.J. and Brigham, R.M. (2003) An experimental test of clutter tolerance in bats. *Journal of Mammalogy*, 84, 216-224.

Smit, C. Ruifrok, J.L. van Klink, R. and Olff, H. (2015) Rewilding with large herbivores: The importance of grazing refuges for sapling establishment and wood-pasture formation. *Biological Conservation*, 182, 134-142.

Snowdonia Rhododendron Partnership (2015) *The Ecosystem Benefits of managing the invasive non–native plant Rhododendron ponticum in Snowdonia* [Online] Available at: http://www.eryri.llyw.cymru/__data/assets/pdf_file/0019/546112/Rhododendron-in-Snowdonia.pdf [Accessed 22 January 2018].

Stein, A. Gerstner, K. and Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866-880.

Stewart, A.J.A. (2001) The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. *Forestry: An International Journal of Forest Research*, 74, 259-270.

Stimpert, A.K. Au, W.W. Parks, S.E. Hurst, T. and Wiley, D.N. (2011) Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring. *The Journal of the Acoustical Society of America*, 129, 476-482.

Stirnemann, I.A. Ikin, K. Gibbons, P. Blanchard, W. and Lindenmayer, D.B. (2015) Measuring habitat heterogeneity reveals new insights into bird community composition. *Oecologia*, 177, 733-746.

Storchová, L. and Hořák, D. (2018) Life-history characteristics of European birds. *Global Ecology and Biogeography*, 27, 400-406.

Stout, J.C. (2007) Pollination of invasive *Rhododendron ponticum* (Ericaceae) in Ireland. *Apidologie*, 38, 198-206.

Stowell, D. and Plumbley, M.D. (2014) Automatic large-scale classification of bird sounds is strongly improved by unsupervised feature learning. *PeerJ*, 2, e488.

Suarez-Rubio, M. Ille, C. and Bruckner, A. (2018) Insectivorous bats respond to vegetation complexity in urban green spaces. *Ecology and Evolution*, 8, 3240-3253.

Sueur, J. Aubin, T. and Simonis, C. (2008b) Equipment review: seewave, a free modular tool for sound analysis and synthesis. *Bioacoustics*, 18, 213-226.

Sueur, J. and Farina, A. (2015) Ecoacoustics: the Ecological Investigation and Interpretation of Environmental Sound. *Biosemiotics*, 8, 493-502.

Sueur, J. Farina, A. Gasc, A. Pieretti, N. and Pavoine, S. (2014) Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acoustica*, 100, 772-781.

Sueur, J. Gasc, A. Grandcolas, P. and Pavoine, S. (2012) Global estimation of animal diversity using automatic acoustic sensors. *In*: J.F. Le Galliard, J.M. Guarini & F. Gaill, eds. *Sensors for ecology: Towards integrated knowledge of ecosystems*. Paris, France: CNRS, 99-117.

Sueur, J. Pavoine, S. Hamerlynck, O. and Duvail, S. (2008a) Rapid acoustic survey for biodiversity appraisal. *PLOS One*, 3, p.e4065.

Svenning, J.C. Munk, M. and Schweiger, A. (2019) Trophic rewilding: Ecological restoration of top-down trophic interactions to promotes self-regulating biodiverse ecosystems. *In*: N. Pettorelli, S. Durant & J. Du Toit, eds. *Rewilding (Ecological Reviews)*. Cambridge, UK: Cambridge University Press, 73-98.

Swanson, M.E. Franklin, J.F. Beschta, R.L. Crisafulli, C.M. DellaSala, D.A. Hutto, R.L. Lindenmayer, D.B. and Swanson, F.J. (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, 9, 117-125.

Sweeney, O.F.M.D. Wilson, M.W. Irwin, S. Kelly, T.C. and O'Halloran, J. (2010) The influence of a native tree species mix component on bird communities in non-native coniferous plantations in Ireland. *Bird Study*, 57, 483-494.

Swift, S.M. (1980) Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology*, 190, 285-295.

Taherzadeh, S. (2007) *Assessing Noise in Our Environment*. Milton Keynes, UK: The Open University Press, ISBN 9780749218638.

Taylor, A. McCallum, H.I. Watson, G. and Grigg, G.C. (2017) Impact of cane toads on a community of Australian native frogs, determined by 10 years of automated identification and logging of calling behaviour. *Journal of Applied Ecology*, 54, 2000-2010.

Taylor, R.S. Penrose, L. and Rotherham, I.D. (2003) *Rhododendron and Its Management (No. 6)*. Bingley, UK: STRI.

Terraube, J. Archaux, F. Deconchat, M. Van Halder, I. Jactel, H. and Barbaro, L. (2016) Forest edges have high conservation value for bird communities in mosaic landscapes. *Ecology and Evolution*, 6, 5178-5189.

Tews, J. Brose, U. Grimm, V. Tielbörger, K. Wichmann, M.C. Schwager, M. and Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31, 79-92.

Thinh, V.T. (2006) Bird species richness and diversity in relation to vegetation in Bavi National Park, Vietnam. *Ornithological Science*, 5, 121-125.

Thomas, R.J. (1999) Two tests of a stochastic dynamic programming model of daily singing routines in birds. *Animal Behaviour*, 57, 277-284.

Thomas, A. (2019) *RSPB Guide to Birdsong*. London: Bloomsbury Publishing Plc.

Tiedeken, E.J. and Stout, J.C. (2015) Insect-flower interaction network structure is resilient to a temporary pulse of floral resources from invasive *Rhododendron ponticum*. *PLOS One*, 10, e0119733.

Tishechkin, D.Y. and Bukhvalova, M.A. (2009) Acoustic communication in grasshopper communities (Orthoptera: Acrididae: Gomphocerinae): segregation of acoustic niches. *Russian Entomological Journal*, 18, 165-188.

Titley Scientific (2019) *AnaBat™ Swift Bat Detector User Manual V. 1.6* [Online] https://www.titley-scientific.com/uk/downloads/dl/file/id/44/product/0/anabat_swift_user_manual_v1_6.pdf [Accessed 9 May 2019].

TLUG (2017) *Linfos: Thüringer Arten-Erfassungsprogramm der TLUG, Liste der Arten: Brutvögel*. Jena, Germany: Thüringer Landesanstalt für Umwelt und Geologie.

Torres, A. Fernández, N. zu Ermgassen, S. Helmer, W. Revilla, E. Saavedra, D. Perino, A. Mimet, A. Rey-Benayas, J.M. Selva, N. and Schepers, F. (2018) Measuring rewilding progress. *Philosophical Transactions of the Royal Society of London B*, 373, 20170433.

Towsey, M. Wimmer, J. Williamson, I. and Roe, P. (2014b) The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecological Informatics*, 21, 110-119.

Towsey, M. Zhang, L. Cottman-Fields, M. Wimmer, J. Zhang, J. and Roe, P. (2014a) Visualization of long-duration acoustic recordings of the environment. *Procedia Computer Science*, 29, 703-712.

Tree, I. (2017) The Knepp Wildland project. *Biodiversity*, 18, 206-209.

Tree, I. (2018) *Wilding: The Return of Nature to a British Farm*. London, UK: Pan Macmillan.

Trimpop, M. and Mann, P. (2014) Determination of noise damping by forests. *In: INTER-NOISE and NOISE-CON Congress and Conference Proceedings*, Melbourne, Australia 16-19 November 2014, 3399-3405.

Turner, A. Fischer, M. and Tzanopoulos, J. (2018) Sound-mapping a coniferous forest-Perspectives for biodiversity monitoring and noise mitigation. *PLOS One*, 13, e0189843.

Ulyshen, M.D. (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management*, 261, 1479-1489.

van Der Plas, F. Manning, P. Soliveres, S. Allan, E. Scherer-Lorenzen, M. Verheyen, K. Wirth, C. Zavala, M.A. Ampoorter, E. Baeten, L. Barbaro, L. *et al*. (2016) Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences of the USA*, 113, 3557-3562.

van Klink, R. Ruifrok, J.L. and Smit, C. (2016) Rewilding with large herbivores: Direct effects and edge effects of grazing refuges on plant and invertebrate communities. *Agriculture, Ecosystems and Environment*, 234, 81-97.

van Klink, R. and WallisDeVries, M.F. (2018) Risks and opportunities of trophic rewilding for arthropod communities. *Philosophical Transactions of the Royal Society of London B*, 373, 20170441.

van Schaik, J. Janssen, R. Bosch, T. Haarsma, A.J. Dekker, J.J. and Kranstauber, B. (2015) Bats swarm where they hibernate: compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. *PLOS One*, 10, e0130850.

Vaughan, N. Jones, G. and Harris, S. (1997) Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *Journal of Applied Ecology*, 34, 716-730.

Veen, T. Sheldon, B.C. Weissing, F.J. Visser, M.E. Qvarnström, A. and Sætre, G.P. (2010) Temporal differences in food abundance promote coexistence between two congeneric passerines. *Oecologia*, 162, 873-884.

Vera, F.W.M. (2000) *Grazing Ecology and Forest History*. Wallingford, UK: CABI Publishing.

Vera, F.W.M. Bakker, E. and Olff, H. (2006) Large herbivores: Missing partners of western European light-demanding tree and shrub species? *In:* K. Danell, R. Bergström, P. Duncan & J. Pastor, eds. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Cambridge, UK: Cambridge University Press, 203-231.

Verheyen, K. Vanhellemont, M. Auge, H. Baeten, L. Baraloto, C. Barsoum, N. Bilodeau-Gauthier, S. Bruelheide, H. Castagneyrol, B. Godbold, D. and Haase, J. (2016) Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio*, 45, 29-41.

Vidaña-Vila, E. Navarro, J. and Alsina-Pagès, R. (2017) Towards automatic bird detection: An annotated and segmented acoustic dataset of seven *Picidae* species. *Data*, 2, 18.

Villanueva-Rivera, L.J. (2015) *Soundecology* [Online]. Available at: http://ljvillanueva.github.io/soundecology [Accessed 20 February 2016].

Villanueva-Rivera, L.J. Pijanowski, B.C. Doucette, J. and Pekin, B. (2011) A primer of acoustic analysis for landscape ecologists. *Landscape Ecology*, 26, 1233-1246.

Visser, M.E. Holleman, L.J. and Gienapp, P. (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, 147, 164-172.

Walsh, A.L. and Harris, S. (1996) Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology*, 33, 508-518.

wa Maina, C. Muchiri, D. and Njoroge, P. (2016) A Bioacoustic Record of a Conservancy in the Mount Kenya Ecosystem. *Biodiversity Data Journal*, 4, e9906.

Waring, P. and Townsend, M. (2017) *Field guide to the moths of Great Britain and Ireland.* Third ed. London, UK: Bloomsbury Publishing.

Warren, M.R. Spurrier, M.S. Roth, E.D. and Neunuebel, J.P. (2018) Sex differences in vocal communication of freely interacting adult mice depend upon behavioral context. *PLOS One*, 13, e0204527.

Webb, W.H. Brunton, D.H. Aguirre, J.D. Thomas, D.B. Valcu, M. and Dale, J. (2016) Female song occurs in songbirds with more elaborate female coloration and reduced sexual dichromatism. *Frontiers in Ecology and Evolution*, 4, 22, DOI: 10.3389/fevo.2016.00022

Welch, J.N. Fordyce, J.A. and Simberloff, D.S. (2016) Indirect impacts of invaders: A case study of the Pacific sheath-tailed bat (*Emballonura semicaudata rotensis*). *Biological Conservation*, 201, 146-151.

Welch, J.N. and Leppanen, C. (2017) The threat of invasive species to bats: a review. *Mammal Review*, 47, 277-290.

Weller, T.J. and Zabel, C.J. (2002) Variation in bat detections due to detector orientation in a forest. *Wildlife Society Bulletin*, 30, 922-930.

Wesołowski, T. Fuller, R.J. and Flade, M. (2018) Temperate Forests: A European Perspective on Variation and Dynamics in Bird Assemblages. *In:* G. Mikusiński, J. Roberge & R.J. Fuller, eds. *Ecology and Conservation of Forest Birds*. Cambridge, UK: Cambridge University Press, 253-317.

Whytock, R.C. and Christie, J. (2016) Solo: an open source, customizable and inexpensive audio recorder for bioacoustic research. *Methods in Ecology and Evolution*, 8, 308-312.

Wickramasinghe, L.P. Harris, S. Jones, G. and Vaughan, N. (2003) Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *Journal of Applied Ecology*, 40, 984-993.

Wildlife Acoustics (2016) *Song Meter SM4 Acoustic Recorder* [Online] www.wildlifeacoustics.com/images/product_brochures/WA_Brochure_SM4.pdf [Accessed 15 February 2016].

Wildlife Acoustics (2017) *Song Meter user manual* [Online]. Available at: https://www.wildlifeacoustics.com/images/documentation/SM1-user-manual.pdf [Accessed 8 May 2019].

Wildlife Acoustics (2019a) *Song Meter SM4 User Guide* [Online]. Available at: https://www.wildlifeacoustics.com/images/documentation/SM4-USER-GUIDE.pdf [Accessed 8 May 2019].

Wildlife Acoustics (2019b) *Song Meter SM4BAT FS user guide* [Online]. Available at: https://www.wildlifeacoustics.com/images/documentation/SM4-BAT-FS-USER-GUIDE.pdf [Accessed 9 May 2019].

Wildlife Acoustics (2019c) *Kaleidoscope Pro 5: User Guide* [Online]. Available at: https://www.wildlifeacoustics.com/images/documentation/Kaleidoscope-Pro-5-User-Guide.pdf [Accessed 11 May 2019].

Wildlife Acoustics (2019d) *Kaleidoscope Pro analysis software* [Online]. Available at: https://www.wildlifeacoustics.com/products/kaleidoscope-pro [Accessed 12 May 2019].

Wiley, R.H. and Richards, D.G. (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, 3, 69-94.

Willmott, J.R. Forcey, G.M. and Hooton, L.A. (2015) Developing an automated risk management tool to minimize bird and bat mortality at wind facilities. *Ambio*, 44, 557-571.

Willson, M.F. (1974) Avian community organization and habitat structure. *Ecology*, 55, 1017-1029.

Wilson, M.W. Pithon, J. Gittings, T. Kelly, T.C. Giller, P.S. and O'Halloran, J. (2006) Effects of growth stage and tree species composition on breeding bird assemblages of plantation forests. *Bird Study*, 53, 225-236.

Wimmer, J. Towsey, M. Roe, P. and Williamson, I. (2013) Sampling environmental acoustic recordings to determine bird species richness. *Ecological Applications*, 23, 1419-1428.

Wolfgang, A. and Haines, A. (2016) Testing automated call-recognition software for winter bird vocalizations. *Northeastern Naturalist*, 23, 249-259.

WWF (2018) *Living Planet Report - 2018: Aiming Higher*. M. Grooten & R.E.A. Almond, eds. Gland, Switzerland: WWF.

Wrege, P.H. Rowland, E.D. Keen, S. and Shiu, Y. (2017) Acoustic monitoring for conservation in tropical forests: examples from forest elephants. *Methods in Ecology and Evolution*, 8, 1292-1301.

Wyman, M.T. Mooring, M.S. Mccowan, B. Penedo, M.C.T. Reby, D. and Hart, L.A. (2012) Acoustic cues to size and quality in the vocalizations of male North American bison, *Bison bison*. *Animal Behaviour*, 84, 1381-1391.

Yip, D. Leston, L. Bayne, E. Sólymos, P. and Grover, A. (2017) Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data. *Avian Conservation and Ecology*, 12, 11.

Zellweger, F. Roth, T. Bugmann, H. and Bollmann, K. (2017) Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. *Global Ecology and Biogeography*, 26, 898-906.

Zimov, S.A. (2005) Pleistocene park: return of the mammoth’s ecosystem. *Science*, 308, 796-798.

Zsebők, S. Moskát, C. and Bán, M. (2017) Individually distinctive vocalization in Common Cuckoos (*Cuculus canorus*). *Journal of Ornithology*, 158, 213-222.

Zuur, A.F. Ieno, E.N. and Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3-14.