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The Tallgrass Prairie Soundscape; Employing an Ecoacoustic Approach to Understand Grassland Response to Prescribed Burns and the Spatial and Temporal Patterns of Nechrophilous Invertebrate Communities

Sarah Dodgin
University of New Hampshire, Durham

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THE TALLGRASS PRAIRIE SOUNDSCAPE; EMPLOYING AN ECOACOUSTIC APPROACH TO UNDERSTAND GRASSLAND RESPONSE TO PRESCRIBED BURNS AND THE SPATIAL AND TEMPORAL PATTERNS OF NECROPHILOUS INVERTEBRATE COMMUNITIES

BY

SARAH R. DODGIN

Bachelor of Science in Biology at Bloomsburg University of Pennsylvania, 2014

THESIS

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This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Integrative and Organismal Biology by:

Thesis Director, Dr. Daniel R. Howard
Assistant Professor of Neurobiology and Behavior

Dr. Jeff Garnas
Assistant Professor of Forest Ecosystem Health

Dr. Carrie L. Hall
Assistant Professor of Ecology and Biology Education Research

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Abstract

The Tallgrass Prairie Soundscape; Employing an Ecoacoustic Approach to Understand Grassland Response to Prescribed Burns and the Spatial and Temporal Patterns of Necrophilous Invertebrate Communities

By

Sarah R. Dodgin

University of New Hampshire, September 2018

Tallgrass prairies are rapidly vanishing biodiversity hotspots for native and endemic species, yet little is known regarding how spatial and temporal variation of prairie soundscapes relates to seasonal changes, disturbance patterns and biological communities. Ecoacoustics, the study of environmental sounds using passive acoustics as a non-invasive tool for investigating ecological complexity, allows for long-term data to be captured without disrupting biological communities. Two studies were carried out by employing ecoacoustic methodology to study grassland carrion food webs and to capture the phenology of a grassland soundscape following a prescribed burn. Both studies were conducted at the Nature Conservancy's Tallgrass Prairie Preserve (36°50'N, 96°25'W) and used six acoustic indices to quantify the ratio of technophony to biophony, acoustic complexity, diversity, evenness, entropy, and biological acoustic diversity from over 70,000 sound recordings. Acoustic index values were used to determine the relationship between *Nicrophorus* burying beetle species composition and the prairie soundscape (Chapter 1) and to determine if prescribed burning changes the composition of the soundscape over time (Chapter 2). In Chapter 1, I found that associations between *Nicrophorus* burying beetles and the soundscape were unique to particular species, acoustic indices and times of day.

For example, *N. americanus* trap rates showed a positive correlation to areas of increased acoustic complexity specifically at dawn. In addition to positive associations with the soundscape, we found that *N. marginatus* was consistently negatively correlated to higher levels of biophony, while *N. tomentosus* was consistently positively correlated to places with higher levels of biophony. Although reproduction of all species examined is dependent upon securing small carrion for reproduction, I found that known habitat and activity segregation of five *Nicrophorus* beetle species may be reflective of the soundscape. Finally, I show that favorable habitat for a critically endangered necrophilous insect, the American burying beetle (*Nicrophorus americanus*) can be identified by the acoustic signature extracted from a short temporal window of its grassland ecosystem soundscape. Using the same suite of acoustic indices from Chapter 1, in Chapter 2 I examined acoustic recordings at a much larger time scale to determine distinctive acoustic events driven by biophony and geophony across a 23-week period. In addition to examining acoustic changes over time, I examined differences between 11 burned and unburned pastures. Results from this study indicate that prescribed burning does alter the soundscape, especially early in the post-burn period, but the effects are ameliorated by a significant increase in biophony as the growing and breeding season progressed into the warmer summer months. Both studies demonstrate that passive acoustic recording is a reliable method to assess relationships to acoustic communities over space and time.

INTRODUCTION

Soundscapes represent the acoustic signature of an ecosystem, capturing at a single space and time the cumulative acoustic output of biotic and abiotic forces and their interactions as they play out across the landscape. Dimensions of a soundscape, especially when considering the presence of anthropogenic noise, can influence the behavior of organisms across trophic levels spanning from arthropods (Morley et al., 2014; Shamble et al., 2016; Bunkley et al., 2017; to birds (Patricelli and Blickley, 2006), fish (Ladich, 2013) and whales (Parks et al., 2007; Rossi-Santos, 2015). Additionally, soundscapes are highly variable according to season (Krause et al., 2011), climate (Krause and Farina, 2016), elevation (Campos-Cerqueira and Aide, 2017) and disturbance patterns (Alvarez-Berríos et al., 2016; Deichmann et al., 2017). Ambient sounds that contribute to this acoustic phenotype can be generated by biological (biophony), geophysical (geophony), or anthropogenic (technophony) factors (Pijanowski et al., 2011; Farina and James, 2016). Sounds are not only distinguishable based on origin, but usually have predictable spectral signatures and temporal patterns (Sueur et al., 2014). When considered together, these sounds contribute to a complex acoustic arrangement stemming from individual fauna to communities interacting with the landscape (Farina, 2014). Any uninformative sound, regardless of origin is considered noise and is dependent upon the perspective of the organism perceiving the sound (Brumm and Slabbekoorn, 2005; Wollerman and Wiley, 2002). In the well-established field of terrestrial and marine bioacoustics, sound caused by human activity is defined as anthropogenic noise and has been shown to have profound negative impacts on wildlife (Rabin et al., 2003; Wright et al., 2007; Barber et al., 2010; Francis and Barber, 2013; Tennessen et al., 2014; Bunkley et al., 2015. In the context of soundscape ecology or ecoacoustics, anthropogenic noise is defined more explicitly as technophony and is considered separately from biotic and abiotic sounds (Gage and Axel, 2014; Merchant et al., 2015; Mullet et al., 2016). Ecoacoustics combines fundamental concepts of two long-standing disciplines, bioacoustics (aquatic and terrestrial) and landscape ecology, and melds their methodological and analytical techniques into a unique discipline that holds the potential to answer a new suite of pressing ecological questions (Farina and Pieretti, 2012).

Required to answer these questions however, are sophisticated audio recording and analysis technologies familiar to bioacousticians that are faced with similar obstacles (Rempel et al., 2005; Obrist et al., 2010; Beason et al., 2018). Software and statistical packages must then overcome the hurdle of processing files that may contain anywhere from one minute to 24 hours or more of continuous sound. This is a recognized limitation in making soundscape ecology methods practical on a large scale (Villanueva-Rivera et al., 2011; Villanueva-Rivera and Pijanowski, 2012). Data storage however, is becoming less of a barrier to conducting acoustic surveys due to the decreased cost of high capacity data storage devices and cloud-based storage and processing systems including REAL (Kasten et al., 2012), Pumilio (Villanueva-Rivera and Pijanowski, 2012) and ARBIMON (Aide et al., 2013). As such, algorithms to aid in sifting through voluminous sound file collections have been developed for invasive species monitoring (Boelman et al., 2007), rapid biodiversity assessments (Sueur et al., 2008), the quantification of anthropogenic disturbance effects on wildlife (Francis and Barber, 2013; Reed et al., 2012) and wilderness (Barber et al., 2011; Mullet et al., 2017) both logistically tractable and practically useful to the natural resource and conservation communities.

Since the emergence of the field in the late 1980's (Krause, 1987), attributes of soundscapes have been used as an ecological assessment tool across diverse contexts. This approach has been used to map areas most heavily influenced by anthropogenic noise effects

(Barber et al., 2011; Reed et al., 2012; Mennitt et al., 2014; Buxton et al., 2017; Turner et al., 2018) and for qualitative and quantitative sound composition analysis in National Parks (Miller, 2008; Krause et al., 2011; Lynch et al., 2011), rapid biodiversity assessments in ecologically sensitive environments (Sueur et al., 2008a; Gasc et al., 2013) to detect presence/absence of species of rare or endangered species (Digby et al., 2013; Marques et al., 2013; Towsey et al., 2014; Ribeiro et al., 2017) and to monitor the effects of climate change (Krause and Farina, 2016).

Equally as diverse as the context in which ecoacoustic methods are applied are the techniques and equipment used to gather and analyze sound data. Most recorders and microphones deployed in terrestrial settings are commonly used to capture biophony generated by birds, mammals, insects, and/or amphibians (Celis-Murillo et al., 2009; Fuller et al., 2015; Xie et al., 2017; Ferreira et al., 2018) between 20 Hz and 20 kHz which parallels the human range of hearing (Heffner and Heffner, 2007). Until recently, ultrasonic frequencies (>22 kHz) commonly emitted by insects and small mammals had to be captured using recorders specifically designed to conduct bat surveys (Britzke et al., 2013; Bunkley et al., 2015; Bunkley and Barber, 2015). Now, a diverse suite of recording options has become available ranging from mobile smart phones with time-lapse audio recording apps (Towsey and Planitz, 2011) to more sophisticated and expensive programmable recorder units with higher sampling rates (up to 96 KHz) like the Wildlife Acoustics^{TM} SM-series (Maynard, MA, USA) and Frontier Labs BAR recorders (Brisbane, Australia). More complex methods include the use of omnidirectional microphones in a 4-directional arrangement or a series of recorders distributed in an array to estimate bird, elephant and bat populations or to inform directionality of a signal from an individual (Jensen and Miller, 1999; Celis-Murillo et al., 2009; Thompson et al., 2010;

Blumstein et al., 2011). This method of deploying microphone arrays have been shown to increase the probability of detecting and correctly identifying bird vocalizations and estimating abundance over point-count data from human observers (Celis-Murillo et al., 2009). Using both analog (point counts) and digital (audio recordings) observation methods for the same survey effort usually yield most accurate results (Leach et al., 2016; Silva and Bernard, 2017).

While improvements within the field of soundscape ecology continue, the incorporation of consideration of the soundscape in conservation management plans is still limited (Miller, 2008). Acoustic surveys add a rich temporal and spatial dimension to conservation that has long been overlooked (Mazaris et al., 2009). Biological diversity is often reflective of the sounds in an environment (Truax, 1996; Sueur et al., 2008b; Obrist et al., 2010; Gasc et al., 2013). Passive acoustic monitoring, a method fundamental to soundscape ecology, ecoacoustics and bioacoustics is a minimally invasive technique that is well suited for long-term ecological monitoring (Ross et al., 2017). Soundscape recordings have the ability to document daily and seasonal, as well as climate and disturbance-related changes in biodiversity. A benefit to this approach is the ability for acoustic recorders to operate remotely, programmed to collect data at biologically relevant time intervals or scales (Farina et al., 2015). Using remote acoustic sensing techniques allows researchers to monitor at large spatial and temporal scale, both limiting observer bias and producing more robust datasets (Digby et al., 2013; Gasc et al., 2015).

Inter- and intra-observer biases and variable observer auditory acuity and identification expertise present issues in the reliability of many commonly used survey methods (Cyr, 1981; Kepler and Scott 1981; Bart 1985; Emlen and DeJong 1992; Sauer et al., 1994; Kendall et al., 1996; McLaren and Cadman 1999; Hobson et al., 2002, Alldredge et al., 2007, Celis-Murillo et al., 2009). Sound analysis and machine learning tools have been developed that allows for the extraction of relevant spectral and/or temporal data valuable for species identification and biodiversity evaluation across a wide range of acoustic space (Farina et al., 2016; Gage et al., 2017; Farina et al., 2018). Extended periods of time recording, however lead to massive datasets, and while programs and machine learning systems developed to identify specific species are available they have not yet been perfected and usually require an additional validation component to distinguish all ranges of species-specific spectral ranges or for spectrally complex species, especially in birds (Jennings et al., 2008; Aide et al., 2013; Digby et al., 2013; Ferreira et al., 2018). Given the robust capabilities of sound recorders to capture acoustic patterns across greater spectral, temporal and spatial extents, it is now feasible to answer ecological questions from a more comprehensive, community-level perspective in a non-invasive manner where data collection and equipment can be managed by technicians with minimal training (Farina and Pieretti, 2012; Xie et al., 2017; Ulloa et al., 2018). Given these advantages, acoustic monitoring can be used as an alternative or used in addition to such methods for population data collection, especially those that rely heavily on visual observations (point counts, transect surveys, game cameras) and physical capture (mist netting, trapping). Additionally, when large-scale rapid biodiversity assessments are not feasible due to challenging terrain, geographic isolation, and lack of locally available trained experts, sound-based surveys may be beneficial (Wrege et al., 2010; Gasc et al., 2013). Soundscape surveys rely on autonomous, remotely operated recorders that are deployed for days to months at a time and automatically create and securely store a permanent record of recordings (Farina and Pieretti, 2012; Aide et al., 2013; Farina et al., 2018;). Accordingly, such studies do not require the direct presence of a surveyor, thus observer biases inherent to methods traditionally used to collect population data are minimized (Celis-Murillo et al., 2009; Harris et al., 2016). Further, animal behavior is not modified due to the presence of a human observer which has been shown to startle, elicite alarm calls and increase stress and heart rate in animals (Lobel, 2001; Constantine et al., 2004; Jack et al., 2008). When the observer is removed, biophony that reflects normal, unperturbed behavior is captured. Remote operation does have both a beneficial and negative component as one could come back to a recording station only to discover that equipment has been vandalized by humans or wildlife, rendering the survey effort futile. Conversely, the recording unit could detect rare or unique acoustic events that would have otherwise gone unnoticed and is especially useful to monitor elusive or rare species in aquatic and terrestrial ecosystems (Rebelo and Jones, 2010; Marques et al., 2011; Funk et al., 2012). For example, unexpected calling times of Southern Leopard Frogs (*Rana sphenocephala*) which would have gone undetected if not for the deployment of an automatic recording system provided evidence that long-standing protocols should be updated to reflect newly discovered activity patterns of focal species surveys (Bridges and Dorcas, 2000). Although some ecoacoustic studies focus on automated techniques to identify focal fauna or to cluster acoustically similar events in recordings using automated detection algorithms such as Kaleidoscope Analysis Software (Wildlife Acoustics Inc.), Arbimon Bioacoustic Analysis Platform (Sieve Analytics 2015), Multiresolution Analysis of Acoustic Diversity (MAAD) (Ulloa et al., 2018) and Ecoacoustic Event Detection and Identification (EEDI) (Farina et al., 2016; Farina et al., 2018), a substantial emphasis in soundscape ecology remains focused on the use of acoustic indices to quantify acoustic complexity by evaluating spectral parameters of large quantities of sound recordings (see Table 1.1). The putative function of these indices is to create a comparative measure of acoustic diversity not unlike traditional indices of biodiversity or species richness (i.e. Simpson's diversity (Shannon, 1948; Lande, 1996). Ambient sounds can be characterized by biological, geophysical, or anthropogenic origin which have predictable spectral signatures and temporal patterns (Farina et al., 2011; Sueur et al., 2014). Acoustic indices are designed to take advantage of these predictable characteristics of each sound source since low frequency sounds are typically abiotic (geophony and technophony) and higher frequency sounds (>2000 Hz) are biotic. Within the biophonic spectrum, acoustic partitioning is observed at the species level of acoustic signal evolution, allowing individuals to minimize errors in the interpretation of signals from heterospecifics and conspecifics. (Krause, 1993; Amézquita et al., 2006; Amezquita et al., 2011; Sueur et al., 2012; Wilkins et al., 2013). Acoustic partitioning is seen in the evolutionary history of species that rely on sound production for communication and is supported by the Acoustic Niche Hypothesis (Krause, 1993) which suggests that to avoid interspecific competition, communication signals are partitioned by time and frequency. The Acoustic Complexity Index (ACI) (Pieretti et al., 2011) the Normalized Difference Spectral Density Index (NDSI) (Kasten et al., 2012) the Bioacoustic Index (BIO) (Boelman et al., 2007) and the Acoustic Diversity and Evenness Indices (ADI and AEI) (Villanueva-Rivera et al., 2011) are commonly applied to interpret ecoacoustic phenomena. These indices can be calculated using the open access R packages *Seewave* (Sueur, 2015) and *soundecology* (Villanueva-Rivera and Pijanowski 2018) packages in R (Table 1.1). While the algorithms incorporated into the suite of acoustic indices available for soundscape data analysis are suitable for answering many ecological questions where sound plays a role, there are several factors that can confound the analytical process and interpretation of sound recordings. These include: (1) understanding how the values of a particular acoustic index relates other ecological metrics and (2) the frequency limitations (i.e., sample rate) of the recorder that are preset by the researcher to limit the range of acoustic space sampled or limited by the recorder codec, which may yield an incomplete representation of the faunal contributors to the soundscape. In the first case, most ecoacoustic research omits from study design the pairwise comparison of acoustic index values with relevant in-situ ecological data, especially when it comes to non-soniferous fauna. Measures have been taken in controlled settings to determine the effectiveness of alpha acoustic complexity indices by way of simulated soundscapes in order to control the signal to noise ratio and number of (bird) species per recording (Kendrick et al., 2016). It becomes important to know which index will yield most accurate results under favorable vs unfavorable environmental conditions. In the second case, until recently, many ecoacoustic surveys omit a biologically relevant range of frequencies (those above 22 kHz) due to the limited sampling rate of the employed recorders or the sensitivity range of the microphones. Additionally, many acoustic indices include default parameterization that relegates all low frequency dimensions of the soundscape (<2kHz) as anthropogenic noise, despite many species contributing sound to this spectral range. Few studies explicitly address these omissions and limitations (see Ritts et al., 2016 for exceptions). Depending on the research objective, acoustic surveys may offer an attractive alternative to traditional surveys of soniferous fauna all together given the shortcomings of traditional survey methods. However, terrestrial acoustic surveys are a relatively new approach for ecological monitoring with their own limitations. Disadvantages to implementing soundscape ecology methods include: unless an array of microphones are used (as described in (Celis-Murillo et al., 2009), relative species abundance cannot be easily quantified, recording equipment can be expensive, storage of sound files requires large volumes of digital storage and backup space, uploading and analyzing hours of files can be labor and time-intensive. Nonetheless, soundscape ecology has the potential to enhance our understanding of ecosystem function from individual behavior (Bridges and Dorcas, 2000; Nattier et al., 2011; Wood and Yezerinac, 2006) to community assemblage structure (Solla et al., 2006; Farina and Pieretti, 2012; Deichmann et al.,

2017) to long-term ecological change. Ecoacoustics is an inherently integrative field which combines elements from landscape ecology, bioacoustics, computer science, animal behavior, population and community ecology, geophysical sciences, and evolutionary biology. Similar to questions driving landscape ecology research, soundscape ecology considers the myriad of interactions which occur in functional ecological spaces and land-use by humans and natural inhabitants (plants, animals, microorganisms, soil, hydrology, etc.) (Mazaris et al. 2009). Data collection however, more closely resembles bioacoustics because researchers rely on recording instruments. Because this field is still in its developmental stages and is constantly being built upon with new terminology, definitions, recording technology and analysis methods, publications and open communication is necessary to advance the field to better inform management plans and policy (Farina and James, 2016). My research uses soundscape recordings to 1) address gaps in knowledge related to how non-soniferous species may respond to the environment in similar-enough ways to the soniferous taxa that the soundscape can help predict their abundance and 2) assess how grassland phenology can be described through the soundscape in relation to fire disturbance.

I evaluated spatial and temporal relationships between *Nicrophorus* burying beetle community members and the acoustic signature of an ecosystem (Chapter 1) and the acoustic signature of ecological disturbance by fire of a tallgrass prairie over space and time (Chapter 2). Although the focal species of my first experimental chapter produce stridulations resulting in air-borne sounds, they are low amplitude signals (Hall et al., 2013) that functionally do not contribute to the soundscape. In addition to their inability to produce sounds detectable using conventional soundscape recording methods, there is no evidence that burying beetles can perceive air-borne sound due to the lack of obvious hearing structures (Hall et al., 2013). Their reproductive behavior however, is inherently linked to sound-producing organisms. Small vertebrate carcasses (birds and mammals) are central to the life history of burying beetles (genus *Nicrophorus*) (Trumbo, 1990; Scott, 1998; Rozen, 2008; Woelber et al 2018). Instead of auditory cues to detect this stochastic resource, they rely on chemoreception to locate carcasses and attract a mate where they will copulate, bury the carcass underground and most notably, provide biparental care for their offspring (Conley, 1982; Lomolino and Creighton, 1996). Because of their dependence on carrion of soniferous animals, I hypothesized that burying beetle species and burying beetle community assemblages would be positively correlated with acoustics signatures that indicate a higher diversity, complexity and abundance of biophony as described by a suite of six acoustic indices (ACI, ADI, AEI, BIO, H, NDSI; Table 1.1).

In my second experimental chapter, I employed the same six acoustic indices to describe the phenology of a tallgrass prairie before and after a disturbance event. Prior to European settlement expansion in the early 1800's, fires in prairies were caused primarily by Native Americans and lightning strikes (Axelrod, 1985; Hulbert, 1988; Umbanhowar, 1996). In addition to a combination of factors including climate, soil and topography, this form of disturbance subsequently discourages the invasion of woody shrubs and trees and allows for grasses and forbs to become established as the dominant primary producers (Bell and Hulbert, 1974; Bragg and Hulbert, 1976; Gibson and Hulbert, 1987; Abrams, 1992; Briggs and Knapp, 1995; Briggs et al., 2002). Following this period of European settlement expansion, major landscape and ecosystem alterations occurred resulting in a more than 90% reduction in the historic extent of the Great Plains grasslands (Samson and Knopf, 1994). Alterations to the Great Plains landscape is driven primarily through conversion of prairie to agriculture (Fuhlendorf et al., 2002; Samson et al., 2004). What remains of intact prairie have been sequestered into protected lands where human development is minimal; however, oil and gas extraction is ubiquitous in this region of the United States and still exists in ecologically sensitive areas (Francis et al., 2011; Blickley et al., 2012; Hovick et al., 2014). Today, protected native prairie is managed by private, federal, state, tribal and non-profit conservation entities where controlled fire prescription, mowing and grazing throughout the year is a common practice (Collins et al., 1998; Hamilton, 2007). At the Tallgrass Prairie Preserve, the most intensive burning takes place in late winter/early spring to remove dead standing grasses and detritus from the previous seasons. This action allows for decreased interception of inorganic nitrogen-containing rainwater by detritus, thus allowing for more nitrogen to reach the soil which can be taken up by living grass roots (Knapp and Seastedt, 1986; Hulbert, 1988; Hobbs et al., 1991; Ojima et al., 1994; Pepper et al., 2005). Following this disturbance, bird migrants establish nesting sites and later in the spring and summer, insects emerge to make their advertisement calls until late summer/ early fall. Grassland bird (Reinking, 2005; Sandercock et al., 2015; Fuhlendorf et al., 2017) and insect (Römer, 1993; Callaham et al., 2002; Howard and Hill, 2009) species have been well-studied regarding burn stage preference. Factors influencing this preference range from soil moisture and soil temperature to the physical properties of sound transmission depending on different heights, ages and densities of grass. Because grassland floristic and faunal communities are adapted to be resilient to fire disturbance (Fuhlendorf & Engle, 2004) and based on what is known regarding tallgrass prairie seasonal phenology, I hypothesized that areas of the Tallgrass Prairie Preserve that were burned in early spring 2017 will support greater biological acoustic diversity by the time grass regeneration has reached its peak in late July compared to areas that remained undisturbed by fire in the previous year.

Chapter 1: Temporal and spatial heterogeneity of a tallgrass prairie soundscape in relation to the distribution and composition of a *Nicrophorus* burying beetle community

Introduction

Acoustic communities comprising interacting populations of sound-producing species engaged in intra- and interspecific communication, represent the biotic component of a soundscape (Luther, 2009; Depraetere et al., 2012; Farina & James, 2016; Campos-Cerqueira & Aide, 2017; Xie et al., 2017; Ulloa et al., 2018). Evolving in the context of competition for acoustic space imposed by the presence of biotic signals (biophony) along with both geophysical (geophony) and human-generated (technophony) sources of sound, the emergent acoustic properties of these communities represent an acoustic signature of an ecosystem (Pijanowski et al., 2011; Bormpoudakis et al., 2013; Rodriguez et al., 2014; Sueur et al., 2014; Lomolino et al., 2015). The unique signature of an acoustic community emerges from and encodes information about the numerous sender-receiver dyads actively exchanging information across the landscape (Morton, 1975; McWilliam & Hawkins, 2013; Pieretti et al., 2015; Aide et al., 2017). These dyads span trophic (Tuttle & Ryan, 1981; Boelman et al., 2007; Simpson et al., 2008) and taxonomic [(insects (Sueur, 2002), frogs (Garcia-Rutledge and Narins, 2001), mammals (Stimpert et al., 2007), birds (Ryan and Brenowitz, 1985), bats (Kloepper et al., 2017)] levels, and their interactions vary over space and time (Bormpoudakis et al., 2013; Rodriguez et al., 2014; Farina et al., 2015; Job et al., 2016; Mullet et al., 2016). Moreover, sender-receiver communication is shaped by environmental constraints (Wiley and Richards, 1978; Forrest, 1994; Tyack, 1998 Parris, 2002; Ey and Fischer, 2009; Merchant et al., 2015). Thus, the soundscape represents the acoustic fingerprint of a place resulting from the interacting biotic and abiotic forces that shape the adaptive processes underlying an ecosystem.

The adaptive structure of acoustic communities is governed by processes explained by three underlying hypotheses: 1. The Acoustic Adaptation Hypothesis (AAH; Morton, 1975; Ey and Fischer, 2009) which explains the relationship between a species physiological, anatomical and signal evolution that results in optimized communication and signal propagation in conjunction with their physical environment; 2. The Acoustic Niche Hypothesis (ANH; Krause, 1993; Stone, 2000; Villanueva-Rivera, 2014) describes the adaptive evolution of signal spectral, temporal and spatial attributes that reduce intra-specific competition for acoustic space; 3. The Acoustic Habitat Hypothesis (AHH; Mullet et al., 2017) which postulates that animals sense or actively seek acoustic environments that provide suitable habitats with respect to communication, competition, predation risk, access to mates, or foraging opportunities. Treating acoustic spaces as a limited resource, these models identify different axes of competition that may occur and result in the segregation and occupation of acoustic niches within a soundscape (Brumm, 2006; Bradbury & Vehrencamp, 2011; Farina, 2014). Acoustic spaces are regarded as limited resources because of masking in the frequency, timing and amplitude domain of acoustic signal transmission which is mainly be driven by habitat structure and noise from other calling animals and non-natural human generated noise. These factors ultimately interfere with or aid in interspecific communication (Schmidt & Balakrishnan, 2015). Over time, the unique sounds animals have evolved for a variety of life history functions at the species level thus represent a unique and specialized acoustic signature that contributes to the acoustic complexity of the biological community. Because these signatures often exhibit temporal and spectral features resulting from inter- and intra-specific competition, acoustic communities frequently exhibit spectral, temporal and spatial variability in order to adapt to environments that optimize signal transmission and avoid masking (Bormpoudakis et al., 2013; Rodriguez et al., 2014; Farina et al., 2015; Job et al., 2016; Mullet et al., 2016). This variability results in fluctuations in acoustic complexity that often exhibit daily and seasonal cycles such as the dawn and dusk avian chorus, (Pijanowski et al., 2011b; Farina et al., 2015; Celis-Murillo et al., 2016; Izaguirre et al., 2018); spring and fall bird migration (Saunders, 1947; Brennan & Kuvlesky, 2005; Van Buskirk et al., 2009; Ehnes et al., 2018); and the anuran (frog) and insect emergence in the spring and summer, (Callaham et al., 2002; Nattier et al., 2011; Klaus & Lougheed, 2013; Solla et al., 2006)). While models are informative and help to explain the evolution and ecology of animal signals in the context of community competition for acoustic niche space, sensory adaptation, and preferred habitats for signaling, it is highly likely that the cumulative acoustic signature of a community, resulting from these selective forces, also has adaptive or functional significance for non-soniferous species that co-exist in the soundscape.

Non-soniferous animals often receive direct benefits from acoustic community interactions. Sound-producing fish and crustaceans provide important auditory cues for planktonic marine larval settlement on temperate and tropical coral reefs (Simpson et al., 2008a; Simpson et al., 2008b; Harris et al., 2016; Rossi et al., 2016). Although these larval-stage organisms may or may not mature into adults with auditory and/or sound producing structures, the role of sound for these species and in these particular communities transcends intraspecific communication to include a function of heterospecific habitat selection. This acoustic community interaction has been observed in birds (Mukhin et al., 2008), fish (Lecchini et al., 2005) and frogs (Oldham, 1967; Pupin et al., 2007) and has led to the call for the formation of a new field dubbed soundscape orientation (Slabbekoorn & Bouton, 2008). Embedded in the principles of this emerging field is the notion that all trophic levels of an ecosystem can influence the characteristics of a soundscape; in other words, the acoustic signature of a place is intimately linked to both the biotic and abiotic structure of the landscape (Boncoraglio & Saino, 2007; Bormpoudakis et al., 2013; Farina et al., 2011; Lomolino et al., 2015; Pijanowski et al., 2011a). For example, native vegetation diversity and biomass in Hawaii Volcanoes National Park correlated with low abundance of invasive bird species and was found to be related to an intact native species-dominated soundscape (Boelman et al., 2007). Additionally, by classifying habitat characteristics such as distance from human disturbance, Mazaris et al. (2009) was able to explain most of the variation in foreground and background soundscape composition. This insight further suggests that soundscapes are dynamic and serve as a sensory cue for communities contributing to and interacting with the acoustic environment. Like plants, the abundance and biodiversity of non-soniferous animals persisting at lower or auxiliary trophic levels should likewise covary with measures of acoustic diversity when the species share a direct or indirect but critical trophic interaction with soniferous community members. This dynamic has been shown to contribute to shifts in pollinator and plant community structure (Francis et al., 2009). If this is the case, attributes of a local soundscape produced by the acoustic community could potentially be used to predict the abundance and biodiversity of these non-soniferous species.

Similar to biodiversity indices used to evaluate and compare species richness and evenness, acoustic indices have recently proliferated for the purpose of evaluating the acoustic (typically spectral) diversity of soundscapes in marine (Parks et al., 2014; Butler et al., 2016; Harris et al., 2016) and terrestrial ecosystems (Boelman et al., 2007; Sueur et al., 2008; Gage et al., 2001; Pieretti et al., 2011; Villanueva-Rivera et al., 2011; Depraetere et al., 2012; Gasc et al., 2013; Kasten et al., 2012; Sueur et al., 2014; Lellouch et al., 2014; Rodriguez et al., 2014; Towsey et al., 2014; Fuller et al., 2015; Gasc et al., 2015; Farina et al., 2016; Kendrick et al., 2016; Ferreira et al., 2018; Izaguirre et al., 2018). For example, repeated recordings over time can produce time-series data that captures spectro-temporal trends across and within acoustic communities based on acoustic parameters evaluated by the particular algorithm coded in the acoustic index (Sueur, 2015). All acoustic indices used in soundscape assessment weight various parameters of biophony, geophony, technophony, frequency bands, and sound pressure intensities differently within a sound recording (Sueur et al. 2014; see Table 1.1.). Acoustic index choice typically relates to the breadth and scale of a study question, along with empirical knowledge of the functional dynamics of the acoustic community or ecosystem in question. For example, Fuller et al. (2015) found that after independent application of six acoustic indices to recordings from a subtropical Australian landscape, H (acoustic entropy), ADI (acoustic diversity index) and NDSI (normalized difference soundscape index) most accurately described nocturnal biophony, while ACI (acoustic complexity index) was linked more closely to daytime avian song intensity. The few studies in which acoustic indices have been validated in the field used aural and visual bird count and or vegetation data to assess correlations between acoustic and in situ ecological data (Boelman et al., 2007; Celis-Murillo et al., 2009; Farina et al., 2014). Correlations between measures of habit and soniferous species abundance and diversity have been long noted. MacArthur & MacArthur (1961) demonstrated a critical relationship between bird diversity and botanical community composition in North and Central American forests. Few studies (Francis et al., 2009) have examined how non-soniferous species abundance and biodiversity, especially in invertebrates, may correlate with parameters of the soundscape.

Nicrophorine burying beetles (Insecta: Coleoptera: Silphidae) belong to a guild of necrophilous invertebrates that obligately feed or reproduce on the carcasses of small birds and mammals and are thought to be ecologically important in facilitating soil nutrient cycling (Scott, 1998; Rozen, 2008). Relying on vertebrate carrion for reproduction (Conley, 1982; Trumbo & Robinson, 2004), burying beetle mated pairs quickly bury a carcass and defend it while providing facultative biparental care to offspring (Scott and Traniello, 1990), and can optimize the brood structure based upon ambient environmental cues (Woelber et al 2017). Burying beetles produce sounds via stridulation, the action of rubbing together file and scraper structures (Hall et al., 2013) during carcass burial and offspring care, but adults lack auditory organs (Pers. Comm. C. Hall) and the low amplitude signals (~55-58 dB SPL) lack the intensity to functionally contribute to an acoustic community or soundscape. With around 75 species in the Northern Hemisphere and 4-6 species co-existing in most locations at any time (Scott, 1998), burying beetle species exhibit diel temporal, seasonal, habitat and carrion resource niche segregation across a variety of ecosystems (Anderson, 1982; Conley, 1982; Hocking et al., 2007; Wilson et al., 1984). Burying beetle habitat preferences within ecosystems are known to relate to soil type, soil moisture, canopy/land cover, soil temperature, along with inter- and intraspecific competition gradients (Anderson, 1982; Wilson et al., 1984), but how burying beetles assess cues related to potential carrion availability remains unstudied. Mullet et al. (2017) developed the hypothesis that particular species pay attention to the soundscape produced by acoustic communities as a cue to decipher suitable habitat conditions. While carrion beetles breed on vertebrate species that contribute directly to the local soundscape, it is not known if burying beetle species abundance or biodiversity covaries with measures of acoustic community diversity.

Here, I examined whether variation in burying beetle abundance and/or biodiversity is related to variation in the local acoustic community in a grassland setting with multiple sympatric *Nicrophorus* species. While we assume that the eco-field, which is the physical space in which an animal can perceive biotic and abiotic cues essential for securing resources (Farina & Belgrano, 2004) applies to Nicrophorine burying beetles in the context of chemical cues related to carcass localization, it is unknown if sonotopes, or acoustic habitats (Farina et al., 2014), are a relevant factor in their eco-field. For the endangered N. *americanus* (Fig. 1) for example, while loss of habitat is thought to explain one dimension of population decline, the biotic and abiotic parameters that represent optimal habitat remains under evaluation (Sikes & Raithel, 2002). However, due to their dependence upon soniferous species for reproduction, burying beetle habitat quality might presumably covary with the acoustic diversity of a site. To test whether burying beetle habitat quality might covary with the various acoustic parameters, and to address the question of how Nicrophorine burying beetle population demographics relate to the local soundscape, we conducted a field study that directly measured burying beetle abundance through systematic pitfall trapping of five sympatric species (*N. americanus*, *N. marginatus*, *N. tomentosus, N. orbicollis, N. pustulatus*) while simultaneously collecting acoustic recordings at the 34 field sampling sites. I hypothesized that the abundance and diversity of these necrophilous grassland community constituents would correlate with measures of acoustic diversity and utilized six commonly deployed acoustic indices (Table 1.1.) for rapid soundscape assessment as instruments to test for these hypothesized relationships. Due to putative niche segregation between the five focal species, along with high levels of landscape heterogeneity across the tallgrass prairie study site (Table 2.), I predicted that the magnitude and direction of significant relationships between Nicrophorine species demographics and soundscape structure would differ by species, and that both would exhibit significant spatial effects.

Fig. 1.1. A pair of breeding *N. americanus* prepare a quail carcass for burial where they will provide biparental care to their larval brood (Scott, 1998). While numerous studies have sought to understand the habitat requirements for this endangered species, data from this study show for the first time that the acoustic conditions of a site may predict occupancy and abundance.

Table 1.1. Six alpha-level complexity indices (within-group diversity) used in the investigation of a tallgrass prairie soundscape in relation to Nicrophorine burying beetle composition. These metrics were selected to further understand the limitations and adaptability of acoustic indices for rapid soundscape assessment as they relate to known biotic and abiotic features of the landscape. Each acoustic index is uniquely parameterized to detect spectral, temporal or intensity nuances within individual sound recordings. Replicating acoustic index calculations allows one to analyze acoustic patterns across a landscape at distinct time intervals.

Index	Original Publication	Interpretation
H	Entropy (Sueur et al., 2008)	Values range from 0 to 1 where 0 = pure tone, 1 = numerous and even frequency bands. Evaluates a combination of spectral and temporal entropy.
BIO	Bioacoustic Index (Boelman et al., 2007)	Considers sound intensity (dB) and frequency. Large numbers indicate acoustically rich recordings i.e. loud sounds occupying many frequency bands. Low numbers indicate the opposite i.e. acoustically poor recordings while quite sounds occupied by fewer frequency bands.
ACI	Acoustic Complexity Index (Pieretti et al., 2011)	Considers intensity (dB) and length of recording in the calculation. Originally created to estimate avifauna populations in areas of constant, low-frequency anthropogenic noise where an ACI value is calculated independent of low frequencies.
AEI	Acoustic Evenness Index (Villanueva-Rivera et al., 2011)	Values range from 0 to 1 where 0 = extremely even acoustic community and 1 = uneven or diverse acoustic community. The Gini index is applied to proportions of binned frequencies to measure the evenness of the occupancy distribution.
ADI	Acoustic Diversity Index (Villanueva-Rivera et al., 2011)	The Shannon Diversity Index is applied to binned frequencies of a sound file at 1000 Hz intervals
NDSI	Normalized Difference Soundscape Index (Kasten et al., 2012)	Values range from -1 to 1 where -1 = predominant anthropogenic sounds and 1 = predominant biotic sounds. Computes the normalized power spectral density (watts/kHz) of technophony:biophony

Table 1.2. Life history and ecological characteristics of the burying beetle community at the Tallgrass Prairie Preserve, OK. Adapted from Creighton, Vaughn, & Chapman, 1993; Scott, 1998; Scott & Traniello, 1990; Shubeck, 1971; Trumbo & Bloch, 2000.

Species	Habitat	Activity	Reproductive Period
N. americanus	Generalist	Nocturnal	June – July
N. marginatus	Field	Diurnal	Late June – Early August
N. tomentosus	Generalist	Diurnal	August – October
N. orbicollis	Hardwood forest	Nocturnal	June – August
N. pustulatus	Hardwood forest	Nocturnal	June - August

Methods

Study area

The Nature Conservancy's (TNC) Tallgrass Prairie Preserve (TGPP) in Osage County, Oklahoma (36°50'N, 96°25'W) encompasses ~16,000 ha of one of the largest remaining stands of tallgrass prairie in North America and is located at the southern terminus of the Greater Flint Hills region of Kansas. Since its purchase in 1989, the TNC has aimed to restore natural heterogeneity patterns typical of this ecoregion through a mix of bison and cattle grazing coupled with prescribed fire, mowing and haying (Hamilton 1996; Palmer, 2007). Using a 3-year fire return schedule, TNC biologists randomly select pastures for prescription burns; 40% of burns are conducted in the spring, 20% in the summer, and 40% in the fall/winter months. The TGPP is 90% grassland with the remaining 10% composed of cross-timber forests characterized predominately by two oak species: *Quercus stellata* and *Quercus marilandica* (Hamilton 2007). Dominant C^4 grass species include *Andropogon gerardii*, *Sorghastrum nutans*, *Sporobolus compositus*, *Panicum virgatum* and *Schizachyrium scoparium* with an additional 763 plant species in 411 genera and 109 families with 12% non-native (Palmer 2007). This diverse botanical composition leads to high invertebrate biomass and diversity, which in turn supports numerous resident and neotropical bird species that nest at the site during the summer months (May-July). Additionally, the preserve sits within the historic boundaries of the Osage Nation. The Osage Nation retains the mineral rights to the land, and therefore maintains a network of gravel roads that provide access to the many oil and natural gas wells that operate across the site.

Burying beetle abundance

In order to evaluate how the abundance and diversity of necrophilous invertebrates related to the tallgrass prairie soundscape, I conducted field surveys in the summer of 2017 for five species of *Nicrophorus* beetles known to co-occur at the study site. Using above-ground 18.9 liter pit-fall traps (Figure 1.2.) baited with aged chicken liver, traps were deployed in a grid across the preserve at 34 sampling locations between 6-30 July 2017 (as described in Woelber et al 2018). Each site was sampled for three nights, unless weather events or scavenger disturbance of the trap required the site be resampled for additional nights. All traps were checked between dawn and 10am, with all collected *Nicrophorus* burying beetles identified to species, counted, and released. Due to their endangered status, all collected *N. americanus* were marked with temporary identification tags and released immediately. Collection data for each trap for each day were recorded in the field on hard copy data sheets designed by the U.S. Fish and Wildlife Service for use in field surveys of American burying beetles. Data were then digitized, with mean values of species abundance and trap-rates (beetles-trap night^{-1}) for each 3-night sample period and were incorporated into a Geographic Information System (GIS) attribute table for use in spatial analyses. Shannon’s Index (H), Simpson Diversity Index (Gini coefficient), species richness, and species evenness values were calculated from survey data and likewise incorporated into the GIS.

Acoustic Data Acquisition

In order to examine how sonic variation (i.e. the sonotope) relates to variation in Nicrophorine species composition and abundance across the field site, each pitfall trap was co-located with a single programmable acoustic recorder. We simultaneously deployed up to eight Frontier Labs BAR recorders (Brisbane, AU) fitted with Primo EM179 a microphone (Primo Co. Ltd., Tokyo, JP) and eight Arbimon portable recorders (Sieve Analytics, San Juan, PR) fitted with a Monoprice model 600200 condenser microphone (Monoprice Inc., Brea, CA, USA). Recorders were mounted to temporarily installed metal posts positioned 5m from the baited pitfall trap (Figure 2.). All recording units (16 bit/44kHz sampling rate) were set to record for one minute every ten minutes over each 24 hr period (144 recordings/day) for 72 hours. Recordings were stored on internal San Disk (Western Digital, CA, USA) Ultra 128 GB SD cards in wav file format at the time of recording and transferred to an external hard disk and the University of New Hampshire Box cloud storage at the end of each 3-night round of the field survey.

Acoustic data processing

All recordings were subject to a high pass filter using Adobe Audition 3.0 (San Jose, CA, USA) to eliminate microphone self-noise present from 0-300Hz. Prior to calculating acoustic index values for each 24-hr period of the study at each site, all 60-second audio files were inspected for biotic recording quality by visually examining spectrograms. Audio files impacted by >7.5 seconds of broad-spectrum wind or rain noise that could not be eliminated by the initial high pass filter were not included in subsequent analyses. Ultimately, after filtering and quality check, 8,826 acoustic files were used in subsequent analysis.

Acoustic Indices

We quantified the acoustic information captured in soundscape recordings from multiple perspectives by way of using six assessment metrics: Acoustic Complexity Index (ACI; Pieretti, et al., 2011), Acoustic Diversity Index (ADI; (Villanueva-Rivera et al., 2011), Acoustic Evenness Index (AEI; Villanueva-Rivera et al., 2011), Bioacoustic Index (BIO; Boelman et al., 2007), Acoustic Entropy (H; Sueur et al., 2008), and the Normalized Difference Soundscape Index (NDSI; Kasten et al., 2012) (see Table 1.1. for original publications and descriptions). Acoustic indices were parametrized to reflect the 44.1 kHz sampling rate of the field recorders, and NDSI, which computes the normalized power spectral density (watts/kHz) of technophony:biophony ratio in each recording, was further modified to appropriately categorize low frequency technophony ("anthro_min = 300, anthro_max = 1500, bio_min = 1501, bio_max = 22000").

Acoustic index values for each were calculated for each 60-sec sound recording using the R (R Development Core Team 2017) packages *Soundecology* (Villanueva-Rivera et al., 2011) and *Seewave* (Sueur et al., 2008) and run through Premise (the University of New Hampshire's Research Computing Center High-performance Computing Cluster). Premise consists of a head node and 14 compute nodes along with 225TB of usable storage, and wav files were run in serial using the "multiple_files" function in R (ver. 3.4.1; see Appendix).

In addition to preprocessing raw sound files to screen for wind distortion artifacts, once calculated, we also identified and removed acoustic index value outliers produced by irregular biotic or abiotic acoustic events as performed by Depraetere et al. (2012). Similarly, Rankin and Axel (from Ecoacoustics 2017, pg 129) examined spectrograms with BIO values 60 – 90 and >90 to determine if the output was artificially inflated due to broad spectrum cicada choruses or rain events. In the cases where over inflation was confirmed, values were removed from subsequent analyses. Similarly, ACI was shown to increase for the same reasons. We thus removed from analyses all ACI values exceeding 2500 (see Table 2. for details on acoustic index value data dispersion and final values incorporated into analysis). After screening for outliers, median values for each three-day sample period and for each intra-diel time range for all six acoustic indices were calculated and incorporated into the GIS along with the burying beetle field collection data.

To facilitate a more detailed examination of intra-diel relationships between the prairie soundscape and Nicrophorine burying beetle abundances, we divided daily recording periods into acoustically-distinct time ranges for additional analyses. Two-hour windows representing dawn and dusk periods were determined from sunrise and sunset parameters obtained from the U.S. Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php. Dawn was represented by two hours following sunrise and dusk was represented by two hours following sunset. Day and night were assigned as the time periods following the end of the dawn and dusk periods respectively. Dawn and dusk temporal windows are known to be important for diel soniferous species due to optimal signal transmission conditions and lowered predation risk (Burt and Vehrencamp 2005). Although reasons for dawn and dusk chorusing may have different adaptive values for different species, this behavior can be observed in anurans (Grafe & Meuche 2005), birds (Farina 2015), coyotes (Laundré, 1981) and some insects (Howard and Hill, 2009) at the TGPP. Once time blocks were established and assigned to all recordings in a sampling period, we used a Kruskal-Wallis test to compare ranked differences of each acoustic index between groups defined by four time blocks in a 24-hour period. If the Kruskal-Wallis test showed that groups were significantly different, we used the Wilcoxon rank test (Mann-Whitney

U test) to determine which groups differed from one another (alpha = 0.05). Results were then interpreted into boxplots and violin plots in R.

Data Analysis

I first evaluated the spatial heterogeneity of the soundscape using spatial statistics in GIS (ESRI ArcGIS ver. 10.3.1) (ESRI, Redlands, CA, USA). I used the Anselin Local Moran's test with an inverse Euclidean distance parameter to identify statistically significant acoustic hot spots, cold spots, and spatial outliers for each of the five time periods for each of the six acoustic indices. To test for spatial heterogeneity of Nicrophorine beetle distributions, I used a Kernel Density Estimation (KDE) using Hawth's Analysis Tools (developed by Hawthorne Beyer; http://www.spatialecology.com.) in conjunction with ArcMap 10.3.1 to create 50 percentile volume contours to estimate Nicrophorine burying beetle hot spots using trap-rate values across the study site. In addition to using acoustic indices to explain variation in beetle species composition and the soundscape, I tested the strength of association between beetle species trap rates and acoustic index values to distances from reliable sources of biophony and technophony at the TGPP from the 34 survey sites. For this analysis, I measured planar distances in meters using the measure tool in ArcGIS 10.3.1 from nearest: forest edge, oil and gas wells, private road and county road and used a Spearman Rank correlation in R to determine significance covariation.

Fig. 1.2. Pictured is a typical sampling site which includes one above-ground pitfall trap (foreground) and one Arbimon portable recorder (Sieve Analytics, San Juan, PR) mounted to a temporary metal fence post situated 5-m away (background). Each recorder was placed askew so that the microphone would not interfere with the post from behind which may have been disturbed by wind or with the post itself by creating a notch in the frequency spectrum. All materials were removed at the completion of each trapping period.

Table 1.3. Dispersion/Distribution of acoustic index values from thirty-four sites

Index	Min	1st Q	Median	3rd Q	Max	Index	Min	1st Q	Median	3rd Q	Max
$\text{ACI}_{\text{total}}$	765.8	1709.2	1809	1885.8	2497.2	$\text{BIO}_{\text{total}}$	1.651	34.061	43.445	51.412	79.968
ACI_{dawn}	864.2	1819.3	1878.7	1933.9	2062.9	BIO_{dawn}	5.893	37.415	44.189	51.242	56.222
ACI_{day}	818.4	1792.5	1883.2	1923.9	2077.4	BIO_{day}	3.566	36.037	45.162	50.205	60.76
ACI_{dusk}	878.2	1808.9	1844.4	1897.6	1975.5	BIO_{dusk}	4.752	35.253	44.817	49.72	79.457
$\text{ACI}_{\text{Nnight}}$	863	1769	1806	1864	2001	$\text{BIO}_{\text{night}}$	4.879	40.145	46.79	51.828	73.33
$\text{ADI}_{\text{total}}$	0	1.162	2.063	2.633	3.091	H_{total}	0.255	0.673	0.789	0.869	0.983
ADI_{dawn}	0.043	1.551	2.027	2.422	3.087	H_{dawn}	0.323	0.686	0.802	0.875	0.972
ADI_{day}	0.004	0.255	0.978	2.081	2.274	H_{day}	0.264	0.491	0.663	0.778	0.877
ADI_{dusk}	0	1.538	2.279	2.704	3.045	H_{dusk}	0.278	0.763	0.86	0.892	0.934
$\text{ADI}_{\text{Nnight}}$	0.07	1.545	2.325	2.811	3.089	H_{night}	0.363	0.731	0.826	0.877	0.962
$\text{AEI}_{\text{total}}$	0.001	0.501	0.716	0.877	0.955	$\text{NDSI}_{\text{total}}$	-0.99	-0.215	0.479	0.839	0.997
AEI_{dawn}	0.023	0.601	0.732	0.834	0.954	$\text{NDSI}_{\text{dawn}}$	-0.72	0.018	0.35	0.733	0.966
AEI_{day}	0.624	0.706	0.895	0.947	0.955	NDSI_{day}	-0.9	-0.678	-0.374	0.33	0.776
AEI_{dusk}	0.118	0.459	0.665	0.831	0.955	$\text{NDSI}_{\text{dusk}}$	-0.74	0.25	0.536	0.779	0.968
$\text{AEI}_{\text{night}}$	0.016	0.409	0.644	0.83	0.953	$\text{NDSI}_{\text{night}}$	-0.727	0.091	0.432	0.82	0.978

Results

I collected 17,280 1-minute sound files while simultaneously collecting 596 total *Nicrophorus* beetles (*N. americanus* = 272, *N. marginatus* = 290, *N. tomentosus* = 4, *N. orbicollis* = 2 and *N. pustulatus* = 28, Table 1.4.) across the 34 sample sites between 9 – 22 July 2017. After screening files that were rendered unusable by wind distortion, I incorporated 8,826 sound files into subsequent analyses. Excessive wind effects were most pronounced during the day (63.8% of files impacted) and dusk (45.9%) periods, and lowest during the dawn (29.4%) and night (30.1%) periods. The 300 Hz – 1500 Hz range correctly assigned nearly all sounds emitted by oil and gas wells, along with vehicular and air traffic (mean dominant frequency = 914 Hz) as technophony. I found a similar effect of orthopteran species inflating BIO as an artifact of close proximity to the microphone as described by Rankin and Axel (from Ecoacoustics 2017, pg 129) and thus for a small sample of files, removed index values greater than 80. H values from all sites produced a median of 43.5 (34.1 to 51.4). Similarly, ACI values would occasionally increase to 2500 - 3000 during high wind or when birds with frequency modulated calls would sing while perched on top of a recording post. In these cases, ACI values were removed which helped to reduce fallacious variability (median ACI was 1850.3 (Q1 = 1791.5, Q3 = 1961.7)). I found significant differences in the distributions of acoustic activity across a 24-hour period as described by all six acoustic indices. In all figures letters above the violin plots indicate significant differences between time blocks (Figure 3). To identify clusters of high and low values of acoustic indices across the preserve, we used the the Anselin Local Moran’s I Test in ArcGIS and found that clustering was specific to time of day and geographic location on the preserve (Table 1.5.).

Burying beetles were likewise distributed heterogeneously across the preserve landscape (Figure 1.4.) with some species located in high abundances in particular locations and low in others, likely related to species-level habitat associations. To identify clusters and outliers of beetle species based on trap rates of each, we used the Anselin Local Moran's I Test in ArcGIS (Table 6.). For example, the endangered American burying beetle was found in high abundance at sites 3 (LMI Index = -0.003, LMI Z = -4.479, P < 0.001) and 26 (LMI Index = -0.003, LMI Z = 5.195, P < 0.001), while we observed unexpectedly low values at site 10 (LMI Index = -0.002, LMI Z = -1.996, P = 0.045). The most common species found at the site, *N. marginatus*, was found in high abundances at sites 1, 8, 32 and 26, and low abundances at sites 4, 18, 19, 24, 25, 37 and 38 (total = 0), however did not appear in the final resulting table. This species is known to exhibit a preference for open grassland habitats, whereas *N. americanus* is thought to be a habitat generalist.

Using mean capture rates from above-ground pitfall traps (Table 4.), we found three out of five *Nicrophorus* species exhibited significant correlations with one or more acoustic indices (Table 1.7.). With the exception of overall and dawn median ADI values, AEI at dusk, and BIO at dusk, both acoustic index values and beetle survey data failed normality tests, were resistant to transformation and were found to be non-normally distributed (Table 1.3). Therefore, we used a non-parametric correlation test (Spearman rank correlation) to examine relationships between acoustic index values and burying beetle abundance and biodiversity. For those pairs of variables that yielded significant correlation coefficients (alpha = 0.05), I created plots of the median acoustic index values and mean beetle trap-rates fitted with a line (Figure 1.5).

We found that capture rates of two diurnal species, *N. marginatus* and *N. tomentosus* were negatively correlated with Acoustic Diversity Index (ADI), Acoustic Entropy Index (AEI) and the Normalized Difference Soundscape Index (NDSI) values calculated from dusk, night and dawn recordings. Conversely, abundances of the endangered and nocturnal species *N. americanus* were positively correlated with Acoustic Complexity Index (ACI) values calculated from dawn recordings (Figure 2.). Despite numerous species-level relationships with the soundscape, we found no significant association between overall burying beetle biodiversity, evenness or richness and any of the calculated acoustic indices.

In addition to the relationship between burying beetle abundance and acoustic structure, I found beetle trap rates and acoustic index values themselves related to several landscape features that likely contributed to increased biophonic diversity (forest stands) or technophony (roads, oil and gas wells; Table 8). We found two species exhibited strong correlations with distances from county roads, private roads and forest edges. *Nicrophorus orbicollis* was negatively correlated with distances from forest: as distance from forest increased, *N. orbicollis* trap rates decreased (Spearman rho = -0.392, p = 0.024). This is a nocturnal species and is reported as a forest obligate species which supports our finding that distance from forest and *N. orbicollis* trap rates would negatively covary. Trap rates of *N. tomentosus*, a generalist diurnal species, however showed contradictory results in relation to distance from county and private roads. This suggests that for this site, roads are not a reliable covariable to assess trends in beetle capture rates of specific species: *N. tomentosus* was positively correlated with private roads (Spearman rho = 0.384, p = 0.028) and negatively correlated with county roads (Spearman rho = -0.356, p = 0.042). We chose to delineate road types because the is one county road that is runs through the middle of the preserve in a north/south direction and receives regular traffic from tourists, TNC employees, and private oil and gas workers while private roads make up an expansive network of smaller distances and widths across the preserve and are less frequently trafficked. Acoustic indices: negative to distance from roads except for BIO_{day}, positive to distance from oil and gas and negative to distance from forest.

Table 1.4. Summary of July 2017 trapping effort results (trap nights = 3).

Species	**Total**	**Mean Capture Rate (beetles/trap night)**
N. americanus	272	1.82
N. marginatus	290	2.32
N. tomentosus	4	0.03
N. orbicollis	2	0.02
N. pustulatus	28	0.22
Total	596	

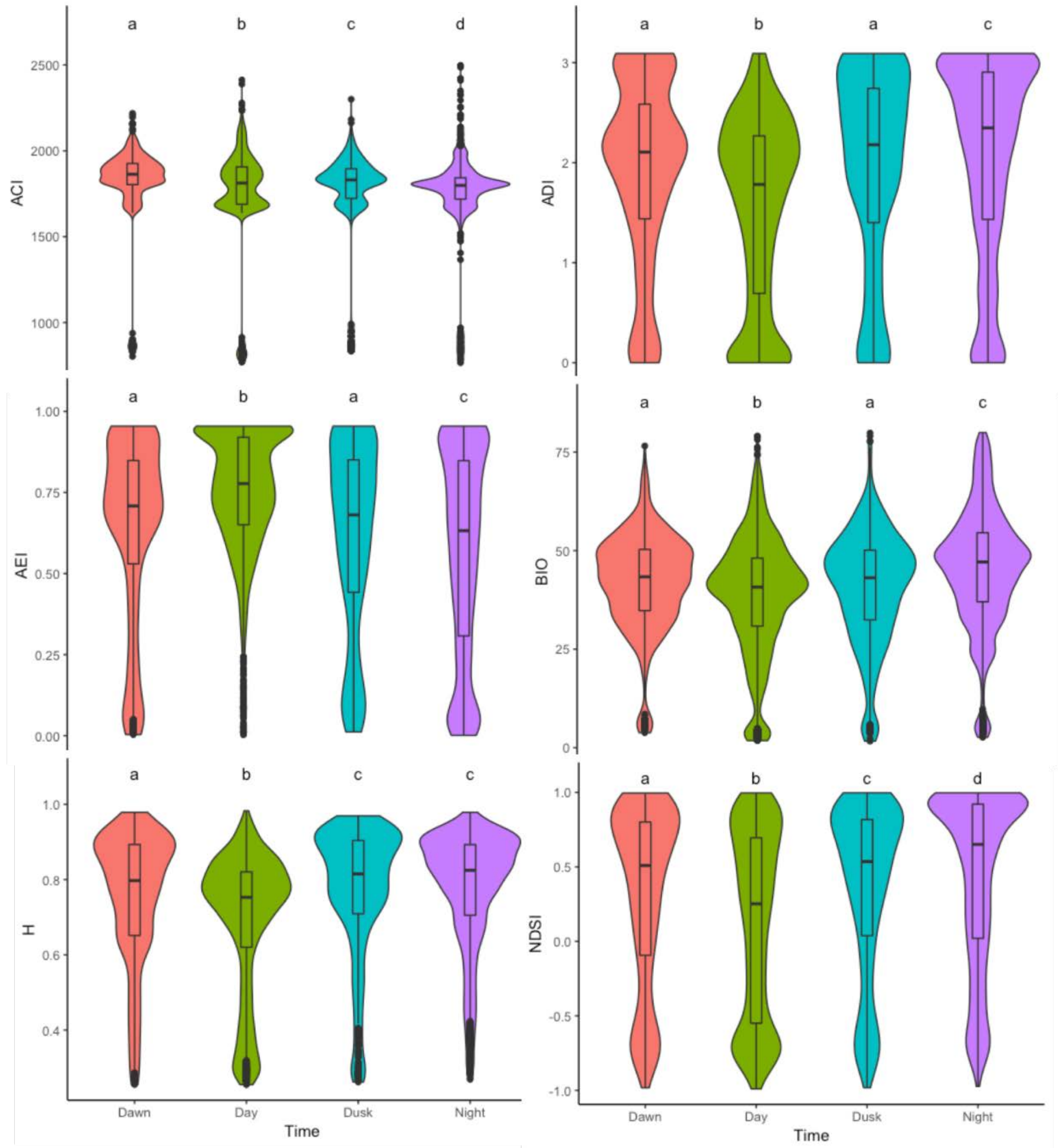


Fig. 1.3. Values generated from each acoustic index at four time blocks were interpreted into violin plots. Plots show the shape of the distribution of acoustic index values by weight. A Kruskal-Wallis rank sum test was used to determine if significant differences existed between time blocks. A post-hoc Dunn/ Mann Whitney U test was used to identify which time blocks where different from one another: ACI (chi-squared = 285.78, df = 3, p-value < 0.001); ADI (chi-squared = 657.02, df = 3, p-value < 0.001); AEI (chi-squared = 600.69, df = 3, p-value < 0.001); BIO (chi-squared = 390.43, df = 3, p-value < 0.001); H (chi-squared = 566.45, df = 3, p-value < 0.001); NDSI (chi-squared = 536.23, df = 3, p-value < 0.001). Letters indicate significant differences between time blocks. While p-values less than the set alpha of 0.05 would suggest significant differences exist, each time block still maintains a large amount of variation. Although median values are trending towards what I would expect the response of each acoustic index to be at each time block, the effect of over-sampling could be causing variation to inflate.

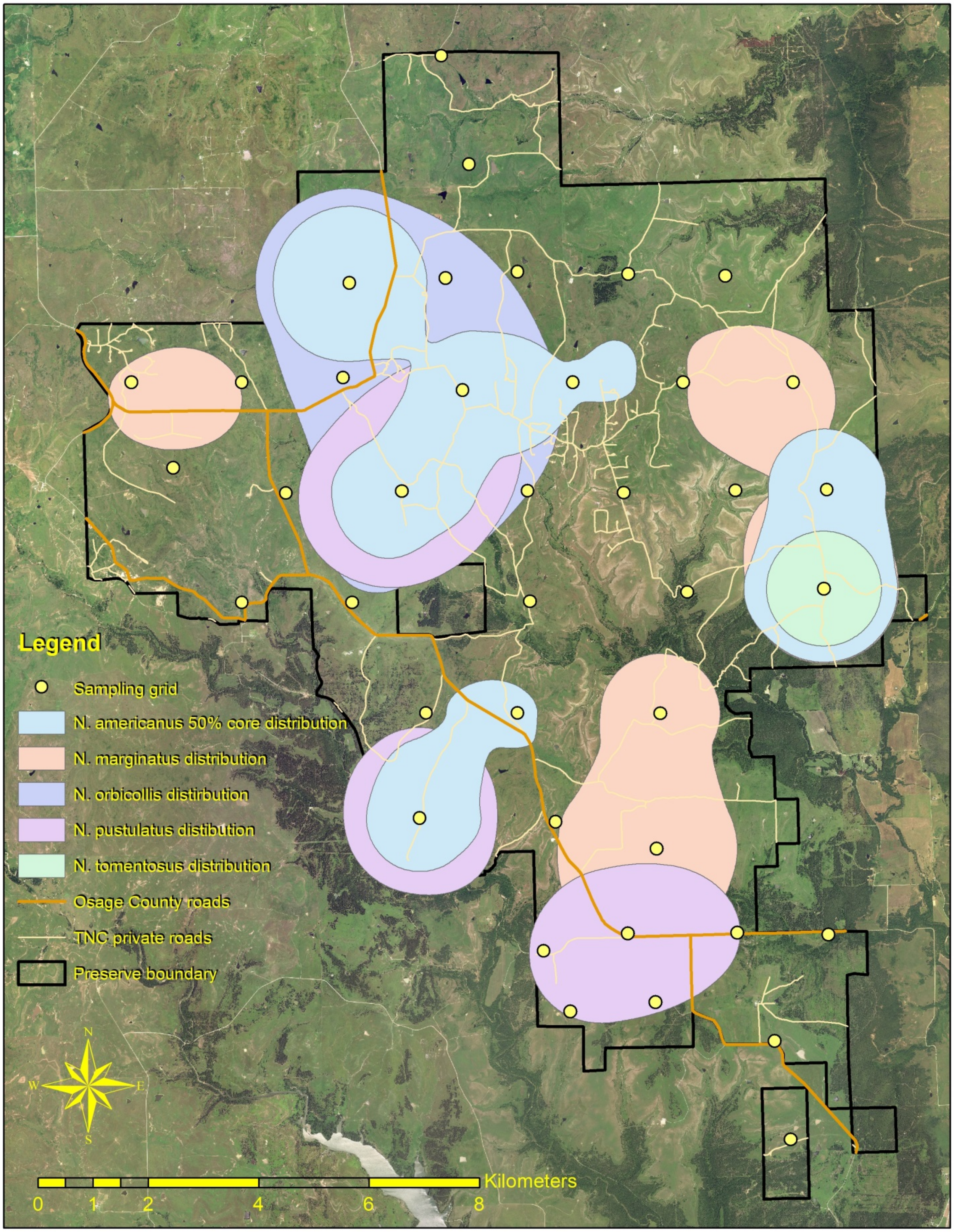


Fig. 1.4. Spatial distribution of Nicrophorine burying beetle species collected in the study. Polygons represent the 50% core distribution of the five *Nicrophorus* burying beetle species based on capture rates calculated from three trap nights.

Table 1.5. Cluster and Outlier Analysis (Anselin Local Moran's I) results for high median acoustic index values surround by low median acoustic index values (HL), high median acoustic index values clustered around high median index values (HH), low median index values surrounded by high median index values (LH) and low median index values surrounded by a cluster of low median index values (LL).

Acoustic Index	Site	Acoustic Index Value	LMiIndex	LMiZScore	LMi p-value	COType	Acoustic Index	Site	Acoustic Index Value	LMiIndex	LMiZScore	LMi P-value	CO Type
ADI$_{dusk}$	1	3.045	-0.001	-2.567	0.010	HL	H$_{day}$	11	0.877	-0.002	-2.026	0.043	HL
AEI$_{dawn}$	1	0.169	-0.001	-2.263	0.024	LH	AEI$_{night}$	13	0.064	-0.002	-1.987	0.047	LH
AEI$_{dusk}$	1	0.118	-0.001	-3.053	0.002	LH	ACI$_{total}$	15	1958.071	-0.002	-2.559	0.011	HL
AEI$_{dusk}$	2	0.954	-0.003	-3.376	0.001	HL	ACI$_{day}$	15	2074.268	-0.003	-3.992	<0.001	HL
ADI$_{dusk}$	2	0.005	-0.003	-4.036	<0.001	LH	ACI$_{dusk}$	15	1906.458	-0.001	-2.415	0.016	HL
H$_{dusk}$	2	0.464	-0.003	-3.030	0.002	LH	ACI$_{night}$	15	1907.236	-0.002	-2.969	0.003	HL
ADI$_{night}$	8	2.781	-0.002	-2.142	0.032	HL	ADI$_{total}$	15	1958.071	-0.002	-2.559	0.011	HL
Ht$_{otal}$	8	0.860	-0.002	-2.716	0.007	HL	AEI$_{total}$	17	0.949	-0.002	-1.972	0.049	HL
H$_{day}$	8	0.850	-0.001	-2.062	0.039	HL	AEI$_{night}$	17	0.942	-0.003	-3.134	0.002	HL
H$_{night}$	8	0.899	-0.002	-3.036	0.002	HL	ADI$_{dawn}$	17	0.096	-0.002	-2.598	0.009	LH
NDSI$_{night}$	8	0.802	-0.002	-2.133	0.033	HL	ADI$_{dusk}$	17	0.000	-0.002	-2.057	0.040	LH
ACI$_{total}$	8	841.826	-0.005	-8.731	<0.001	LH	ADI$_{night}$	17	0.380	-0.003	-3.578	<0.001	LH
ACI$_{day}$	8	818.364	-0.004	-8.366	<0.001	LH	H$_{total}$	17	0.406	-0.002	-2.392	0.017	LH
ACI$_{dusk}$	8	878.159	-0.003	-5.464	<0.001	LH	H$_{dawn}$	17	0.323	-0.002	-2.189	0.029	LH
ACI$_{night}$	8	862.967	-0.003	-6.149	<0.001	LH	H$_{dusk}$	17	0.278	-0.003	-3.830	<0.001	LH

ADI_{total}	8	841.826	-0.005	-8.731	<0.001	LH	H_{night}	17	0.498	-0.003	-3.846	<0.001	LH
BIO_{total}	8	4.395	-0.002	-2.745	0.006	LH	$NDSI_{dawn}$	17	-0.720	-0.002	-2.416	0.016	LH
BIO_{dawn}	8	5.893	-0.001	-2.325	0.020	LH	$NDSI_{dusk}$	17	-0.740	-0.003	-4.071	<0.001	LH
BIO_{day}	8	3.566	-0.002	-2.788	0.005	LH	$NDSI_{night}$	17	-0.439	-0.002	-2.049	0.041	LH
BIO_{dusk}	8	4.752	-0.001	-1.981	0.048	LH	$NDSI_{night}$	20	0.820	-0.002	-2.075	0.038	HL
H_{total}	10	0.897	-0.002	-2.084	0.037	HL	$NDSI_{total}$	22	0.732	-0.001	-2.351	0.019	HL
$NDSI_{total}$	10	0.786	-0.003	-2.278	0.023	HL	$NDSI_{night}$	22	0.842	-0.001	-2.123	0.034	HL
AEI_{total}	10	0.326	-0.002	-2.044	0.041	LH	AEI_{dawn}	24	0.023	-0.002	-2.757	0.006	LH
							H_{dawn}	35	0.443	-0.002	-2.865	0.004	LH

Table 1.6. Cluster and Outlier Analysis (Anselin Local Moran's I) results for high mean trap-rates surround by low mean trap-rates (HL), high mean trap-rates clustered around high mean trap-rates (HH) and low mean trap-rates surrounded by high mean trap-rates (LH). Only sites where significant spatial clustering was observed are included.

Species	**Site**	**Trap-rate**	**LMiIndex**	**LMiZScore**	**LMiPValue**	**COType**
N. tomentosus	1	0.33	0.005	11.12	<0.001	HH
N. tomentosus	2	0.33	0.004	5.47	<0.001	HH
N. americanus	3	9.67	-0.003	-4.48	<0.001	HL
N. orbicollis	3	0.67	-0.001	-4.32	<0.001	HL
N. americanus	10	0.33	-0.002	-2.00	0.0459	LH
N. pustulatus	11	1	0.002	2.71	0.0066	HH
N. pustulatus	17	2	0.004	6.05	<0.001	HH
N. americanus	26	8.5	0.003	5.20	<0.001	HH

Table 1.7. Spearman rho correlation matrix of significant relationships observed between acoustic indices and beetle abundance across the study site (n = 11).

Acoustic Index	**Beetle spp.**	**Spearman rho**	**p-value**
ACI_{dawn}	*N. americanus*	0.362	0.042
ADI_{dawn}	*N. tomentosus*	-0.365	0.040
AEI_{dawn}	*N. tomentosus*	0.365	0.040
BIO_{total}	*N. tomentosus*	0.555	<0.001
BIO_{day}	*N. tomentosus*	0.460	0.0092
BIO_{dusk}	*N. tomentosus*	0.520	0.002
BIO_{night}	*N. tomentosus*	0.562	<0.001
H_{total}	*N. marginatus*	-0.343	0.047
H_{dusk}	*N. marginatus*	-0.357	0.041
H_{night}	*N. marginatus*	-0.435	0.011
$NDSI_{dusk}$	*N. marginatus*	-0.383	0.028

Table 1.8. Correlation matrix of acoustic indices, beetle species and distance from potential sources of sources of technophony. Forests stands tended to introduce increased acoustic diversity due to supporting acoustic communities that differed from those in the grasslands. Since county and private roads yielded mixed results, treating both variable as the same factor of "roads" might depict a more accurate association between beetle species and acoustic indices.

Species/Index	**Factor**	**Rho value**	**p-value**
N. tomentosus	Private Roads	0.384	0.028
N. tomentosus	County Roads	-0.356	0.042
N. orbicollis	Forest	-0.392	0.024
BIO_{total}	County Roads	-0.347	0.045
BIO_{day}	Private Roads	0.456	0.008
H_{total}	Private Roads	-0.398	0.020
ADI_{total}	Private Roads	-0.433	0.013
ADI_{night}	Private Roads	-0.375	0.032
ACI_{day}	Oil and Gas	0.343	0.059
BIO_{day}	Oil and Gas	0.402	0.025
BIO_{day}	Forest	-0.424	0.014
$NDSI_{dusk}$	Forest	-0.501	0.003

Discussion

In examining the relationship between the tallgrass prairie soundscape and Nicrophorine beetle abundances and distributions, I found that associations were unique to particular acoustic indices and beetle species, and that both exhibited temporal and spatial heterogeneity. Results from this study provides the first evidence that the soundscape of a site can reveal significant ecological interactions among organsims in the decomposer role of a food web in addition to identifying the functional composition of the acoustic community. Interestingly however, there was no clear no relationship between the calculated values of four common measures of biological diversity (Shannon diversity, Simpson's diversity, abundance, richness) and those values produced by the most commonly employed indices that describe acoustic diversity. The underpinning of relationships between necrophilous invertebrate abundances and the soundscape are likely related to species-specific life histories, habitat preferences and daily activity patterns (highlighted in Table 2). Nicrophorine burying beetles are thought to exhibit resource partitioning resulting in unique niches; these niches likely drive both the spatial heterogeneity observed in their abundances (Figure 4.) and the fine-scale relationships between these abundances and measures of the soundscape.

Of the six acoustic indices used, three performed the best in regard to drawing significant correlations between soundscape parameters and capture rates of five beetle species: ACI, BIO and H. Although these indices co-varied most closely with *Nicrophorus* beetle capture rates for this study, I had to make considerations unique to the prairie when selecting final values to incorporate in the final analysis. Considerations included the predominance of wind during the day and cicadas at night in sound recordings. ACI and BIO values had to be manually examined and cross-referenced to each value's corresponding spectrogram to ensure values were responding appropriately to the geophony and biophony present. Broad spectrum, high amplitude sounds caused values from these indices to artificially inflate and were removed from further analysis. Although calculating acoustic indices can be done rapidly, a rigorous vetting process must take place before one proceeds with final analyses.

Two diurnal Nicrophorine burying beetle species that showed significant correlations with soundscape indices were also consistently opposed in the direction of the relationship to soundscape composition as reflected in the values of several acoustic indices. *N. marginatus* abundances showed consistently negative correlations with acoustic diversity, while abundances of *N. tomentosus* were consistently positively correlated with acoustic diversity. Although closely related, their life histories exhibit subtle differences which allow them to reduce conflict in terms of habitat use, daily activity patterns, resource allocation and reproduction (Shubeck, 1971; Scott & Traniello, 1990: Creighton et al., 1993; Scott, 1998; Trumbo & Bloch, 2000; Keller et al., in prep). *N. marginatus* is known to be a grassland specialist whereas *N. tomentosus*, a generalist species, can be found in both fields and forests with a preference for dense woody vegetation in some regions (Lomolino & Creighton, 1996). The Tallgrass Prairie Preserve encompasses 16,000 ha of tallgrass and mixed-grass prairie (~90% grassland habitat) and riparian gallery forests (~10% crosstimber forest composed of *Quercus stellata* and *Q. marilandica*) (Hamilton 2007). Our study design closely reflects this ratio where 94% of sites were in prairie habitat while the remaining ~6% of sites were inside forest stands or within 100 meters of the nearest forest edge. The ecoacoustic literature shows mixed results as to whether or not landscape characteristics themselves correlate with attributes of the soundscape as quantified by acoustic indices (Fuller et al. 2015) or by relative soundscape pressure (RSP) (Tucker et al. 2013). However, in our study values for the Bioacoustic Index (BIO) were highest in or near forested regions of a site, where *N. marginatus* abundances were low; *N. tomentosus* did not show an aversion to forested regions. BIO values at night increased with decreasing distances from forests (Spearman rho = -0.425, p=0.0134). Habitat preferences for open grasslands in *N. marginatus* is likely related to the reduction of niche overlap with the other four species of burying beetles found on the preserve. Regions of the preserve with high values of acoustic entropy (H) at dusk and night were not necessarily limited to forest edges as seen in BIO values. This result may indicate habitats where predation risk is elevated during the peak dusk activity period of *N. marginatus*, thus limiting species abundance. Low H values were the best indicator of high occurrences of *N. marginatus*, as indicated by a negative correlation with *N. marginatus* trap rates at dusk (Spearman rho = -0.358, p-value = 0.0412) and night (Spearman rho = -0.435, p-value = 0.0113). Even when variation was not partitioned among time blocks, gross median BIO and H values over three days were still positively correlated with *N. tomentosus* (Spearman rho = 0.555, p-value = 0.0007) and negatively correlated with *N. marginatus* (Spearman rho = -0.343, p = 0.047) trap rates calculated from 34 sites

In addition to evidence of acoustic habitat segregation, *N. marginatus* and *N. tomentosus* exhibit notable morphological differences. While both species possess the trademark black elytra and bright orange markings of other species in the genus, *N. tomentosus* is the only species with a yellow pronotum, appearing strikingly similar to a bumblebee when in flight. Both Milne & Milne (1944) and Heinrich (2012) hypothesized that the species evolved the yellow pubescence as a form of Mullerian mimicry of bumblebees, which most birds tend avoid as prey (Evans & Waldbauer, 1982; Exnerová et al., 2003). Sites with higher BIO values, driven in part by bird song, might indicate higher risk of predation for diurnal burying beetle species, which *N. tomentosus* may be more adapted to avoid. This key difference, given that these species share the same active period and exhibit potential habitat overlap, could explain why *N. tomentosus* is positively correlated with acoustic diversity while *N. marginatus* generally exhibits a negative correlation with the local soundscape. Experimental field work would be required to test this hypothesized link between aposematism and acoustic habitat preferences in burying beetles however.

High BIO values were the best indicator of observed high occurrences of *N. tomentosus*. BIO was positively correlated with *N. tomentosus* trap rates during day, dusk, and night time blocks. During the mid-summer trapping period of the study, documented abundances of *N. tomentosus* were low (mean = 0.1 ± 0.3 beetles/trap night; median = 0), as the species is known to emerge in the late spring and have a second flight in late summer (Wilson et al., 1984; Scott & Traniello, 1990). Differences in breeding seasonality between *N. tomentosus* and *N. marginatus* is another explanation for why we observe species contrasts in terms of correlations to soundscape diversity.

Daily acoustic patterns associated with grassland bird diversity are likely indicators of preferred *N. americanus* habitat. Fuller et al. (2015) found that the acoustic complexity index (ACI) and the bioacoustic index (BIO) followed a cyclic diel pattern, with corresponding peaks in the dawn and dusk hours driven by increases in the prevalence of avian song intensity (Figure 3). Similarly, we observed predictable fluctuations of ACI values in response to avian activity and that dawn values were positively correlated with abundance in the critically endangered *N. americanus*. In one instance when median ACI was especially low over the course a three-night trapping period (median = 841.6, all other sites ACI median = 1876.7), *N. americanus* capture rates were also low (0.5) (Figure 5.). This particular site is located in close proximity to a number of active oil wells where internal combustion diesel engine pumps were operating 24-hours per day. This source of anthropogenic noise could be causing *N. americanus* to avoid the site. Although this is only one example of decreased presence of *N. americanus* near a constant source of technophony, the significant correlation further supports evidence provided by Bunkley et al. (2017) that some arthropod communities are altered by anthropogenic noise. This finding has even more profound conservation and management implications for a critically endangered arthropod species like *N. americanus*, whose rapid decline over the last century remains poorly understood (Sikes & Raithel, 2002).

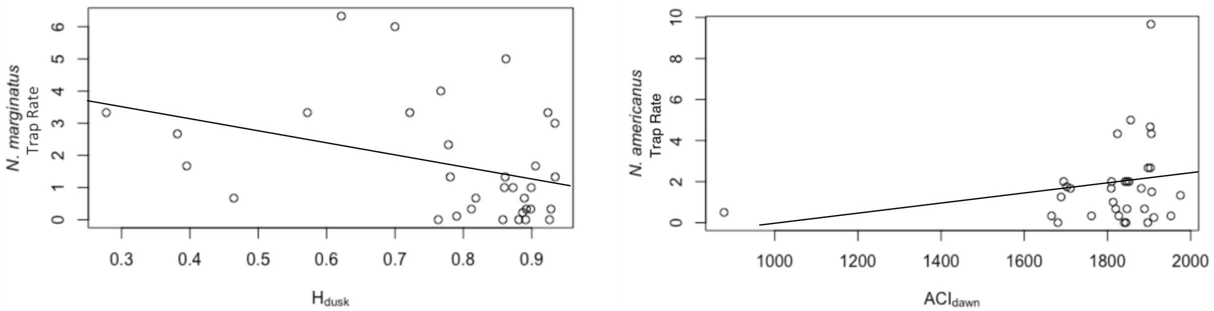


Fig. 1.5. *N. marginatus* trap rates (left) are significantly correlated with night time entropy (H) values (Spearman rho = -0.358; p-value = 0.0412). *N. americanus* trap rate (right) positively covaries with acoustic complexity index (ACI) values at dawn (Spearman rho = 0.362, p-value = 0.042). When the outlier in the right plot is removed (ACI = 864, *N. americanus* trap rate = 0.5), the strength of the correlation is reduced (Spearman rho = 0.35, p-value = 0.056). Although this ACI value is ~11 standard deviations (SD = 89) below the median ACI value of 1879 at dawn, these data were retained in the analysis because it represents a site where an active oil pump was next to a trap/ recording station. In all audio files recorded over the course of 72 hours, technophony from the oil pump was constantly present and may have created an unfavorable acoustic environment for biophony which could explain why the ACI value for this particular site was so low. This result is important to include in order to understand how anthropogenic noise may influence necrophilous invertebrate communities.

Arthropod diversity, even in relatively undisturbed, intact ecosystems are known to be vulnerable to decline in the Anthropocene (Dirzo et al., 2014). Although most scientific surveys and public and policy attention is focused on Lepidoptera and Hymenoptera (butterflies and bees), Dirzo et al’s (2014) findings suggest that the Coleoptera have followed the same trend of world-wide insect decline as other more well-studied orders (Cardoso et al., 2011; IUCN, 2013; Dirzo et al., 2014). Anthropogenically driven causes for invertebrate faunal decline is complex and includes habitat loss, pathogens, pollution, and competition from intentionally or accidentally introduced invasive species (Kotz and O'Hara 2003; Potts et al., 2010). Understanding the relationship between the acoustic signature of a place and the process of defaunation may provide managers with a viable and rapid assessment method to assess current habitat suitability or biodiversity change over time. Our findings show that ecoacoustic recordings collected during the *N. americanus* summer reproductive season, analyzed using the appropriate acoustic index, may hold promise to gauge suitable habitat for this endangered species.

Invertebrate species are sensitive to environmental changes and can be reliable indicators of ecosystem health (Hilty & Merenlender, 2000). In some instances, the population dynamics of insects such as beetles and grasshoppers may also predict the biodiversity of unrelated taxa (Pearson & Cassola, 1992; Rodríguez et al., 1998; Michael & Samways, 2011). Similarly, Aide et al. (2017) showed that insect acoustic morphospecies richness, quantified through the manual evaluation of acoustic recordings, was highly correlated with regional bird species richness. Here we found a similar ecological relationship at play, with Nicrophorine burying beetle abundance reflected in a soundscape dominated by avian song. This is intuitive, as these necrophilous community members rely in part on bird carcasses for reproduction. Given that passerine and other small vertebrate carcasses are their primary food and reproductive resource, carrion beetles may face the ripple effects of a trophic cascade if bird populations are in decline. Through the use of acoustic indices, Fuller et al. (2015) found that NDSI, H, and AEI were positively correlated with bird species richness, ecological condition and landscape configuration of fragmented Australian forests. It is thus not surprising that acoustic indices that relate robustly to avian biodiversity also point to increased abundance of non-soniferous community members that rely facultatively on them.

Chapter 2: Phenology of a tallgrass prairie soundscape in response to prescribed burns

Introduction

Acoustic monitoring and soundscape analysis is increasingly being integrated into management practices to document disturbances to wildlife (Alvarez-Berríos et al., 2016; Burivalova et al., 2017; Deichmann et al., 2017; Raynor et al., 2017; Rossi et al., 2016; Rossi-Santos, 2015), to estimate species richness in acoustically complex environments (Aide et al., 2017; Celis-Murillo et al., 2009; Pieretti et al., 2011; Ribeiro et al., 2017; Towsey et al., 2014; Ulloa et al., 2018) and to describe changes to the landscape as reflected by the soundscape over space and time (Gage & Axel, 2014; Job et al., 2016; Krause et al., 2011; Lomolino et al., 2015; Mazaris et al., 2009; Mennitt et al., 2014; Mullet et al., 2016; Reed et al., 2012; Rodriguez et al., 2014). The way an environment sounds at any given place and time has shown strong correlations with bird diversity (Gasc et al., 2013), levels of habitat fragmentation (Fuller et al., 2015; Burivalova et al., 2017) and shifts in elevational gradients (Leach et al., 2018). Because of the diverse applications and the autonomy of acoustic recording deployment and operation, ecoacoustics has developed into a code-driven, big-data field requiring as much computing and data storage capabilities for information processing rivalling other data intensive fields such as genomics. Because of their low maintenance and minimal energy demands, passive acoustic recording stations minimize disturbances to floral and faunal communities during biomonitoring and survey efforts. As such, cryptic species that would normally go undetected are documented and fragile or difficult to access habitats can be monitored at any time of day or night.

Grasslands harbor vastly diverse native and endemic floral and faunal species (Brennan and Kuvlesky 2005; Palmer 2007) and serve as important carbon sinks to help offset rising atmospheric carbon emissions (Pepper et al., 2005). Short grass and tallgrass prairies, however, are facing rapid decline. In 1994 it was estimated that tallgrass prairies covered a mere 4% of the original 68,371,000 ha extent from 13 North American states (Samson & Knopf 1994). Nitrogen availability, water, temperature and disturbance (fire, grazing or mowing) are the primary factors driving production of grasses and forbs. These factors aid in maintaining a grass-dominated landscape and prevent the encroachment of forests (Hobbs et al., 1991; Pepper et al., 2005). Fire disturbance in particular is known as a biodiversity-maintaining process for communities in many ecosystems (Richards et al., 1999). When applied in combination either through habitat management intervention (by Native Americans and post-European settlers) or by natural causes (lightning), grazing and fire promotes biodiversity and increases heterogeneity of C4 grasses and forbs (Hulbert 1988; Howe 1994; Collins et al. 1998; Hamilton 2007). However, responses can be variable. For example, Collins et al. (1995) found that the response of floral species richness to fire disturbance in a tallgrass prairie was mixed. In addition to generally promoting vegetative biodiversity, regular fire events encourage a greater biodiversity of some avian assemblages which aids in the establishment of nesting and mating display sites (Johnson et al., 1997). Similar to plant communities, avian responses can also be variable. Research by Reinking et al. (2000; 2005) reported that not all bird species found in tallgrass prairies prefer the same habitat management regime and that nest success rate was lower at burned sites (Shochat et al., 2005). Studies on insect communities in grasslands support a similar conclusion in that there are differences in the assemblages between burned and unburned sites and that not all species respond similarly (Chambers and Samways, 1998; Hansen, 1986; Panzer and Schwartz, 2000;

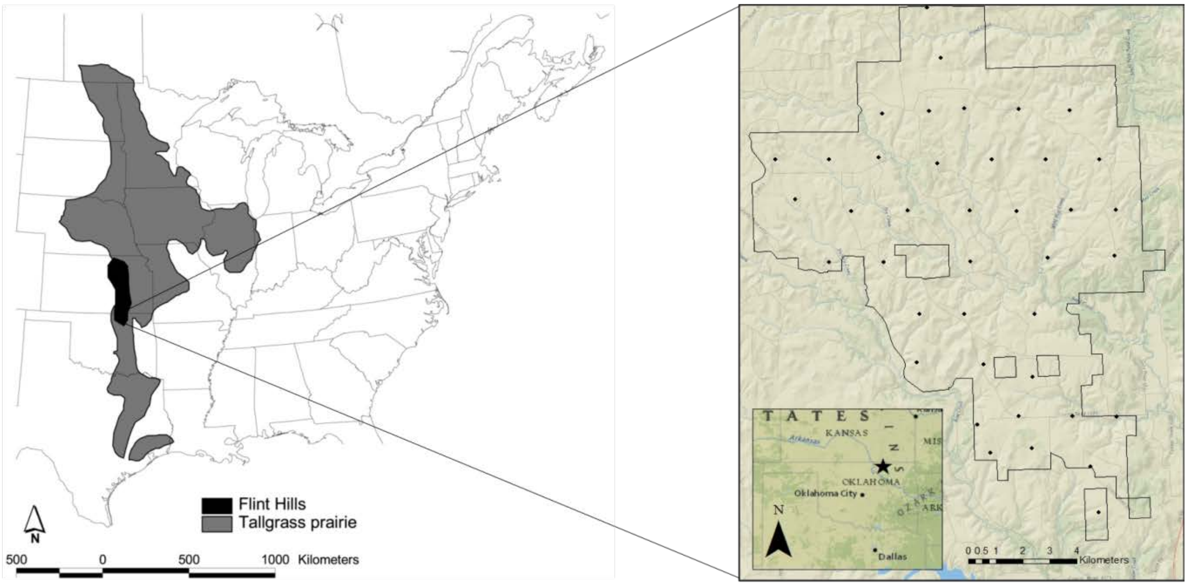
Armitage and Ober, 2012). Since fire presicption is now a common practice in many managed North American grassland ecosystems, it is important to periodically evaluate if a traditionally used practice is still appropriate to achieve optimal habitat for any given species (Howard and Hill, 2007). A novel method to evaluate the efficacy of historic management practices in order to determine if intended goals are met, is to compare soundscape recordings before and after intervention.

Grassland ecosystems are good candidates for ecoacoustic surveys because of their vast expansiveness, the seasonal and daily changes of acoustic biotic activity, and because of the management practices grasslands are subject to such as mowing, burning and grazing which can have a strong influence on the soniferous faunal assemblages. Soundscape ecology aims to understand the composition of sound energy in the context of the environment from which sounds emanate (Turner et al. 2018). These sounds include those of biological, geophysical, and anthropogenic (non-natural sounds cause by humans themselves (anthrophony) or by machinery (technophony; Pijanowski et al., 2011; Sueur et al. 2012; Fuller et al., 2015; Mullet et al., 2017) origin. Soundscapes are heterogeneous in time and space and thus create patches of sonic activity called sonotopes (Farina 2014). Landscapes are thus comprised of a heterogeneous arrangement of sonotopes that together create an acoustic signature unique to a particular place and time. Often, the biophony of a site is evaluated dimensions of ecosystem health. Biophonies from multiple faunal origins form an acoustic community which is defined as the sum of all sound-producing species and as such, can be considered an appropriate measure of biodiversity (Farina & James, 2016; Lellouch et al., 2014).

The Acoustic Niche Hypothesis (Krause 1993) asserts that soniferous organisms have evolved to communicate using difference frequencies and temporal patterns to avoid interspecific competition for a shared acoustic space. Although rarely empirically tested, this phenomenon has been reported in bird (Luther 2008; Planqué and Slabberkoorn, 2007), cicada (Sueur, 2002; Hart et al., 2015), anuran (Duellman and Pyles, 1983) and bat (Heller and Helveren, 1989) acoustic communities. Although it is informative to understand the evolutionary ecology driving the inter and intra-specific interactions documented in an acoustic recording, soundscape assessment does not require species identification. Because automatic species detection software can be time consuming to train and have low levels of accuracy in correctly identifying some species within an acoustic community, a less identification-based means for rapid biodiversity assessment through the use of passive acoustic recording was required. Acoustic indices are designed to exploit frequency, time and amplitude partitioning within acoustic communities (Sueur et al. 2012), using an evaluation of the Fast Fourier Transform (FFT) to identify spectrally distinct acoustic events. An acoustic index produces a unitless number which summarizes the distribution of sound energy within a single recording using an algorithm that measures aspects of the structure and distribution of the acoustic information found therein (Ecoacoustics, 2017). Seewave (Sueur et al., 2008) and Soundecology (Villanueva-Rivera et al., 2011) are packages in R developed to calculate a suite of indices that can be parametrized for site-specific needs. To contribute to the effort to determine the best practices associated with use of acoustic indices and their and interpretation, six were tested in 19 Australian forest stands (Fuller et al., 2015), 21 sites of varying urban intensity in a North American city (Gage and Joo from Ecoacoustics 2017), 24 sites across of mosaic of land-use types in Okinawa, Japan (Ross et al. 2017), and 73 sites in a man-made forest in lowland UK (Turner et al., 2018). The reliability it acoustic indices are dependent on many factors including habitat type, acoustic community composition and the ratio of biophony:geophonic:technophony (Sueur et al. 2012).

Previous studies that have used acoustic indices to describe the soundscape have reported that wind and increases in sound intensity of biophony due to close proximity to the microphone will produce unexpected results from some acoustic indices (Rankin and Axel from Ecoacoustics 2017, pg 129). Although intensive ecoacoustic studies have been conducted on many continents and ecosystem types, here I describe a first test of the use of acoustic indices to assess biodiversity and response to disturbance in a tallgrass prairie ecosystem, where wind is a prevailing geophysical factor year-round.

The Tallgrass Prairie Preserve (TGPP) provides substantial refugia for species experiencing habitat loss in the southern Great Plains ecoregion. As one of the largest remaining stands of contiguous, untilled tallgrass prairie remaining in North America, the TGPP provides important habitat for mammals, reptiles, migratory nesting birds and bats. Insectivorous faunal groups benefit from the tremendous insect diversity and biomass during the spring and summer. Land management practices including haying, mowing, grazing from bison and cattle in addition to prescribed burning employed by the Nature Conservancy (TNC) allow the prairie to flow through the disturbance cycles and nutrient influxes that it would normally experience pre-European settlement (Reinking 2000; Payne et al., 2001; Hamilton 2007; Palmer 2007). However, the preserve is not without anthropogenically induced habitat alterations which include the construction of a network of gravel roads to access oil and gas extraction sites. In addition, vehicular and air traffic are common sources of anthropogenic noise which comes from visitors who want to experience an increasing rare ecosystem and from training flights originating from a local Air Force base. Because the preserve is expansive (16,000 ha), broad spectrum passive acoustic monitoring is a practical solution for a non-invasive method to monitor spatial and temporal fluctuations in biotic and abiotic community interactions over time.



Adapted from Steinauer and Collins (1996) and Reichman (1987).

Fig. 2.1. The Tallgrass Prairie Preserve (TGPP), located in northeastern Oklahoma (36°50’N, 96°25’W), encompasses ~16,000 ha and is owned by the Nature Conservancy (TNC). The preserve is situated in the southern terminus of the Flint Hills where remnant prairies of the Great Plains still exist. Left image was adapted from Steinauer and Collins (1996) and Reichman (1987).

The primary goal of this study was to describe 1) how the soundscape of the tallgrass prairie changes over the growing season, and 2) how this pattern of growing season phenology compares in sites exposed to spring prescribed burns. Additionally, we hope to 3) provide evidence to land managers and conservation professionals that acoustic monitoring can be used as a rapid biodiversity assessment method to monitor the dynamic responses of grasslands to disturbance over time and for long-term ecological monitoring of acoustic communities.

We hypothesized that 1) there would be a significant increase in the activity and complexity of acoustic communities during all time periods as the mean daily temperature increased from Februrary to July and 2) recordings taken in pastures that had been burned in the spring of the study period (April 2017) would produce acoustic indices that acurrately reflect greater acoustic complexity (ACI), entropy (H), overall acoustic diversity (ADI), and acoustic biodiversity (BIO) and decreased evenness (AEI) of the burned sites. Additionally, I predict the ratio of technophony to biophony as measured by the normalized difference soundscape index (NDSI), will decrease over time as the acoustic community in burned sites will be restored over the growing season, eventually outcompeting any technophonies present.

Methods

Study Area

The Nature Conservancy's (TNC) Tallgrass Prairie Preserve (TGPP) in Osage County, Oklahoma (36°50'N, 96°25'W) encompasses ~16,000 ha of one of the largest remaining stands of tallgrass prairie in North America and is located at the southern terminus of the Greater Flint Hills region of Kansas. Since its purchase in 1989, the TNC has aimed to restore natural heterogeneity patterns typical of this ecoregion through a mix of bison and cattle grazing coupled with prescribed fire, mowing and haying (Hamilton 1996; Palmer, 2007). Using a 3-year fire return schedule, TNC biologists randomly select pastures for prescription burns; 40% of burns are conducted in the spring, 20% in the summer, and 40% in the fall/winter months. The TGPP is 90% grassland with the remaining 10% composed of cross-timber forests characterized predominately by two oak species: *Quercus stellate* and *Quercus marlinadica* (Hamilton 2007).

Dominant C^4 grass species include *Andropogon gerardii*, *Sorghastrum nutans, Sporobolus compositus*, *Panicum virgatum* and *Schizachyrium scoparium* with an additional 763 plant species in 411 genera and 109 families with 12% non-native (Palmer 2007). This diverse botanical composition leads to high invertebrate biomass and diversity, which in turn supports numerous residents and neotropical bird species that nest at the site during the late-spring and summer months (May - July). Additionally, the preserve sits within the historic boundaries of the Osage Nation. The Osage Nation retains the mineral rights to the land, and therefore maintains a network of gravel roads that provide access to the many oil and natural gas wells that operate across the site via tribal leases.

Recording Stations

A combination of 11 cattle grazed, bison grazed, and ungrazed pastures were burned by TNC staff in March and April 2017. To test the effect of fire disturbance on the local acoustic community, I determined the centroid of each burn pasture in (ESRI ArcGIS ver. 10.3.1) (ESRI, Redlands, CA, USA) and used this location to establish a "treatment" recording station for five months (February – July) during the grassland growing season to collect pre-burn and post-burn/recovery recordings. Each of the 11 treatment recording stations were paired with a control (unburned) recording station that best matched TNC management history characteristics of its corresponding treatment recording station (Figure 2.2.). A minimum distance between recorders of 500 meters was chosen and was based on microphone sensitivity to avoid pseudo sampling (Eldridge et al. 2016). Additional criteria used in control recording station selection to minimize variation between sites included grazing and fire treatment history and distance from natural and non-natural landscape features (Table 2.1).

Due to the sparsity of woody vegetation suitable for mounting recorders, 2m metal T-posts posts were installed to establish the recording stations and provide a mounting surface for the acoustic recorders. Fence posts were driven ~0.5m into the ground and secured with concrete (The Quikrete Cos., Atlanta, Georgia, USA) for the duration of the five-month recording period. Upon completion of the study, all fence posts and concrete were removed and holes that were created as a result of retiring the recording stations were filled in with displaced soil.

Soundscape Recordings

Many studies using passive acoustic recorders will employ an automated sampling schedule to coincide with the activity patterns of the acoustic community of interest (birds: Sueur et al. 2008; Farina et al. 2011; Depraetere et al. 2012; Krause & Farina 2016; Ritts et al., 2016; fish: Harris et al. 2016). Because we wanted to understand how the overall sound signature of an environment may change in response to fire disturbance, we deemed it important examine all periods of the day in order to evaluate the nocturnal, diurnal and crepuscular species contributions to the soundscape. Thus, to represent sounds throughout a full solar and lunar cycle and to incorporate ultrasonic soundtopes (>25kHz), which describe the spectral activity unique to each species present in a sonotope (Farina 2014), Frontier Labs BAR (Brisbane, AU) recorders fitted with custom EM179 microphones (Primo Microphones, McKinney, TX, USA) were programmed to record 1 minute every 10 minutes for 24 hours at a 16 bit/ 96kHz sampling rate. Recording six one-minute samples every hour is one of the suggested optimal sampling schedules out of the five recording schedules empirically tested to capture an accurate representation of an acoustic community in terms of spectral and temporal heterogeneity (Pieretti et al., 2015). In order to make direct comparisons between burned and unburned pastures of a similar landscape configuration, BARs at treatment and control recording stations were set to record simultaneously for the entire 24-hour period. We rotated ten recorders every 48 hours among the 11 pairs of recording stations (Table 2a. & 2b.).

Data pre-processing

Prior to calculating acoustic index values, we inspected all 60-second audio files for biotic recording quality by visually examining spectrograms. A 300 Hz high pass filter was applied to all recordings in Adobe Audition 3.0 to reduce self-noise generated from the microphone and low levels of wind noise (Merchant et al. 2015). Audio files impacted by high levels of wind or rain to the extent that the >12.5% of the acoustic signature was obscured were not included in subsequent analyses.

In addition to tracking hourly changes in acoustic diversity every ten minutes from the one-minute files, and to aid in a more detailed examination of relationships between phenological changes in the soundscape and prescribed burns, we subdivided daily recording periods into acoustically-rich time ranges for additional analyses. Local sunrise and sunset times were obtained from the Astronomical Applications Department (U.S. Naval Observatory website: http://aa.usno.navy.mil/data/docs/RS_OneYear.php). Similar to findings from Buxton et al. (2016), we observed an increase in avian activity within one hour of sunrise. These temporal windows are hypothesized to be important for soniferous species because wind and humidity are at optimal signal transmission conditions, and the periods are thought to incur lower predation risk (Burt and Vehrencamp 2005). To capture the distinctive crepuscular chorusing activity of anurans (Grafe & Meuche 2005), birds (Farina et al., 2015), coyotes (Laundré, 1981) and some insects (Howard and Hill, 2009) at the TGPP, we designated two-hour windows to represent dawn (two hours following sunrise) and dusk (two hours following sunset). Day and night were assigned to the remaining hours following the end of the dawn and dusk periods respectively.

Acoustic Indices

In order to rapidly assess changes in the tallgrass prairie soundscape over the growing season, and to assess how prescribed burning influenced this phenological change, we chose six acoustic indices to characterize the soundscape: Acoustic Complexity Index (ACI), Acoustic Diversity Index (ADI), Acoustic Evenness Index (AEI), Bioacoustic Index (BIO), Entropy (H), and Normalized Difference Soundscape Index (NDSI) (see Table 3. for original publications and descriptions).

Acoustic indices were calculated for each 60-sec sound recording using the R (R Development Core Team 2017), packages *Soundecology* (Villanueva-Rivera et al., 2011) and *Seewave* (Sueur et al., 2008) run through Premise (the University of New Hampshire's Research Computing Center High-performance Computing Cluster). Premise consists of a head node and 14 compute nodes along with 225TB of usable storage, and wav files were processed in serial using the "multiple_files" function in R (ver. 3.4.1; see Appendix). All acoustic indices were parameterized to accommodate the 96 kHz sampling rate (maximum frequency set to 48kHz) to capture the ultrasonic night calling insects (mostly katydids) and bats. NDSI was modified from the default setting of anthrophony (1000 Hz to 2000 Hz) and biophony (2000 Hz to 11000 Hz) to include technophonic sounds emitted by oil and gas air compressors and vehicular and air traffic from 300 to 3000 Hz (mean dominant frequency = 914 Hz, n=8) and biophonic sounds emitted from 3001 Hz to 48,000 Hz. An additional modification was done NDSI was also done to conserve low frequency soundtopes from coyotes and some bird species (night hawks, great horned owls) when appropriate. If biophony from these sources were detected, we lowered the minimum value to 300 Hz.

In addition to removing geophonic events that mask most frequencies before using index values in final statistical analyses, it is common in the pre-processing stage to manually remove outliers if spectrograms confirm that indices responded disproportionate to biotic or (more commonly) abiotic acoustic events (Depraetere et al. 2012). Values from each index were sorted by size and were cross-referenced to its corresponding spectrogram. If a value was deemed to behave unexpectedly and was identified through analysis as a statistical outlier, it was removed from further analysis. ACI values were observed to spike to 2500 - 3000 during extreme wind events or when birds with frequency modulated calls would sing while perched on top of a recorder post. Given that the median ACI for this study was 1665 (1st quartile = 1649, 3rd quartile = 1693) values exceeding 2500 were removed as outliers.

Data Analysis

We used median values to describe the central tendency for each time block examined (hour, day, week) in our time series analyses (Feys 2016). Median values were calculated for each week of the study (1-23) for each acoustic index value and for each larger time block from each day (dawn, day, dusk, night). Median values were then plotted over 23 weeks with each index on a separate y axis represented by multiple time-series plots for visual analysis. We then used Kruskal-Wallis test to compare the weekly acoustic index values for each distribution of control versus burned sites over the 23-week period and ran this comparison for all six indices tested. I used a non-parametric Dunn-Bonferroni multiple comparisons test to examine week to week differences in the grassland soundscape to assess acoustic divergence and convergence over time.

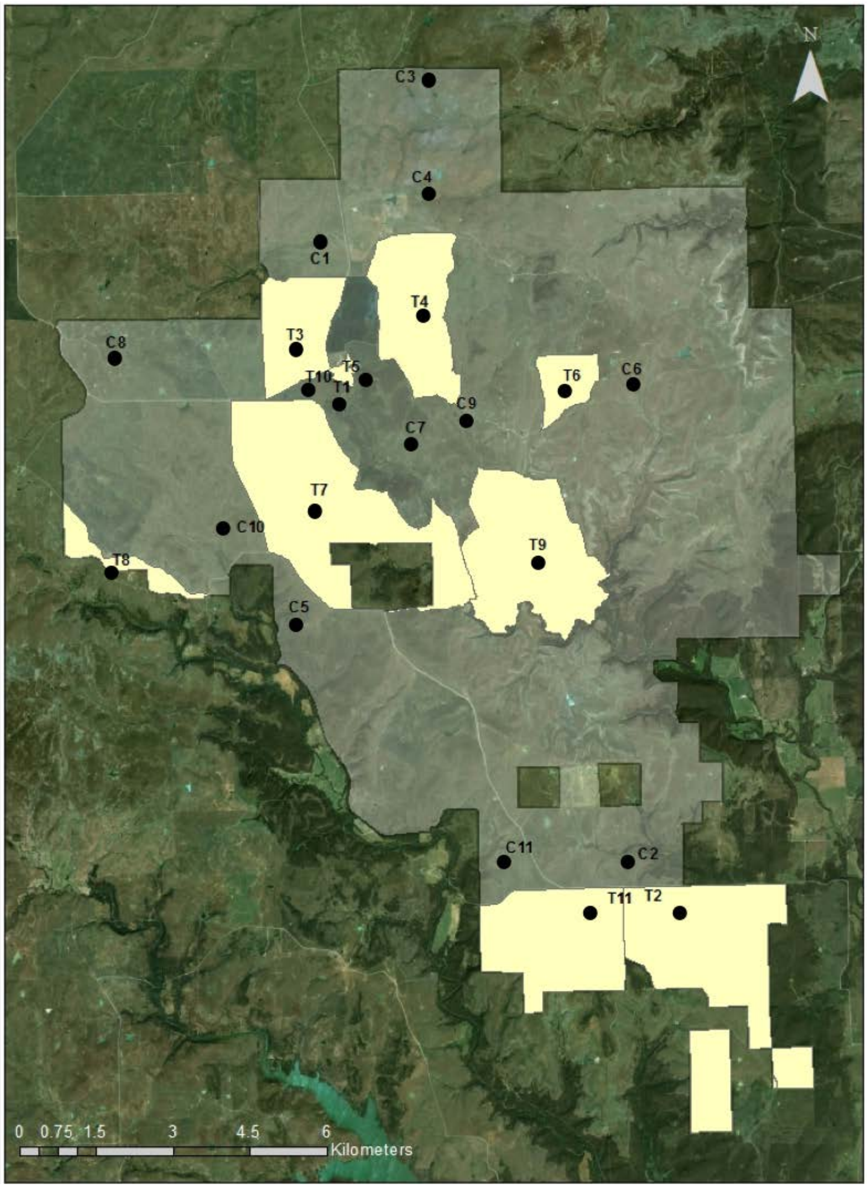


Fig. 2.2. Map of recording stations established at the Tallgrass Prairie Preserver, Osage County, OK, USA for February – July 2017. Opaque polygons represent pastures that received a prescribed burn. The centroid of each polygon was identified and was assigned a point ID (T1-11) to mark the location of recording station installation. Once treatment pastures were identified, a counterpart control (unburned in the last 12 months) location was determined using criteria identified in Table 1.

Table 2.1. Criteria used to select a control recording station to pair with eleven treatment recording stations. Listed in order of importance to control for variation in landscape attributes in this particular ecosystem where regular land management practices dictate landscape and potential soundscape attributes.

Factor	**Site-specific attribute**
Fire	Outside 2017 burn 2016 burn < 2016 burn
Herbivory	Grazing regime (bison or cattle)
Anthropogenic	Proximity to oil wells Proximity to roads
Environmental	Proximity to streams Proximity to forest

Table 2.2. Sites at the TGPP were burned in the beginning of March 2017 and ended in April 2017.

Site	**Burn Date**
T6	3-Mar
T3	15-Mar
T5	15-Mar
T4	18-Mar
T8	20-Mar
T7	28-Mar
T9	29-Mar
T2	1-Apr
T11	1-Apr
T1	24-Apr
T10	24-Apr

Table 2.3a. Deployment schedule blocked by week. Ten recorders were rotated across the twenty-two study sites between late February and the end of July 2017. An average of twelve 24-hour recordings were made at each site at the conclusion of the study (~2.4 recordings periods per month).

Recording Station	Pre-burn recordings	Post-burn recordings
1	1	11
2	1	13
3	2	12
4	2	13
5	3	13
6	2	13

7	3	12
8	2	11
9	2	11
10	2	10
11	2	12

Table 2.3b.

Week	Dates	Recording Periods
1	Feb 20 - 26	13
2	Feb 27 - March 5	4
3	March 6- 12	6
4	March 13 - 19	6
5	March 20 - 26	6
6	March 27 - April 2	8
7	April 3 -9	6
8	April 10 - 16	5
9	April 17 - 23	6
10	April 24 - 30	6
11	May 1 - 7	6
12	May 8 - 14	8
13	May 15 - 21	4
14	May 22 - 28	7
15	May 29 - June 4	6
16	June 5 - 11	8
17	June 12 - 18	6
18	June 19 - 25	8
19	June 26 - July 2	8
20	July 3 - 9	14
21	July 10 - 16	4
22	July 17 - 23	6
23	July 24 - 30	6

Table 2.4. Six alpha-level complexity indices (within-group diversity) used in the investigation of the growing season phenological changes to a tallgrass prairie soundscape, and its response to spring prescribed burning.

Index	**Original Publication**	**Interpretation**
H	Entropy (Sueur et al., 2008)	Values range from 0 to 1 where 0 = pure tone, 1 = numerous and even frequency bands. Evaluates a combination of spectral and temporal entropy.
BIO	Bioacoustic Index (Boelman et al., 2007)	Considers sound intensity (dB) and frequency. Large numbers indicate acoustically rich recordings i.e. loud sounds occupying many frequency bands. Low numbers indicate the opposite i.e.

		acoustically poor recordings while quite sounds occupied by fewer frequency bands.
ACI	Acoustic Complexity Index (Pieretti et al., 2011)	Considers intensity (dB) and length of recording in the calculation. Originally created to estimate avifauna populations in areas of constant, low-frequency anthropogenic noise where an ACI value is calculated independent of low frequencies.
AEI	Acoustic Evenness Index (Villanueva-Rivera et al., 2011)	Values range from 0 to 1 where 0 = extremely even acoustic community and 1 = uneven or diverse acoustic community. The Gini index is applied to proportions of binned frequencies to measure the evenness of the occupancy distribution.
ADI	Acoustic Diversity Index (Villanueva-Rivera et al., 2011)	The Shannon Diversity Index is applied to binned frequencies of a sound file at 1000 Hz intervals
NDSI	Normalized Difference Soundscape Index (Kasten et al., 2012)	Values range from -1 to 1 where -1 = predominant anthropogenic sounds and 1 = predominant biotic sounds. Computes the normalized power spectral density (watts/kHz) of technophony:biophony

Results

Soundscape Phenology

In addition to assessing differences in the soundscape of burned and unburned pastures, we are able to report for the first time the soundscape phenology of anurans, birds, insects and bats at the TGPP. The patterns that emerged from notes taken through the visual and aural examination of each spectrogram helped in the interpretation of the patterns we observed after acoustic indices were calculated and generated into time-series plots (Figure 2.a-f.).

Biophony

Anurans

Anurans (frogs and toads) were detected in the evening and night at burned and unburned sites T2, T4, T6, T7, T8, T9, C1, C3, C4, C6, C9. Earliest detections include the first week of recording before burns had occurred in late February until late June. No calls were identified to species.

Birds

We regularly detected Common Nighthawk (*Chordeiles minor*), Dickcissel (*Spiza americana*), Eastern Meadowlark (*Sturnella magna*), Grasshopper Sparrow (*Ammodramus svannarum*), Field Sparrow (*Spizella pusilla*), Henslow's Sparrow (*Ammodramus henslowii*) and Killdeer (*Charadrius vociferous*) throughout the 22 recording stations; all are noted as common species in tallgrass prairies within the Flint Hills region (Reinking, 2005; Reinking et al., 2009). Vocalizations from a recreationally valued game bird in Oklahoma, the Northern Bobwhite (Colinus virginianus), were also common and were detected at every recording station. Our finding is encouraging because this species has been designated as near threatened on the IUCN Red List since 2004 and reports that the current population trend is decreasing (IUCN 2018). At sites T6 and T8 (burned during week 3) we recorded vocalizations from a nesting Upland Sandpiper (*Bartramia longicauda*) which is noteworthy finding because this species has shown population declines for the past two decades in North America (Reinking, 2005; Sandercock et al., 2015). Other bird species we detected but were less common include migrating Canada Geese (*Branta candensis*), breeding Bell's Vireo (*Vireo bellii*), Chuck-Will's Widow (*Antrostomus carolinensis*), Yellow-billed Cuckoo (*Coccyzus americanus*), Eastern-wood

Peewee (*Contopus virens*), Indigo Bunting (*Passerina cyanea*), Painted Bunting (*Passerina ciris*), Blue Grosbeak (*Passerina caerulea*), and resident American Crow (*Corvus brachyrhynchos*), Red-bellied Woodpecker (*Melanerpes carolinus*), and Tufted Titmouse (*Baeolophus bicolor*). Although apparently declining in other areas of the Great Plains, this population of Henslow's Sparrows (*Ammodramus henslowii*) at the TGPP may be one of the largest in North America (Reinking et al., 2000). Field Sparrows (*Spizella pusilla*), which were frequently recording during the course of this study, exhibit a poorly understood nocturnal singing behavior. Continued acoustic monitoring similar to this study could reveal seasonal and temporal patterns to this behavior and would allow for the monitoring of other species of conservation concern in the same effort (Celis-Murillo et al., 2016).

Insects

Insect communities in grassland ecosystems are known to differ between burned and unburned sites depending on life history traits of each species (flying vs ground-dwelling), fire periodicity, and season of fire (Hansen 1986; Chambers and Samways 1998; Panzer and Schwartz 2000; Swengel 2001; Perry 2012). At the TGPP, nights at both burned and unburned sites were biologically quiet until the emergence of Prairie Mole Crickets (*Gryllotalpa major* Saussure) during week 8 in mid-April. G. major, a rare endemic species to tallgrass prairies in the south-central United States (Vaughn et al., 1993; Hill 1998; Howard and Hill 2009), has been shown to prefer sites to establish lek mating arenas that have recently been burned (Howard and Hill, 2007). Detections were recorded mid-March through mid-May at sites T3, T4, T10, C4, C5, C8. Detections in unburned sites, although not as common, may indicate previously unknown G. major lek sites. During week 10, prairie mole crickets begin to emerge and contribute to the increase acoustic diversity of the dusk soundscape. Acoustically rich insect diversity occupied a broad spectrum of frequencies which we would not have been able to detect if we had used a lower (44.1 KHz) sampling rate. Cicadas emerged in week 11 becoming acoustically active during the day and dominated the soundscape by, in some cases, occupying the entire frequency spectrum at night by week 18 through the end of the survey in week 23. Interestingly, this acoustic wash effect did not cause an increase in the acoustic evenness index (AEI), rather AEI decreased around this time during the study. This decrease in acoustic evenness could also be due to an increase in bat and other insect species contributing to the soundscape. The first detections of katydids and field (*Gryllus* spp.) and tree cricket (*Oecanthu*s spp.) species occurred during weeks 15 - 19 and could have also contributed to an increase in acoustic diversity and a decrease in acoustic evenness as indicated by ADI and AEI respectively.

Bats

As a result of coupling an ultrasonic-sensitive microphone to a higher recorder sampling rate, we were able to detect bats throughout the duration of this study. Bat community response to fire is a novel topic in fire ecology and as of this current research, undocumented in tallgrass prairies, as most field studies take place in forests and riparian habitats (Perry 2012). We quantified bat detections by counting the number of one-minute files that had bat activity present in the spectrogram. Counts were binned by totaling the number of spectrograms with echolocations from each month of the study (Figure 3.). There was no significant difference in the number of bat calls between burned and unburned sites (chi-square = 0.36, df = 1, p-value = 0.55). While no individual calls from this study were identified to species, two bat species, *Lasiurus borealis* (eastern red bat) and *Nycticeius humeralis* (evening bat) are known to forage near streams and forest edges at the TGPP. Bat species common to the area but not detected on the preserve since the last known survey effort in 2001 include: *Lasiurus cinereus* (hoary bat), *Lasionycteris noctivagans* (silver-haired bat), *Pipistrellus subflavus* (eastern pipistrelle) and *Eptesicus fuscus* (big brown bat) (Payne et al., 2001). Bat populations in this region may soon be threatened by the devastating fungal pathogen White Nose Syndrome, which is now present in seven counties in Oklahoma (White Nose Syndrome Response Team, 2018), and ecoacoustic monitoring may advance our understanding of the effects of this pathogen on bat populations over time.

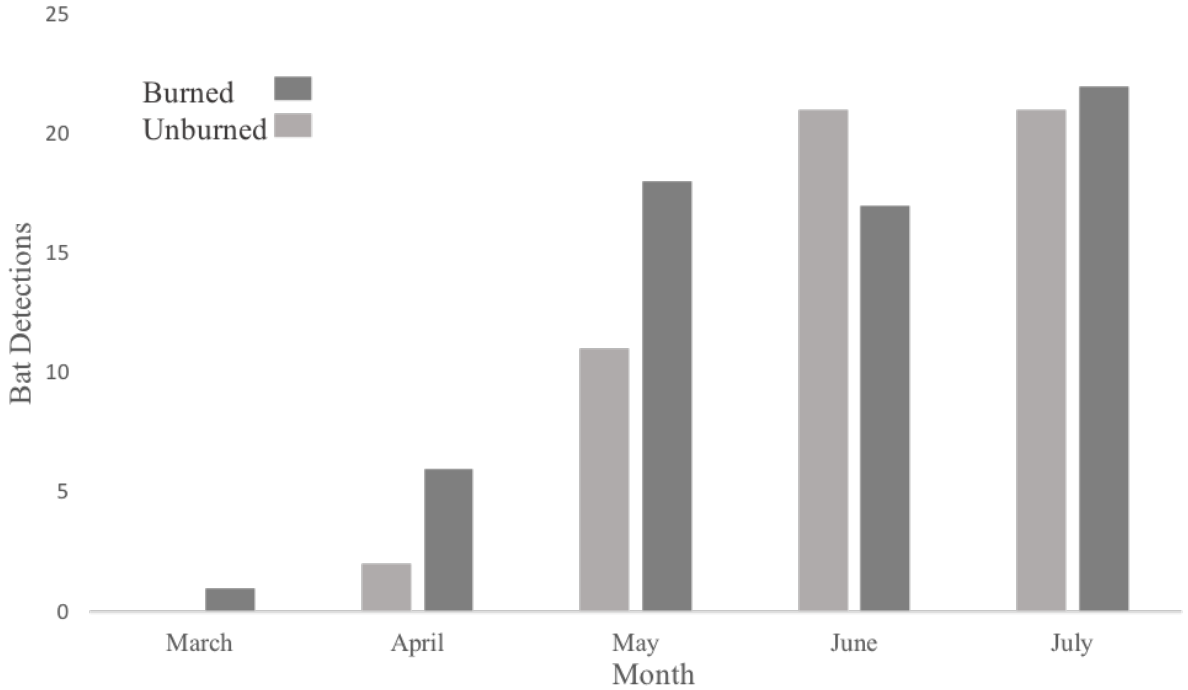


Fig. 2.3. Ecoacoustic recordings indicated no significant difference between the overall number of bat detections between burned and unburned sites (Kruskal-Wallis test, chi-square = 0.36, df = 1, p-value = 0.55) at the Tallgrass Prairie Preserve. However, a distinct increase in bat detections was observed as spring progressed into the warmer summer months as insect activity increased, and early in the post-burn period there were higher bat detections in the burned sites. Access to invertebrate food resources is one of the most important factors in determining insectivorous bat abundance and distribution (Kunz 1982).

Geophony

Wind was the predominant source of sound during the day at the TGPP from February to mid-April around week 9. During this time unsettled weather in the southern plains, wind from severe thunderstorm and tornadic activity would often cause exaggerated acoustic index values, especially those calculated using the ACI. Following this seasonal period of high winds, geophonic activity diminished and was replaced with an increased abundance and diversity of biophony for the remainder of the study.

Technophony

Air traffic was regularly detected at sites T4, T6, C4 during the day. Sites within detection distance from active oil wells where internal combustion diesel engine pumps were operating 24-hours per day include T4, T6, T7, T9, C6, C7, C8, C9. Although technophony was present at these sites throughout the duration of the study, the NDSI is the only index that directly measures the ratio of technophony to biophony in a recording. Overall, human-induced sound was not a prominent component of the TGPP soundscape.

Acoustic Index Response to Disturbance

At the end of the 23-week acoustic survey of the Tallgrass Prairie Preserve, we collected ~ 40,000 1-minute recordings. Using a Kruskal-Wallis test of ranked sums, two acoustic indices identified significant differences in the soundscapes of burned vs unburned sites: ACI (chi-square = 6.24, df = 1, p-value = 0.018) and BIO (chi-squre = 7.5, df = 1, p-value < 0.01) (Figure 2.4). We then used the same test to examine weekly differences between median acoustic index values and found that all acoustic indices revealed statically significant ($p > 0.05$) differences between weeks at burned and unburned sites. We followed up with a post-hoc Dunn-Bonferoni multiple comparisons test to determine which weeks significantly differed. In addition to testing for differences between weeks, we compared the four larger time blocks (dawn, day, dusk and night) between burned and unburned sites. A non-parametric comparison of each pair using the Wilcoxon method revealed no difference across ACI, ADI, AEI, H and NDSI values between sites that were burned and sites that were not burned. Only BIO values at dawn were different between burned and unburned sites (z = -1.96, df = 1, p-value = 0.047) (Figures 5.).

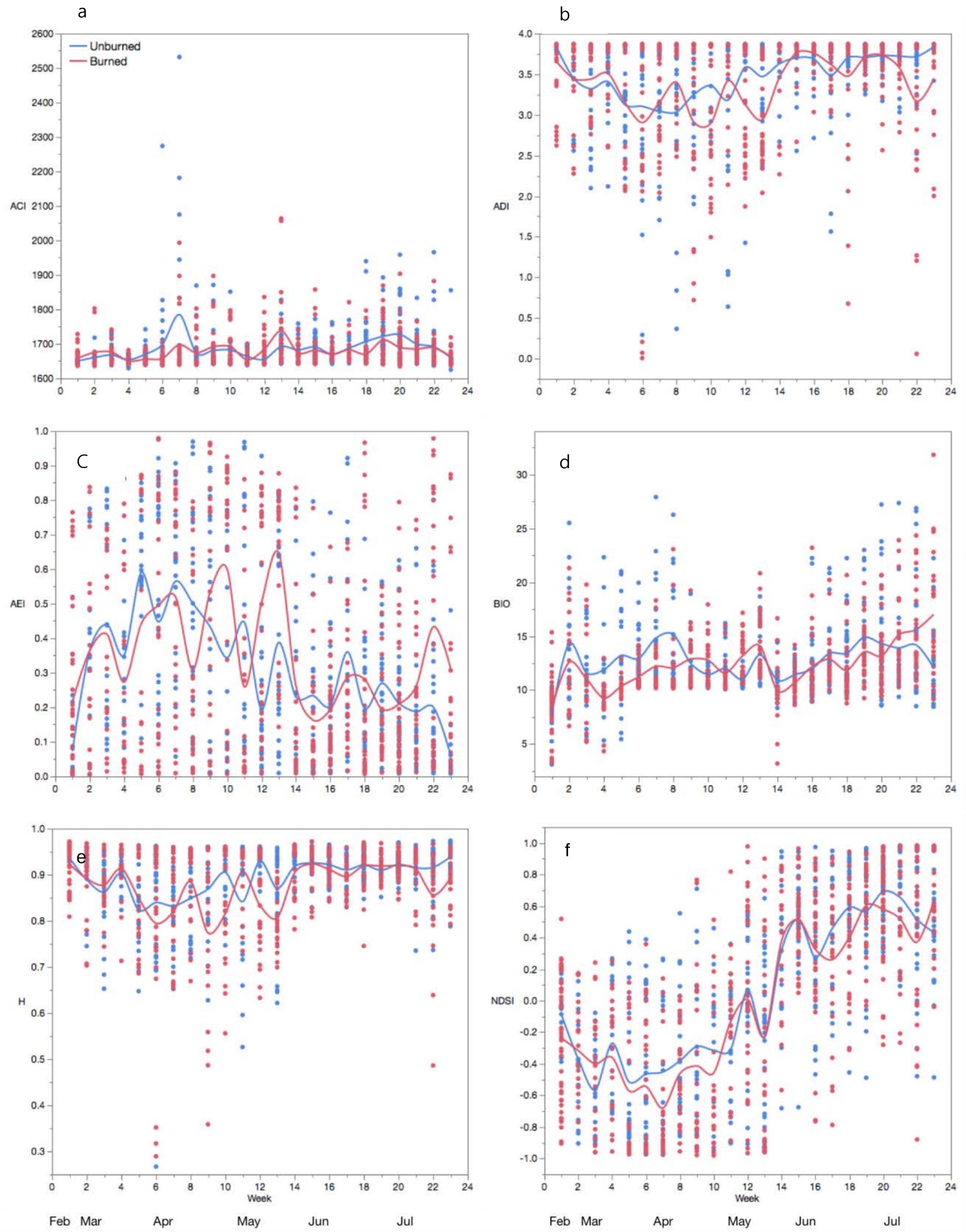


Fig. 2.4 a-f. A panel of six acoustic indices over time in response to fire disturbance which began on March 3 and concluded on April 24, 2017. Acoustic indices all display a unique response which is expected given the purpose of each to evaluate the soundscape differently. ACI appears to fluctuate in the middle of the study and is truncated by converging lines at the beginning and end of the study. In the summer, homogenous broadband signals from insects like cicadas begin to dominate the soundscape, which could be a reason for the decline of ACI. ADI and AEI are roughly opposed in their response to the soundscape, meaning as the season progressed the

soundscape became more diverse and therefore less even. Unburned and burned sites followed a similar trend throughout the data collection effort until the end where lines begin to diverge and bioacoustic activity begins to increase at burned sites. Acoustic entropy (H) follows a similar trend as BIO where unburned and burned sights closely mirrored each other until the middle of July when burned sites begin to decrease in entropy. A noticeable shift in NDSI occurs during week 13. Low values in Fig. 2f represent low frequencies outnumbering high frequencies and higher values represent higher frequencies outnumber low frequencies. This shift could be caused by an increase in bat and insect activity at night where higher frequency bands are occupied by echolocations and ultrasonic interspecific communication. Overall, each acoustic index appears to respond to a shift in burned sites becoming more acoustically diverse around week 13. This trend may reflect a period just before bird, insect and bat activity reach their maximum in mid-May until the end of the season in late July when biotic activity decreases or plateaus.

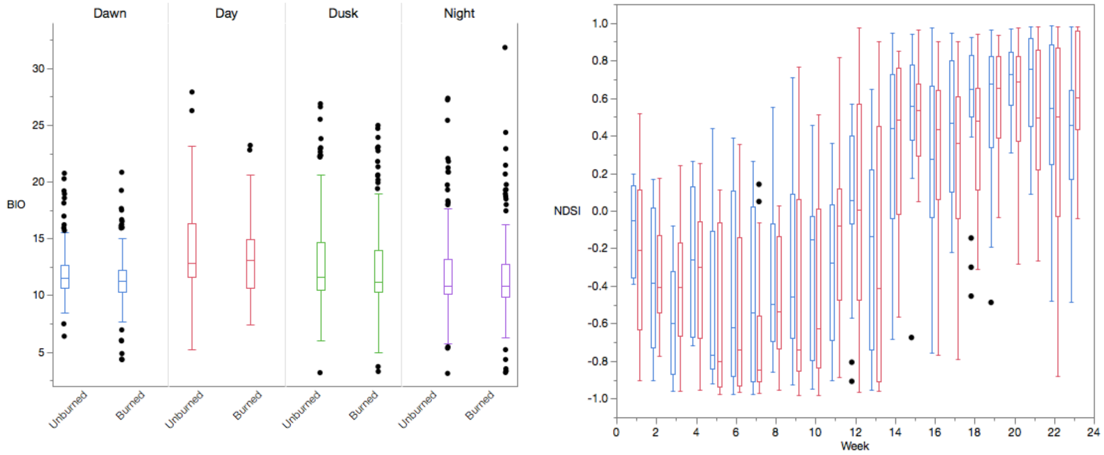


Fig. 2.5. BIO (left) and NSDI (right) appear to be the most responsive acoustic indices to biotic responses to grass recovery and seasonal bird migration and insect emergence in late-spring around week 13 of this study. Cumulative bioacoustic index (BIO) values from burned and unburned sites were significantly different during the dawn time block (z = -1.96, df = 1, p-value = 0.047). BIO was the only acoustic index that revealed significant differences between burned and unburned sites when partitioning values into time blocks.

Discussion

Applications in soundscape ecology are becoming more refined and widely used to inform management practices and policy and have been implemented in U.S. National Parks to measure the impact of noise pollution on wildlife and visitor experience, and extended to temperate reef ecosystems to assess the effects of ocean acidification on marine acoustic communities (Miller 2008; Sueur et al., 2008; Lynch et al., 2011; Rossi et al., 2016; Farina 2018). Research on prairie soundscapes is limited and mostly focused on the potential negative impacts wind energy development may have on species of conservation concern such as Greater Prairie-Chickens (Tympanuchus cypido) and other avifauna and bats (Whalen 2015; Raynor et al., 2017; Bennett and Hale 2018). No studies, however, have examined the soundscape in the context of disturbance due to traditional land management practices like grazing, mowing and prescribed fire regimes. The incorporation of acoustic surveys can help to better understand the dynamic interactions that occur in tallgrass prairies related to these ubiquitous practices and the effects they have on wildlife. Because our understanding of the ecology of the Great Plains is limited to a post-European settlement timeframe, piecing together components of ecosystem interactions using a method that was previously not available is essential to improve conservation efforts of North American prairie remnants. Ecological factors include but are not limited to fire interval, intensity, seasonality and spatial extent (Umbanhowar, 1996), grazing influenced primarily by bison (Collins 1998), and historic endemic and native floral and faunal assemblages. These factors have certainly shaped the acoustic environment prior to dramatic land-use changes that occurred. The Tallgrass Prairie Preserve however, is unique in that due the shallow rocky soils of the Greater Flint Hills ecoregion, it was spared from mass cultivation of the south-central United States (Reinking, 2005; Hamilton, 2007). Because passive acoustic monitoring and ecoacoustic analysis allows for minimal disturbance for deployment and the collection of high-quality, long-term data (Sueur and Farina 2015), this method is an ideal solution to preserving an already vulnerable landscape.

Over the course of five months, we captured a dramatic transformation of the tallgrass prairie soundscape in terms of its acoustic complexity, acoustic diversity, acoustic evenness, acoustic entropy and a shift from human-influences low frequency sounds to high frequency sounds produced primarily biotic communities, all described by six acoustic indices. A prominent shift from the dominance of lower frequency sounds generated by technophonic sources early in the post-winter period to biophony characterized by higher frequencies related to an increase in bird, bat and insect activity later in the early summer was accurately reflected by the NDSI. A reason for an increase in acoustic complexity, particularly in a grassland ecosystem, is due to the highly repetitive and frequency modulated calls of passerines (Morton 1975). This type of vocalization is beneficial to overcome irregular amplitude fluctuations in their open environment (Brown & Handford 1996).

It has been demonstrated that increased acoustic activity at night is attributed primarily to Orthopterans in warm climates such as those of the tallgrass prairie (Fuller et al., 2015; Gasc et al., 2013; Pieretti et al., 2015). We observed a consistent increase during the night hours as temperatures consistently reached and stayed above 4.4 degrees C. A similar phenological trait of a Brazilian forest was observed when ACI values increased during the wet season (Pieretti et al., 2015). Insects are important to tallgrass prairie ecosystems because they provide a stable food source for resident and migratory neotropical breeding birds and bats (Callaham et al., 2002; Whiles 2006). Insects, especially cicadas, have largely been ignored in soundscape studies or are regarded as noise that obstructs the performance of some acoustic indices, yielding dubious results (Ecoacoustics, pg. 112). This difficulty is due their broad-band choruses that interfere with avian acoustic signals in the same manner as geophonies such as wind (Hart et al., 2015; Ross et al., 2017), and emerge particularly when using the ACI to evaluate bird acoustic diversity (Farina et al., 2011). Similarly, ADI and BIO were found to be especially sensitive insect choruses and produced unreliable results when focused on avian diversity because of the wash of broad spectrum sound produced by signing cicadas (Farina et al., 2011; Fuller et al., 2015; Rankin and Axel (from Ecoacoustics 2017, pg 129); Ross et al., 2017). High ACI values indicate high levels of acoustic complexity in terms of the spectral variation of intensities in frequency-modulated avian signals (Pieretti et al., 2011) and these results were consistent with our observations in a tallgrass prairie soundscape.

Comparisons of acoustic indices over time and between burn and unburned sites suggest that soundscapes are altered by prescribed fire, but the changes brought by burning were generally ameliorated by the end of the growing season. Soundscape diversity as measured by six acoustic indices differed significantly between weeks, especially when later recordings were compared to recordings from earlier weeks that were taken before and immediately following a burn. This trend is reflective of the return of grasses and the restoration of the acoustic communities that were eliminated by disturbance effects of the fire. Our hypothesis that burning would yield greater acoustic richness was based on two principles: 1) fire encouraging new growth of grasses which attracts some wildlife and 2) tallgrass prairie plant and animal communities are resilient to disturbance from fire. Fire helps to release nitrogen trapped in leaf and grass detritus. Once liberated, nitrogen can filter back into the soil providing the limiting nutrient essential for grass growth (Knapp & Seastedt, 1986). Furthermore, the ground becomes exposed, it can be warmed by the sun which stimulates seed germination. Combined with the right grazing and fire regime, which have shown strong interactive effects (Fuhlnedorf & Engle, 2004), and annual precipitation, these factors are shown to increase vegetative productivity of tallgrass prairies (Bragg & Hulbert, 1976; Gibson & Hulbert, 1987; Hulbert, 1988; Briggs & Knapp, 1995; Collins & Wallace, 1990). The intermediate disturbance hypothesis, oringially tested in tropical forests and coral reefs, states that species richness is highest when communities are subject to moderate frequencies and intensities of disturbance (Connell, 1978). This hypothesis was testing in a tallgrass prairie to determine floral species richness in response to frequency of fire disturbance (Collins et al., 1995). Findings from this study were mixed. Floral species richness was evaluated in plots representing three stages of disturbance: annual burn, intermediate burn (4 yr interval) and long-term unburned sites. Findings showed a significant negative correlation with disturbance frequency. These results are consistent with results from pervious experiments that fire frequency and plant species richness are negatively correlated (Collins, 1987). However, an intermediate number of years since burning does seem to support maximum species richness which directly correspond to the intermediate disturbance hypothesis. This finding, however is not common and as suggested in an opinion piece by Fox (2013), results in most studies do not support the IDH when biodiversity at differnet levels and frequencies of disturbance is evaluated. In additiont to fire, disturbance grazing and mowing has been show to affect tallgrass floral and faunal species composition (Callaham et al., 2002; Collins et al., 1998; Hobbs et al., 1991; Reinking, 2005; Sandercock et al., 2015; Welti & Joern, 2018). Indeed, disturbance is complex and is usually best evaluated through interactive effects or through multiple linear regressions (Collins, 1987; Krause & Culmsee, 2013). While the current study focused on the influence of prescribed burning on grassland soundscapes, how grazing affects grassland acoustic communities remains another deserving investigative frontier.

CONCLUSIONS AND FUTURE DIRECTIONS

Most research in the soundscape ecology and ecoacoustics literature has focused on soniferous species monitoring, species identification and methodologies to extract and interpret pertinent acoustic information from recorded sound files (Farina et al., 2018). Fewer studies, with the broader aim of using the soundscape as an indicator of ecosystem health, have empirically tested the relationship between soundscape composition and habitat characteristics such as vegetation structure (Boelman et al., 2007) and habitat fragmentation (Fuller et al., 2015; Burivalova et al., 2017). Prior to this study, no work has sought to understand the relationship that non-soniferous species have with the soundscape over space and time. I predicted that all *Nicrophorus* burying beetle species would positively covary with acoustic diversity in a tallgrass prairie soundscape. Results from my study revealed that while some Nicrophorine burying beetle species positively covary in their abundance and distribution with measures of the soundscape as reflected by acoustic indices, one species exhibits an unexpected negative relationship. These relationships were more apparent when acoustic indices were subdivided into four biologically distinctive time blocks. While burying beetles themselves are not known to contribute to or perceive soundscapes, we conclude that their decomposer niche intimately binds them to the acoustic community. The primary reproductive resource Nicrophorine burying beetles depend upon are small mammal and bird carcasses. From this study, I determined that acoustic communities are mainly composed of birds, insects, amphibians and mammals at the Tallgrass Prairie Preserve study site, and that correlations drawn between acoustic indices and the spatial distribution and abundance of burying beetles are species-specific. Relationships between non-soniferous organisms and soundscapes are important to understand because, as in ground beetles that are often used as indicators of disturbance from anthropogenic noise (Bunkley et al., 2017) and of the health of local environmental conditions (Rainio and Niemela 2002), burying beetles may also hold promise as indicators of healthy ecosystem function due to their trophic position. Additionally, knowledge of these relationships between soundscapes and sensitive species may help conservation scientists to further understand declines in beneficial insect populations, particularly species like the critically endangered American burying beetle (*Nicrophorus americanus*). Fundamentally, research from my first chapter demonstrates that measures of the soundscape can be useful in evaluating habitat suitability for non-soniferous species, providing the first test of and support for the Acoustic Habitat Hypothesis (Mullet et al., 2017).

Phenology, the study of the seasonal timing of life cycles, is fundamental to understanding the natural world and is eventually what led to modern experimental ecology (Beaubien and Johnson 1994; Menzel 2002). Studies of phenological patterns are most often applied in the context of monitoring botanical communities, bird migratory behavior and more recently, climate change effects (Leopold and Jones 1947; Sparks 1999; Wilsey et al., 2017). In tallgrass prairies, seasonal transitions are quite dramatic: winter temperatures can be consistently below freezing, spring is characterized by an unstable atmosphere that regularly produces tornadic activity, and warmer summer temperatures lead to a massive influx of insect biomass and migratory breeding birds that remain until early fall (Axelrod 1985). I used an ecoacoustic methodology to document changes to the Tallgrass Prairie Preserve overtime in order to test the hypothesis that new grass growth from prescribed burns and a seasonal increase in photoperiod and daily temperature would be reflected in an increasingly complex soundscape as weeks progressed throughout the duration of the growing season. In addition to phenological characteristics of the prairie over the course of five months, I examined how prescribed burning alters the prairie soundscape. Fire ecology is a well-studied field in both a historical and modern context (Allen and Palmer 2011). Regular fire events are important for reducing fuel loads, cycling limiting nutrients for plant growth such a nitrogen back into the soil and for opening canopies which encourage the recruitment and growth of understory vegetation (Clark 1989; Perry 2012). Fire is especially important in grassland ecosystems, with observations of both positive and negative effects on wildlife being reported; species can be fire averse, neutral, tolerant, resilient or dependent (Hansen, 1986; Chambers and Samways, 1998; Richards et al., 1999; Panzer and Schwartz, 2000; Reinking et al., 2000; Reinking et al., 2005; Armitage and Ober 2012). Because floral and faunal tallgrass prairie communities often exhibit some form of adaptation to fire and generally benefit from regular burning (Collins et al., 1995), I predicted that the acoustic community of a tallgrass prairie would respond positively to prescribed burns and as a result, acoustic diversity would be higher at sites that had been burned in the early spring. I found that the acoustic diversity of the prairie changed over time in unburned grassland settings, and that fire altered the intensity and sometimes the direction of these changes. Prescribed burns altered the tallgrass prairie soundscape, but the changes that reduced the acoustic diversity of the prairie were generally ameliorated by the end of the growing season.

My first field experiment focused on describing a community of five *Nicrophorus* burying beetle species and their relationship to the soundscape of a tallgrass prairie in northeastern Oklahoma. Since 75 species exist in the Northern Hemisphere (Scott 1998), it would be informative to understand the magnitude of the influence community dynamics have on how one species covaries with the soundscape over another in different geographic and ecological regions with different species compositions. We now know that the high acoustic complexity of a soundscape may be an important indicator for preferred habitat of *N. americanus*, the largest and most rare of the burying beetle species monitored in the study. My second experimental chapter focused on seasonal changes of a tallgrass prairie ecosystem and the differences between burned and unburned sites in terms of soundscape composition. Since prescribed burning is one of several common practices in grassland management, it is useful to understand how other habitat management actions such as cattle and bison grazing and mowing potentially alter acoustic communities. Acoustic indices were used in both experimental chapters to interpret acoustic data acquired through passive acoustic recordings. In regard to both the current and future experiments, it is important to know if acoustic indices remain the most robust method to describe acoustic community composition. This investigation would be informative to the ecoacoustics community as acoustic indices have been regularly employed and scrutinized since their creation in the early 2000’s (Boelman et al., 2007; Sueur et al., 2008; Gasc et al., 2015), but rarely validated. Since then, acoustic indices have been used to process field recordings from a number of ecosystems across the globe (Gasc et al., 2013; Sueur et al., 2014; Towsey et al., 2014; Harris et al., 2016; Ferreira et al., 2018). My field experiments were the first to employ this method for the evaluation of a North American tallgrass prairie soundscape. Results from my studies provide empirical evidence that six acoustic indices (ACI, ADI, AEI, BIO, H and NDSI) are reliable indicators of spectral diversity in a grassland ecosystem on a short (several weeks) and long-term (several months) scale.

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APPENDIX

The following Standard Operating Procedure is written to be used on a Windows PC.

Standard Operating Procedure: Using the UNH Premise Cluster to calculate acoustic indices from sound recordings in .wav file format using scripts in R. For more information on Premise, visit http://premise.sr.unh.edu/. Before using Premise, an account must be requested through the UNH Research Computing Center (RCC). To create a Premise account, email the UNH Research Computing Center staff at: rccops@sr.unh.edu.

1. Upload data to Premise

   Files must be transferred from a local machine to the Premise network in order for analysis to occur. However, a SecureSHell (SSH) client program is needed to do this on a PC. An SSH client is a program that allows a user to establish a secure and authenticated SSH connect to SSH servers like Premise.

   - Download an SSH client program to first connect to Premise. On a Windows machine, WinSCP is a commonly recommended option. WinSCP is a free open source Windows client for transferring files with a user-friendly interface and can be downloaded here https://winscp.net/eng/index.php
   - Use WinSCP to login to Premise
   - Enter your username and password
   - Create a create a folder directory in the Premise network in order to have a place to store and organize files including all scripts for analysis
   - Use the WinSCP interface that mirrors your local machine's directory to copy and paste files into the directory you created in Premise

2. Submit a job to Premise

Before you submit a job, you must create a .slurm script using slurm commands. Slurm is the job queuing system used by Premise. Using a slurm script allows for jobs (such as running commands in R) to be executed. For more information on how to create a slurm script using slurm language and syntax, visit http://premise.sr.unh.edu/slurm.html and https://www.slurm.schedmd.com/. When you are ready to submit a job, slurm commands must be used in a terminal interface. A terminal is an interface in which text-based commands can be typed and executed. This allows you to deliver commands to Premise

- To submit a job (i.e. run an analysis), you must first download a terminal for Windows such as PuTTY (https://www.chiark.greenend.org.uk/~sgtatham/putty/latest.html).
- Common Slurm Commands:
    - To view the status of the nodes on the cluster, **type** *sinfo*
    - To view the status of jobs running, **type** *squeue*
    - To cancel a job, **type** *scancel* “JOBID” (where JOBID is the ID of a job)
    - To submit a job, **type** *sbatch* “SCRIPT” (where SCRIPT is a .slurm script).
    - To view the status of a job, **type** *slurm-monitor* “JOBID” (where JOBID is the ID of a job)
- Once PuTTY is downloaded and open, login to Premise. After typing in your username and password, enter the following into the command window. Make sure the .slurm file and the R script is in the folder to which you connect. This will be the folder in which all .wav files and R scripts are stored:

- **cd** “name of folder you wish to connect to”
- *Enter*
- **sbatch** “name of .slurm file”.slurm
- *Enter*

Example

- **cd** Chapter1_data
- *Enter*
- **cd** Unburned_recordings
- *Enter*
- **sbatch** Rscript.slurm
- *Enter*

3. Retrieve Results from Premise

After a job is finished in Premise, retrieve your results by using WinSCP. If you are calculating acoustic indices using the scripts written in R (below) you will need to retrieve .csv files, each of which will correspond to lines of code associated with the calculation of each acoustic index.

- Login to WinSCP
- Navigate to the folder where your data are stored. Multiple .csv files should be found at the same level of the folder which contains all .wav files that were used in the analysis
- Copy and paste .csv files to your local machine using the WinSCP interface

Original Slurm Script

```
#!/bin/bash

## Note - Slurm script comments require two hash symbols (##).  A single
## hash symbol immediately followed by SBATCH indicates an SBATCH
## directive.  "##SBATCH" indicates the SBATCH command is commented
## out and is inactive.

## For jobs running on a single node using multiple threads, the number of
## tasks should be 1.  This reflects how many processes are running (1), and
## not how many threads that process will use.
#SBATCH --ntasks=1

## If it's likely your job will use more than 128GB of RAM, be sure
## to specify a minimum above this to ensure you are allocated a node
## with 512GB of RAM. Note: this value is specified in megabytes.
##SBATCH --mem=512000

## Normal Slurm options
## SBATCH -p shared
#SBATCH --job-name="aci "
#SBATCH --output=aci.output

## Load the appropriate modules first.  Linuxbrew/colsa contains most
## programs, though some are contained within the anaconda/colsa
## module.  Refer to http://premise.sr.unh.edu for more info.
module purge
module load linuxbrew/colsa

## Instruct your program to make use of the number of desired threads.
## As your job will be allocated an entire node, this should normally
## be 24.
srun Rscript script.R
```

Original R script for Chapter 1

```
#Load the package
library(soundecology)

#Load the package
library(tuneR)

#Load the package
library(seewave)

#ACI: calculated from files in the folder multiple_fil, using all cores, and
saving the results to a file called aci_results.csv, type:
multiple_sounds(directory = "multiple_files", resultfile = "aci_results.csv",
soundindex = "acoustic_complexity", min_freq = 0, max_freq = 22000, no_cores
= "max")

#Bioacoustic Index (BI): with change of maximum frequency to 22000 Hz, saved
to a file bioindex_results_22k.csv, type:
multiple_sounds(directory = "multiple_files", resultfile =
"bioindex_results_22k.csv", soundindex = "bioacoustic_index", max_freq =
22000, no_cores = "max")

#ADI: calculated from files in the folder ultiple_files using all cores,
maximum frequency = 22 KHz, and saving the results to a file called
adi_results.csv, type:
```

```
multiple_sounds(directory = "multiple_files", resultfile = "adi_results.csv",
soundindex = "acoustic_diversity", max_freq = 22000, no_cores = "max")

#AEI: calculated from files in the folder ultiple_files, using all cores,
maximum frequency = 22 KHz, and saving the results to a file called
aei_results.csv, type:
multiple_sounds(directory = "multiple_files", resultfile = "aei_results.csv",
soundindex = "acoustic_evenness", max_freq = 22000, no_cores = "max")

#H Index (Acoustic Entropy Index) calculated from seewave, type:
multiple_sounds(directory = "multiple_files", resultfile = "H_results.csv",
soundindex = "H", no_cores = "max"

#NDSI parameters for low frequency biophony (owls and coyotes):
multiple_sounds(directory = "multiple_files", resultfile =
"ndsi_results_c_48k.csv", soundindex = "ndsi", no_cores = "max", anthro_min =
200, anthro_max = 749, bio_min = 750, bio_max = 22000)

#NDSI parameters for all other recordings:
multiple_sounds(directory = "multiple_files", resultfile =
"ndsi_results_22k.csv", soundindex = "ndsi", no_cores = "max", anthro_min =
200, anthro_max = 3000, bio_min = 3001, bio_max = 22000)
```

Original R script for Chapter 2

```
#Load the package
library(soundecology)

#Load the package
library(tuneR)

#Load the package
library(seewave)

#ACI: calculated from files in the folder multiple_files, using all cores,
and saving the results to a file called aci_results.csv, type:
multiple_sounds(directory = "multiple_files", resultfile =
"aci_resultsa.csv", soundindex = "acoustic_complexity", min_freq = 200,
max_freq = 48000, no_cores = "max")

#Bioacoustic Index (BI): with change of maximum frequency to 48000 Hz, saved
to a file bioindex_results_48k.csv, type:
multiple_sounds(directory = "multiple_files", resultfile =
"bioindex_resultsa_48k.csv", soundindex = "bioacoustic_index", max_freq =
48000, no_cores = "max")

#ADI: calculated from files in the folder multiple_files using all cores,
maximum frequency = 48 KHz, and saving the results to a file called
adi_results.csv, type:
multiple_sounds(directory = "multiple_files", resultfile =
"adi_resultsa.csv", soundindex = "acoustic_diversity", max_freq = 48000,
no_cores = "max")

#AEI: calculated from files in the folder multiple_files, using all cores,
maximum frequency = 48 KHz, and saving the results to a file called
aei_results.csv, type:
multiple_sounds(directory = "multiple_files", resultfile =
"aei_resultsa.csv", soundindex = "acoustic_evenness", max_freq = 48000,
no_cores = "max")

#H Index (Acoustic Entropy Index) calculated from seewave, type:
multiple_sounds(directory = "multiple_files", resultfile = "H_resultsa.csv",
soundindex = "H", no_cores = "max")
```

```
#NDSI parameters for low frequency biophony (owls and coyotes): change the
maximum frequency of the biophony of NDSI to 48000 Hz, from the default of
22000, and save the results to a file ndsi_results_48k.csv, with adjustments
to anthro and bio Hz mins and max, type:
multiple_sounds(directory = "multiple_files", resultfile =
"ndsi_results_c_48k.csv", soundindex = "ndsi", no_cores = "max", anthro_min =
200, anthro_max = 749, bio_min = 750, bio_max = 48000)

#NDSI parameters for all other recordings: change the maximum frequency of
the biophony of NDSI to 48000 Hz, from the default of 48000, and save the
results to a file ndsi_results_48k.csv, with adjustments to anthro and bio Hz
mins and max, type:
multiple_sounds(directory = "multiple_files", resultfile =
"ndsi_results_b_22k.csv", soundindex = "ndsi", no_cores = "max", anthro_min =
200, anthro_max = 3000, bio_min = 3001, bio_max = 48000)
```