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LES PAYSAGES ACOUSTIQUES ET SES EFFETS SUR LA STRUCTURE ET LA DYNAMIQUE DES COMMUNAUTÉS

THÈSE PRÉSENTÉE
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my deepest gratitude for your support and encouragement.

In fact, in dealing with nature, the mind must be
on the alert to seize all her conditions;
otherwise we soon learn that our thoughts
are not in accordance with her facts.

John Tyndall 1883

The sound is another case of one plus one equals one.

Bernie Krause 1987

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RÉSUMÉ

L'écologie du paysage sonore est une discipline de recherche très récente. Elle permet d'étudier les relations complexes entre les communautés d'animaux, les dynamiques géophysiques et les systèmes anthropiques. En tant que nouveau domaine de recherche, le développement de bases théoriques et de mesures standards est nécessaire pour identifier et quantifier les processus dans le paysage sonore et les interactions de ce dernier avec les systèmes naturels et anthropiques. Par l'étude des patrons présents à l'intérieur des paysages sonores, nous pouvons également répondre à des questions liées à la structure de la communauté (patrons spatiaux) et à sa dynamique (patrons temporels) tel que la répartition des espèces, leur abondance et leurs interactions biotiques au sein de la communauté. L'expertise que nous avons développée dans cette thèse peut être regroupée sous deux axes principaux de l'écologie du paysage sonore : 1) le développement de bases théoriques et de mesures d'évaluation et 2) l'évaluation des interactions entre le paysage sonore, la structure et la dynamique des communautés animales.

Premièrement, nous évaluons l'utilisation d'indices acoustiques pour différencier systématiquement les contextes du paysage sonore aquatique et terrestre. Les indices acoustiques permettent une quantification standard des propriétés du paysage sonore et ils fournissent une interprétation écologique intuitive de leur variation. Nous utilisons des enregistrements acoustiques des communautés d'oiseaux et d'ensifères dans différentes forêts, tourbières, marais, terres agricoles, zones de végétation urbaine et cours d'eau pour représenter les différents contextes du paysage sonore. En utilisant un modèle de forêts aléatoires, nous comparons la précision de différents indices acoustiques à celle du spectre de puissance du signal pour discriminer différents événements du paysage sonore. Nous montrons que la combinaison d'indices acoustiques particuliers se rapproche à la haute performance du spectre de puissance pour différencier systématiquement les contextes de paysage sonore. Nous introduisons également un nouvel indice acoustique basée sur la taille de compression des fichiers audio numériques.

Deuxièmement, nous développons un nouveau cadre théorique pour étudier les effets du paysage sonore sur les modèles d'assemblage des communautés animales. Nous utilisons une combinaison de modèles de simulation et d'études sur le terrain pour tester les hypothèses suivantes : 1) l'hétérogénéité acoustique augmente avec le nombre d'espèces dans les communautés d'ensifères des écosystèmes tempérés et 2) l'hétérogénéité acoustique d'un assemblage d'ensifères en milieu naturel est plus élevée que celle de communautés assemblées de façon aléatoire. Nous démontrons que l'hétérogénéité acoustique augmente avec la richesse en espèces dans les communautés naturelles. Ceci signifie que des mesures particulières d'hétérogénéité acoustique pourraient être utilisées pour évaluer rapidement la biodiversité dans les communautés d'ensifères. Nous démontrons également que la pente de la relation entre l'hétérogénéité acoustique et la richesse spécifique dans les communautés naturelles ne diffère pas significativement de celle des communautés aléatoires. Ce résultat suggère que la concurrence pour l'espace acoustique est assez faible à l'intérieur des communautés d'ensifères actuelles et qu'il ne semble pas y avoir d'influence sur l'assemblage des communautés locales.

Troisièmement, nous proposons un cadre mathématique simple pour étudier les effets du paysage sonore sur les interactions prédateur-proie dans les milieux aquatiques. Notre modèle lie les captures de poissons à la sensibilité auditive des espèces et au niveau de bruit ambiant dans les écosystèmes d'eau douce. Nous justifions que l'activité d'alimentation des proies dépend de la probabilité d'être détectée par leurs prédateurs. Des simulations de modèles et des résultats préliminaires sur le terrain suggèrent que les proies peuvent profiter d'une augmentation du bruit ambiant sous l'eau pour se nourrir activement en minimisant le risque de prédation encouru. D'ailleurs, les captures de proies par unité d'effort étaient presque trois fois plus élevées lors de jours bruyants (jours de fin de semaine) comparativement aux jours plus calmes (jours ouvrables), ce qui suggère une hausse de l'activité alimentaire en présence de bruit ambiant élevé.

Grâce au travail réalisé dans cette thèse, nous fournissons de nouveaux outils à l'écologie du paysage sonore qui permettront de quantifier et de décrire rapidement la structure et la dynamique des communautés. Nos cadres théoriques sont transposables dans différentes conditions environnementales et systèmes biotiques comme nous l'avons démontré dans ce travail. Nous avons découvert des patrons intéressants concernant l'assemblage des communautés locales et la nature des interactions trophiques dans les groupes d'animaux terrestres et aquatiques. En définitive, nous proposons plusieurs hypothèses qui pourraient conduire à de nouvelles recherches théoriques et appliquées dans l'écologie du paysage sonore.

Mots-clés : Écologie du paysage sonore, espace acoustique, partitionnement acoustique, hétérogénéité acoustique, masquage acoustique, bruit ambiant, assemblage des communautés.

ABSTRACT

Soundscape ecology is an emerging research discipline that formally studies the complex relations between animal communities, geophysical dynamics, and human systems from the point of view of the acoustic properties of the ecosystem. Because it is a new area of research, theoretical bases must be developed and tested to identify and quantify processes within the soundscape and reveal their interactions with natural or human systems. Through the study of soundscape patterns, we can also assess questions related to community structure (spatial patterns) and dynamics (temporal patterns), including species distribution, abundance, and biotic interactions. The subjects developed in this thesis can be integrated into two main axes: 1) developing standard measurements and theoretical frameworks in soundscape ecology 2) evaluating how the environment modulates acoustic (niche) partitioning and acoustic masking principles in animal communities.

First, we evaluate the use of acoustic metrics to differentiate between aquatic and terrestrial soundscape contexts. Acoustic metrics allow a formal quantification of soundscape properties and provide an intuitive ecological interpretation of their variation. We use soundscapes recordings of bird and ensiferan communities in different forests, bogs, marshes, farmlands, urban vegetated areas, and of freshwater streams to represent the different soundscape contexts. Using a random forest model, we compare the ability of different acoustic metrics and the signal power spectrum to discriminate between soundscape events. We show that the combination of particular acoustic metrics has the potential to match the high performance of the power spectrum to differentiate between soundscape contexts. We also introduce a new acoustic metric based on the compression size of digital audio files.

Second, we develop a novel theoretical framework to study the effects of soundscape on the assemblage patterns of animal communities. We use a combination of simulation models and field surveys to test the hypotheses that (1) acoustic heterogeneity increases with the number of species in ensiferan communities from temperate ecosystems and that (2) the acoustic heterogeneity of naturally assembled ensiferan communities is higher than that of regional randomly assembled ones. We show that acoustic heterogeneity increases with species richness in naturally assembled communities, indicating that specific acoustic heterogeneity metrics could be used to perform rapid biodiversity assessments in ensiferan communities. We also show that the slope of the acoustic heterogeneity – species richness relationship in natural communities does not differ from the randomly assembled ones. This result suggests that competition for acoustic space is rather weak in present-day ensiferan communities and does not seem to influence the local community assemblage.

Third, we propose a simple mathematical framework to study the effects of soundscape on predator-prey interactions in aquatic environments. Our model links fish captures to the auditory sensitivities of species and ambient noise levels in freshwater ecosystems. We show that the feeding activity of prey could be dependent on the probability of being acoustically detected by their predators. Model simulations and preliminary field results suggest that prey may take advantage of higher levels of underwater ambient noise to feed more actively at lower predation risk. Prey (yellow perch) captures per unit effort were almost three times higher on noisy (weekend days) versus quiet days (work days), suggesting increased feeding activity in the presence of augmented ambient noise.

Throughout this thesis, we provide new tools related to the soundscape ecology that will allow the rapid quantification and description of community structure and dynamics. We will also show that our theoretical frameworks are applicable to different environmental conditions and biotic systems. We uncover novel patterns concerning local community assemblages and trophic interactions in terrestrial and aquatic animal groups, and we propose several hypotheses that could lead to further theoretical and applied research in soundscape ecology.

Keywords: Soundscape ecology, acoustic space, acoustic partitioning, acoustic heterogeneity, acoustic masking, ambient noise, community assemblage.

GENERAL INTRODUCTION

Soundscape ecology

Soundscape ecology is a nascent area of research that aims to understand the complex interactions of organisms, geophysical dynamics, and human activities using the acoustic properties of the ecosystem. The term soundscape was first used to refer to the sound arising from particular urban spaces, with the practical interest of studying their impact on the spatial perception of humans (Southworth 1969). Later on, the term was extended to include all sounds associated with a particular landscape (Schafer 1977; Truax 1999). The soundscape includes three acoustic elements whose principal differences relate to their source: the *biophony* refers to all sounds produced by living organisms (Krause 1987); the *geophony* to all sounds from non-biological sources (e.g., wind, rain, water currents); and the *anthrophony* to all sounds produced by humans or derived from human activities (Krause and Gage 2003). The soundscape, as defined in soundscape ecology and as it is interpreted in this thesis, represents all sounds – biophony, geophony, and anthrophony – emanating from a given landscape that vary over space and time, reflecting important ecosystem processes and human activities at spatial and temporal scales (Pijanowski et al. 2011a, b).

Soundscape ecology is a booming field of research with a short but rapidly developing history. It was defined as an independent academic discipline for the first time in 2011; it was then that a conceptual framework was developed to describe the underlying processes and dynamics that characterize the soundscape (Pijanowski 2011a, b; Figure 1). Many earlier ecological investigations had incorporated elements of soundscape ecology theory. For instance, a large body of work within the bioacoustics field of research has focused on documenting the effects of anthrophony on wildlife. Soundscape ecology is related to the sciences of bioacoustics (Fletcher 2014) and acoustic ecology (Shafer 1977; Truax 1999), both of which have long been recognized as fields of research in ecology. Bioacoustics studies animal communication, including behavioural patterns, evolution, and the physics of sound production. It concerns a single animal species or involves the comparison of species. Acoustic ecology, in turn, is a human-centred science: it is exclusively concerned with the relationships between humans and the acoustic environment. In contrast, soundscape ecology focuses mostly on macro- or community-related acoustics, it is strongly influenced by the principles of the landscape ecology (Truax and Barrett 2011), and its main purpose is the study of interactions between the soundscape and humans, animal species, and the geophysical environment.

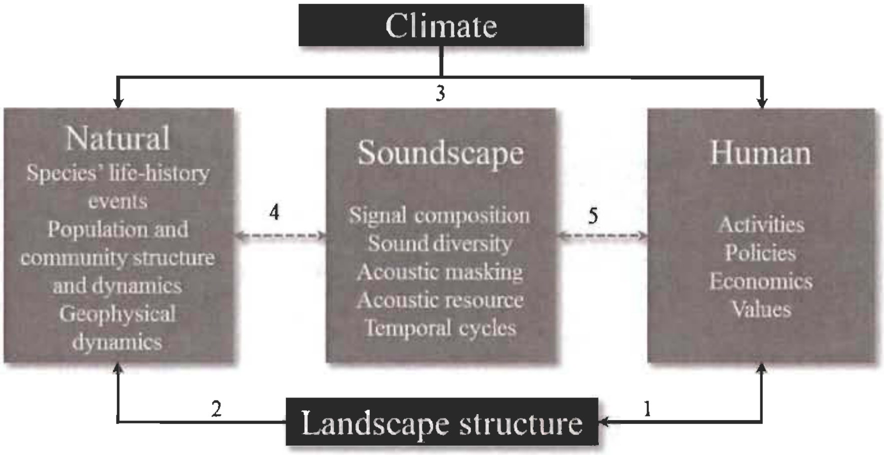

Figure 1. Conceptual framework for soundscape ecology as proposed by Pijanowski et al. 2011b. The landscape structure is transformed by humans through land use and land-cover change (Lambin and Geist 2008; arrow 1). Conversely, human activities, most of which produce sounds of considerable intensity levels (e.g., resource extraction, industrial and transportation networks, and even recreational activities; Barber et al. 2009; Barber et al. 2011), are dependent on landscape features (arrow 1). Landscape structure influences the distribution and abundance of species and their interactions at multiple spatial and temporal scales (MacArthur and MacArthur 1961; arrow 2). Landforms (e.g., valleys, rivers) also provide different geophysical dynamics, some of which produce frequent or constant sounds, such as wind and water (arrow 2). Climate influences species distributions (Currie 1991) as well as the occurrence and extent of life-cycle events, most of which are related to sound production in vocal or stridulating species (e.g., courtship events, breeding, emergence of noisy insects; Brown et al. 1999, Beebee 2002, Ahola et al. 2004; arrow 3). Climate also affects geophonic and anthropic sounds by influencing human activities and the geophysical dynamics in the landscape (arrow 3). Human systems, environmental dynamics, and geophysical attributes influence the soundscape by varying its properties in time and space (arrows 4, 5). Soundscapes provide feedback to natural processes by influencing community dynamics, such as species distributions (e.g., McKinney 2006; Francis et al. 2009; Carvajal-Castro and Vargas-Salinas 2016) and biotic interactions (e.g., Tuttle and Ryan 1982; Simpson et al. 2015; arrow 4). The soundscape can also affect human systems by influencing human well-being, sense of place, and cultural or artistic ideals (Shafer 1977; arrow 5). *Figure and legend adapted from Pijanowski et al., 2011b.*

Because soundscape ecology is a new field of study, many applications and areas of research are opening up to investigation. There are many patterns, mechanisms, and impacts of interactions within the soundscape context to explore. As such, several main themes have been proposed over the last decade to frame future research in soundscape ecology (Pijanowski et al. 2011a, b; Gasc et al. 2017). These themes include the development of theoretical bases and standard measurements to identify and quantify processes within the soundscape and its interactions with natural or human systems; the study of the spatial and temporal dynamics of the soundscape; the evaluation of the effects of environmental factors and human-related sounds on soundscapes; and the study of soundscape effects on humans and animal communities' structure and dynamic.

The physics of sound

All sounds making up the soundscape are basically mechanical disturbances (waves) in the density and pressure of a medium (fluid or solid) that propagate through time and space. Indeed, an acoustical disturbance involves both motion of the medium's particles and changes in its pressure. Every sound has its source at the vibration of a body, and this vibration is transmitted to the medium. In general, sound is transmitted as a longitudinal wave in fluids (air, water), which means that the displacement of the medium is predominantly parallel to the direction of propagation. Each particle undergoes a small excursion to and fro, moving the adjacent particles in turn, and so on, resulting in the propagation of vibratory energy (Tyndall 1883; Bradbury and Vehrencamp 2011). Particles do not travel with the propagating sound wave, but rather transmit the oscillatory motion to their neighbours. The sound pressure is the variation in the medium equilibrium pressure caused by the compression and rarefaction of many synchronized particles as the sound wave propagates (Hartmann 1997; Figure 2). A simple sound emitted as a pure tone can be illustrated and mathematically represented by a sinusoidal wave as it travels over time.

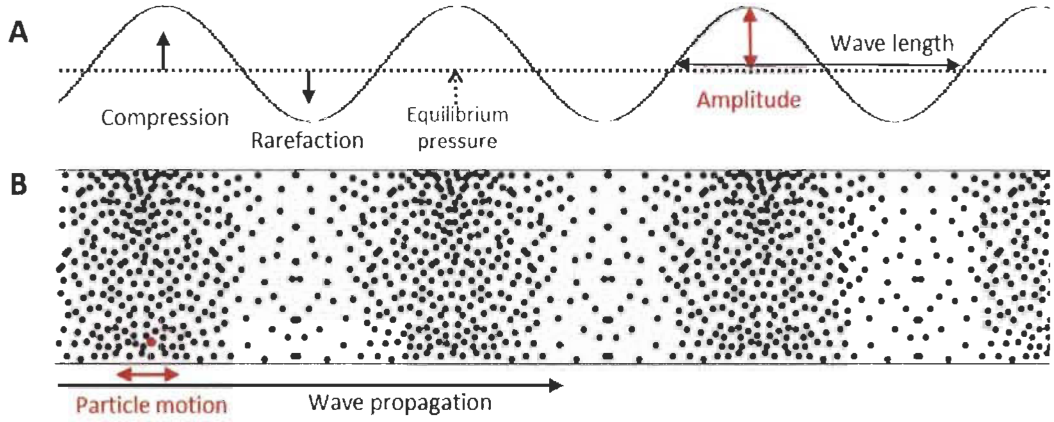

Figure 2. Snapshot of a longitudinal sound wave. A) Sinusoid representation of the sound wave with its physical attributes. B) Schema of the same wave in terms of particle motion in the propagation medium.

Any given sound can be characterized by its temporal and spatial properties: amplitude, intensity, frequency, wavelength, and speed. The amplitude of a sound wave could be interpreted as the distance traveled by each particle in the medium or as the degree of change (positive or negative) in atmospheric pressure caused by the disturbance. In the sinusoidal representation of a sound wave, the amplitude is the peak deviation of the function from zero. It is measured in newtons per square metre ($N \cdot m^{-2}$). The intensity of the sound can be expressed as amplitude over time and over an area. It is proportional to the square of its amplitude and is measured as the rate at which energy (or power) flows through a unit area perpendicular to the wave-traveling direction. The typical units to express sound intensity are watts per square metre ($W \cdot m^{-2}$).

Nevertheless, intensity is frequently measured in decibels (dB). This measurement has a logarithmic (base 10) scale that reflects sound intensity level relative to a reference value. The reference usually corresponds to the minimum intensity that a human ear can perceive in the particular medium. In air, humans can perceive sound from 0 dB to 130 dB ($I_{ref\ in\ air} = 10^{-12}$ $W \cdot m^{-2}$):

$$I\,(dB) = 10 \log_{10} (I / I_{ref}) \qquad (1)$$

The same dB scale is also used to quantify the intensity of the sound by directly measuring the pressure deviation from the ambient, that is, using sound pressure levels (SPL; with reference levels of 20 μPa in air and 1 μPa in water):

$$SPL\ (dB) = 20\ log_{10}\ (P\ /P_{ref}) \qquad (2)$$

The intensity of the sound depends on both pressure and particle velocity ($I = P \times v$, where P = sound pressure and v = particle velocity; Jacobsen and de Bree 2005). Under specific conditions (i.e., plane waves, far from the source), particle motion can be calculated from sound pressure values as $v = P/z$ (where z is the specific acoustic impedance, i.e., the resistance of a medium to wave propagation; Nedelec et al. 2016). For a plane wave, the intensity increases with the square of the pressure and decreases with the specific acoustic impedance of the medium ($I = P^2/z$). This means that when plane waves with equal pressure in air and water are compared, the sound intensity in water is lower than in air ($z_{water}/z_{air} \approx 3700$; Nummela 2009; Bradbury and Vehrencamp 2011). To characterize particle motion in any other condition, it is necessary to make measurements of particle displacement, velocity, or acceleration (Nedelec et al. 2016).

Each oscillation in the sine wave, that is, a complete compression and rarefaction event in the medium, is called a *cycle*. The time that it takes to complete a cycle is called the *period* (T). The number of cycles completed per second determines the characteristic frequency of a particular sound wave. Frequency and period are inversely related ($f = 1/T$). A pure tone will constitute a sinusoid wave with a characteristic frequency, while a complex sound – as are most natural sounds (e.g., a bird song or water surf sound) – will be characterized by the addition of several sinusoids with different characteristic frequencies (Figure 3). It is the frequency of the sound that will differentiate two simple waves (pure tones) as two different notes. The frequency is expressed in hertz (Hz); one Hz is equivalent to one cycle per second. The human ear can detect sounds between 20 Hz and 20 kHz. In soundscape ecology, each soundscape sound element has been associated with a particular frequency range. Biophony has been shown to dominantly occur between 2 and 8 kHz, anthrophony up to 3 kHz, and geophony, while diffuse throughout the entire spectrum, is dominated by low frequencies (Qi et al. 2008).

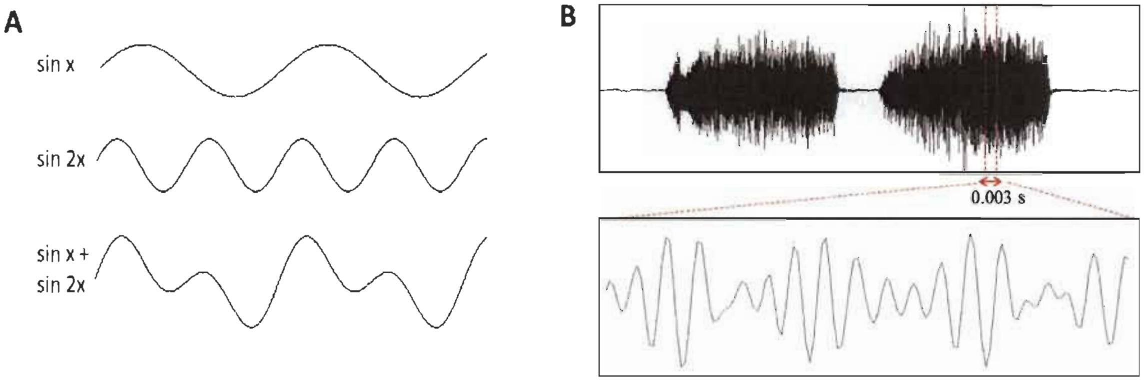

Figure 3. Representation of a complex sound wave. A) Complex sound-wave decomposition. The bottom wave represents a complex sound wave; it is periodic but non-sinusoidal. The waves above represent its decomposition into simple sinusoids. B) Waveform of single call by male boreal chickadee (*Poecile hudsonicus*). Both the upper and lower plots show varying sound pressure relative to ambient pressure on the vertical axis and time on the horizontal axis. The waveform in the dashed section of the top plot is expanded along the time axis in the lower plot to show the complex sound-wave details.

The distance traveled by the wave during a complete cycle is the wavelength of a particular sound. It is related to the sound frequency and speed: $\lambda = c / f$; where λ stands for wavelength, c for the speed of sound, and f for frequency. The wavelength acquires a particular importance in animal communication because it is difficult for most animals to generate an intense sound with a wavelength more than twice their body size (Bradbury and Veherencamp 2011).

Sound transmission speed depends both on the specific acoustic impedance and the density of the propagation media. Sound velocity is directly proportional to the acoustic impedance and inversely proportional to the density of the particular medium (Bradbury and Vehrencamp 2011; Farina 2014). Sound speed is higher in liquids and solids than in gases because the impedance-density ratio of these media is higher than in gases. As an example, the speed of sound in dry air at 20°C is 343.2 $m \cdot s^{-1}$, meanwhile the speed of sound in water at 20°C is 1,484 $m \cdot s^{-1}$ (4.3 times faster than in air). Factors such as media temperature, air humidity, or water salinity also affect sound speed. For instance, sound propagates faster in hot than in cold air.

As the acoustic wave propagates outward from the source, the intensity of the signal is attenuated with increasing range, i.e., there is a *transmission loss*. This attenuation is driven by the processes of reflection, refraction, and absorption (Tolstoy and Clay 1966; Wiley and Richards 1978; Rogers and Cox 1988). Reflection occurs when a sound wave hits the surface of another medium with very different impedance and rebounds off its surface. The reflection coefficient depends on the physical properties of the hit surface as well as the angle of incidence. The air-water interface, for example, is an excellent reflector at all frequencies, while the sea bottom is generally a poor reflector (Rogers and Cox 1988). Refraction occurs when the impedance difference at the interface between the transmission and the hit medium is smaller. In this case, the propagating sound wave will bend after crossing the boundary due to a change in sound speed. It normally occurs inside the same medium when the sound encounters zones with different temperature, pressure, or composition. For example, the earth's surface is cooler at night than during the day, thus any sound produced near the surface will tend to refract in the higher warmer layers towards the ground (Wilson 2003). Absorption occurs to any propagating sound in the medium. It is the constant process by which some energy of the propagating wave is absorbed in the material. It may be converted to heat due to internal friction at a molecular scale (heat loss) or mechanically damped within the medium (spreading loss; Wiley and Richards 1978). Since adjacent layers collide more frequently when propagating a high-frequency sound wave than when propagating a low-frequency one, high frequencies lose more sound energy to heat loss than do low frequencies. This means that for a given amount of energy, low-frequency sounds travel farther than high frequency sounds (Forrest et al. 1993; Bradbury and Vehrencamp 2011). In addition, the medium also affects heat losses. For instance, for a given frequency, heat losses in salt water are about 100 times as high as those in fresh water, and those in air are a 100 times as high as those in salt water.

Sound frequencies undergo degradation during propagation due to absorption (as seen above), reverberation, scattering, and depth in aquatic environments (Wiley and Richards 1978; Rogers and Cox 1988). Scattering is a special case of reflection that occurs whenever there are objects or regions in the propagating medium with different acoustic impedances. When the wavelength of the incident sound is larger than the object encountered, most energy sweeps around the object and continues on. As the ratio of object size to incident sound wavelength increases, increasing amounts of sound energy striking the object will be backscattered. Experiments done in forested areas have revealed that higher-frequency sound waves tend to be strongly scattered by foliage (Marten and Marler 1977; Tang et al., 1986) whereas lower-frequency signals tend to be less attenuated in general (Aylor 1972; Bullen and Fricke 1982; Price et al. 1988). This limits the distance that higher-frequency signals can travel relative to lower-frequency signals in terrestrial environments. Reverberation is caused by the interferences of all reflected and scattered waves of the traveling sound. In aquatic systems, water depth plays an important role in sound propagation (Rogers and Cox 1988). In deep water, sound attenuation is particularly low, since waves can propagate without interactions with the surface or the bottom. On the contrary, the attenuation of low frequency waves in shallow water is very steep. Depending on the bottom's physical properties, the wavelength of the cut-off frequency will be within two to four times the depth of water (Forrest et al. 1993). As an example, in a stream one metre deep with a sandy bottom, frequencies below 700 Hz will hardly propagate at all.

Pressure and particle motion do not attenuate at the same rate. Particle motion decreases more rapidly over a particular distance than pressure does ($1/r^2$ versus $1/r$; where r is the radial distance from the source; Popper and Carlson 1998). This distance is called the near-field. The end of the near-field depends upon the frequency and speed of the sound in the medium as $d_{far\text{-}field} \approx c / 2\pi f$ (Rogers and Cox 1988; Popper and Carlson 1998). Sound sources in air and in water both produce particle motion, but the greater speed of sound in water preserves particle motion over a greater distance. Particle motion is generally not functionally significant for a terrestrial organism, whereas it is very important for aquatic animals, particularly in shallow water and at frequencies less than 1 kHz. In the far-field, both particle motion and pressure attenuate at the same rate (1/r).

To manage and quantify the physical attributes that characterize a sound wave (e.g., spectral and temporal patterns), we need to detect sound pressure and transform the signal into analog (voltage) or digital format to store it. Common microphones detect subtle changes in air pressure, however, to detect sound pressure in aquatic environments, special microphones known as hydrophones are required. Hydrophones are designed to match the higher acoustic impedance of the water and thus accurately perceive underwater pressure differences. Acoustic information is now mostly stored on digital recorders, which have largely replaced analog recorders. A digital recorder stores discrete samples of the signal detected by the microphone at thousands of times per second. To obtain a digital representation of an acoustic signal without phantom frequencies (aliasing effect; Hartmann 1997), the sampling rate must be more than twice the highest frequency present in the signal. For instance, if the sound of interest has an acoustic frequency of 11 kHz, the sampling rate needs to be 22 kHz or greater to detect the high and low peaks of that wave. The highest frequency that can be coded at a given sampling rate without aliasing is referred as the Nyquist frequency (Plichta and Kornbluh 2002). Each sample, or measure of air-pressure variation, is coded and stored in the recorder in bits (8 or 16 bits). This means that each amplitude measure will correspond to a digital value ranging from 0 to 2^8 or 2^{16}.

Digital sound collections may require large storage facilities. As a general guideline, a sound file stored with CD quality (i.e., sampling rate of 44.1 kHz and 16 bits) in two channels requires approximately 10 MB per minute of audio. Although compression of the sound file using algorithms like MP3 can reduce the disk space needed, these algorithms remove part of the acoustic information, for example, sounds humans cannot hear; therefore, modifying the signal recorded and causing information to be lost. For these reasons, sound recorded for analysis should be recorded in uncompressed formats, like Microsoft Wave (.wav), or lossless compression formats such as Free Lossless Audio Codec (.flac)

The sound signal stored in digital format will provide information about the wave amplitude over the recorded time. To extract more useful information for further analysis, we need to apply a Fourier transform (FT) or a discrete Fourier transform (DFT) to the wave. Details of how DFT works are beyond the scope of our work here, but FT is basically a mathematical algorithm that decomposes a complex sound signal into its pure tones in order to extract the frequencies that integrate the complex signal and their corresponding amplitude levels (see Hartmann 1997; Smith 2003).

Animal sound production and reception

Animals use sound to communicate, navigate, locate prey, and detect potential threats. Acoustic signalling is used by many animal groups to defend their territories, warn conspecifics of approaching predators, or attract mates (Bradbury and Vehrencamp 2011). It is a useful communication mode in environments where the visibility is limited (e.g., dense vegetation, ocean depths), where there are great distances (e.g., in the ocean), or as an emergency signal due to its speed. Acoustic communication is found in birds, terrestrial and marine mammals, amphibians, fish, reptiles, insects, and some other arthropods.

There is a great variability in the methods animals use to produce sound. There are four broad categories of vibratory mechanisms that have been identified (Bradbury and Vehrencamp 2011; Kasumyan 2008). In the first group, sound can be produced by the movement of solid body parts against another solid. This can include (i) percussion, where the animal strikes a solid part of its body against the substrate or another body part in a rapid motion (e.g., spiders tapping their legs against a substrate or birds snapping their bills together as a threat); (ii) stridulation, where sound is produced by rubbing certain body parts together. This is typical of many insects (e.g., crickets, katydids, grasshoppers, and some coleopterans) and some fishes; and (iii) tremulation, which is the vibration of an appendage or the complete body and transmitting the resulting vibration to a solid substrate. This technique is used by some ensiferan species.

For the second category, sound can be produced by moving body parts to create surface waves. For example, some hemipteran species generate radiated ripples in the water surface using vertical movements of their legs. The third category includes moving a membrane or body part inside a fluid medium (e.g., cicada's tymbals, the swim bladder of some fish species, or the claw of the snapping shrimp). Finally, the fourth category of sound production involves forcing the vibrating molecules of a fluid medium (e.g., air) to pass over or through a body part. Examples of this include the larynx in amphibians, reptiles, and mammals, and the syrinx in birds.

Sound detection is a generalized ability in many different animal groups; indeed, there are many cases of animal species that can hear sound even though they don't use it for direct communication with conspecifics. Sound detection is basically achieved through two general mechanisms, although animal hearing comprises a great variety of structures and a great variety of sensitivities to sound frequencies and intensities. First, sound can be detected through particle motion sensors. These are normally composed of innervated cilia that move at different rates or degrees relative to any body movement induced by the sound (e.g., lateral line and inner ear in fish). Second, sound can be perceived by sensors detecting media pressure change, such as the eardrum or other membranes with a similar function (e.g., orthopterans and most vertebrates). The human ear detects sound from 20 to 20000 Hz. Infrasound (below 20 Hz) are normally detected by animals that use sound to communicate over long distances, such as cetaceans or elephants (Payne and Webb 1971; Pye and Langbauer 1998). Ultrasound (greater than 20000 Hz) is used, for example, by chiropterans to echolocate because of its high speed (Thomas 2004). While a relatively small percentage of fish species use sound to communicate, most fish have well-developed hearing systems and can discriminate sounds (Kasumyan 2008; Ladich and Schulz-Mirbach 2016; Lugli 2015). In general, fishes hear sound from 100 to 1000 Hz, with a fine hearing range from 200 to 400 Hz (Fletcher 2014). However, there is some evidence that fishes can also detect infrasound (Sand and Karlsen 2000) and ultrasound (Mann et al. 1997, 1998).

The hearing threshold (HT) of a particular species is the minimum intensity at which an individual can hear a pure tone (sound of a particular frequency) without the presence of any other sounds. Any sound, including con- and hetero-specific signals or ambient noise, will only be relevant to a particular individual if it reaches or surpasses its HT level. HT measures are therefore valuable to anticipate the sensitivity of an individual to a particular sound and the potential masking effects of a particular noise (see acoustic masking section below).

The soundscape as an acoustic resource

One of the classical definitions of "niche" is the sum of all environmental conditions that allow a species to satisfy its minimum requirements; thus, niche is defined as an "n-dimensional space" or "hyper-volume" (Hutchinson 1944, 1957). In a particular n-dimensional space, species should differ in their use of vital resources in order to locally coexist – otherwise they would face competitive exclusion (Hutchinson 1978). Niche theory provided conceptual models designed to investigate how many and how similar coexisting species could be within a given community (MacArthur and Levins 1967; MacArthur 1969, 1972).

The soundscape can be conceived as a three-dimensional space (determined by sound intensity, frequency, and time) shared by singing, calling, or stridulating animals. The soundscape is an ecosystem resource that cohabiting species have to share. The acoustic niche hypothesis (ANH), proposed by Krause (1987), postulates that interspecific acoustic interference in animal communities may trigger competition for the acoustic space that would prompt organisms to adjust their signals to exploit vacant niches and thus minimize spectral or temporal overlaps with interspecific vocalizations. This competition may influence community structure (spatial patterns) and dynamics (temporal patterns) at different scales.

The first evidence of acoustic partitioning in an animal community was shown in 2002 in the cicada community of a Mexican rainforest. Organisms showed species-specific spectral and temporal patterns that minimized their acoustic overlap (Sueur 2002). Studies since then have shown how some bird, anuran, insect, and even fish communities also seem to partition their acoustic space (Lüddecke et al. 2000; Chek et al. 2003; Planqué and Slabbekoorn 2008; Henry and Wells 2010; Schmidt et al. 2013; Ruppé et al. 2015; Figure 4), providing strong support for the acoustic niche hypothesis. However, many questions remain unanswered regarding the patterns of this partitioning and its impact in shaping community assemblages. How can we quantify this partitioning to compare its patterns between different communities? How many dimensions (frequency, amplitude, time) and what degree of overlap is permitted before partitioning occurs? Is the acoustic resource a strong (exclusive) competitive factor in current communities? Does the competition for the acoustic space constitutes a selective force in animal communities? How does this competition interact with other environmental factors to shape community structure?

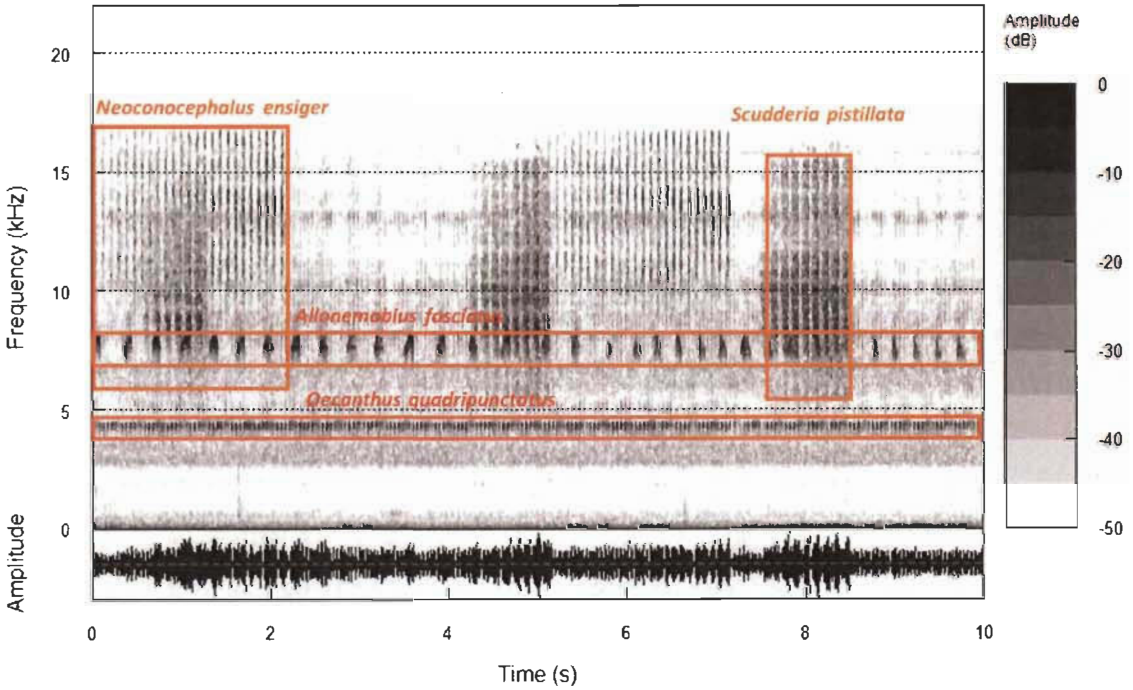

Figure 4. Spectrogram of a 10-second soundscape clip containing the acoustic signals of four species in an orthopteran community. A spectrogram allows a visual representation of the spectral patterns (frequencies and the respective intensity) of an acoustic signal over time. Each point in the plot corresponds to a specific time segment within the signal and a particular band of frequencies. Dark colours represent frequencies whose amplitude is high at that particular moment. An advantage of this representation is that it draws an intuitive image of the three-dimensional acoustic space, with the three dimensions being frequency, intensity, and time. We

can see in this image that signals show species-specific spectral and temporal patterns that allow them to use the acoustic space with a low probability to overlap. The four orthopteran species, whose stridulations are represented in this spectrogram, coexist naturally in farm buffers and meadows in the region of Quebec, Canada.

A consequence of the interspecific acoustic specialization to partition the acoustic space is that the acoustic heterogeneity of a community is predicted to increase with the number of vocalizing species within it. A heterogeneous acoustic space will be filled with signals varying in spectral and temporal patterns, while a homogenous one will be made up of signals showing similar spectral and temporal patterns throughout the acoustic space length. Several acoustic metrics have been recently developed to measure heterogeneity in the spectral and temporal patterns of the acoustic signal of vocalizing or stridulating communities (Sueur et al. 2014). These metrics have been proposed as indices to estimate species richness from soundscape recordings and as tools to perform rapid and inexpensive biodiversity assessments. Rapid biodiversity assessment programs are based on the use of biodiversity proxies, such as heterogeneity indices or recognizable taxonomic units (RTUs), to circumvent many of the logistical difficulties of conventional species surveys (Kerr et al. 2000, Obrist and Duelli 2010). RTUs categorize different sounds in a soundscape recording, in particular groups according to their acoustic similarity (e.g., Ruppé et al. 2015).

The acoustic entropy index (*H*; Sueur et al. 2008) computes the entropy of the temporal and spectral components of an acoustic signal (i.e., a measure of how evenly filled the spectral and temporal acoustic space is); it is one of the most commonly used acoustic metrics in the literature. Other metrics have been derived from *H* that consider only the spectral heterogeneity of the acoustic signal or that reduce the frequency resolution of the average spectra. Some of these are the acoustic complexity index (*ACI*; Pieretti et al. 2011), the acoustic diversity index (*ADI*; Pekin et al. 2012), and the number of peaks in the frequency spectrum (*NP*; Gasc et al. 2013). The normalized difference soundscape index (*NDSI*; Kasten et al. 2012) was developed to compare the acoustic signals of soundscapes with different relative contributions of anthrophony and biophony. *NDSI* is computed as the ratio of the difference between the absolute amplitude of the frequency bands considered typical of biophony (2-8 kHz) and those typical of anthrophony

(1-2 kHz), and the sum of the same bands. Other acoustic metrics have been developed to evaluate the beta acoustic diversity in a rapid, non-intrusive way. Most of these metrics are based on a comparison of the spectral or temporal patterns between two or more acoustic communities to evaluate their similarity or to assess the temporal changes in a specific community (Sueur et al. 2008; Gasc et al. 2013).

Acoustic masking

Acoustic masking refers to the process of one sound overlapping the spectral and temporal patterns of an acoustic signal of particular interest. This masking event increases the probability that the signal in question would be concealed to any potential receiver (Brumm and Slabbekoorn 2005). Acoustic masking can be caused in nature either by interspecific or environmental interferences (e.g., wind, rain, strong water current) or by anthropic noises. Masking may interfere with animal communication and any other activities and behaviours related to sound detection, such as navigation, food search, or predator detection.

Growth in transportation networks, resource extraction, motorized recreation, and urban development are factors responsible for chronic exposure to high levels of ambient noise in many terrestrial and aquatic environments; all in a relatively short period of time (Barber et al. 2010; Slabbekoorn et al. 2010). This fact has raised the concern of many ecologists and conservation biologists for the survival of many terrestrial and aquatic species that use sound to communicate. Acoustic signalling is used by many animal groups to defend their territories, warn conspecifics of approaching predators, or attract mates (Bradbury and Vehrencamp 2011). Any change to the transmission environment that hinders acoustic signals from reaching the intended receiver or that distorts the information content of the signal may have negative consequences for individual fitness and/or the species' persistence (Barber et al. 2010; Ladich 2013).

Ambient noise, when it is dominated by anthropic sources, is characterized by low frequency range sounds (0-3 kHz; Wood and Yerezinac 2006; Goodwin and Shriver

2011; Figure 5) in a more or less regular and constant pattern, the intensity of which varies according to the distance from the source. Possible vocal adjustments that animal species can make to attenuate acoustic masking events include increased call intensity to maintain the individual's active acoustic space, shifts in call frequencies to avoid spectral overlap, or changes in the call's temporal patterns to fill the free temporal gaps in the ambient noise. Species could also simply leave the area. As an example, in the presence of anthropic noise, birds have been shown to increase their dominant frequencies to avoid spectral overlap (Roca et al. 2016), to increase song intensity (Brenowitz 1982; Brumm 2004), to sing during less noisy periods (e.g., at night in areas that are noisy during the day; Fuller et al. 2007), or to adjust their singing rate (Brumm 2006). Other bird species simply prefer to avoid or limit the time spent in urban and traffic environments (Francis et al. 2009; Francis 2015).

While anthropic noise has been shown to drive vocal adjustments in populations of several aquatic and terrestrial species (e.g., Slabbekoorn and Peet 2003; Parks 2007), research still needs to focus on the evaluation of potential loss of signal integrity and species fitness implications before assuming an evolutionary adaptation in response to human-induced rapid environmental change (Sih 2013). It is also important to determine the relative overlap proportion of each soundscape dimensions (frequency, amplitude, time) required to generate an acoustic masking event with fitness implications (Desrochers and Proulx 2016). What is the critical combination, and is it the same for the different animal groups?

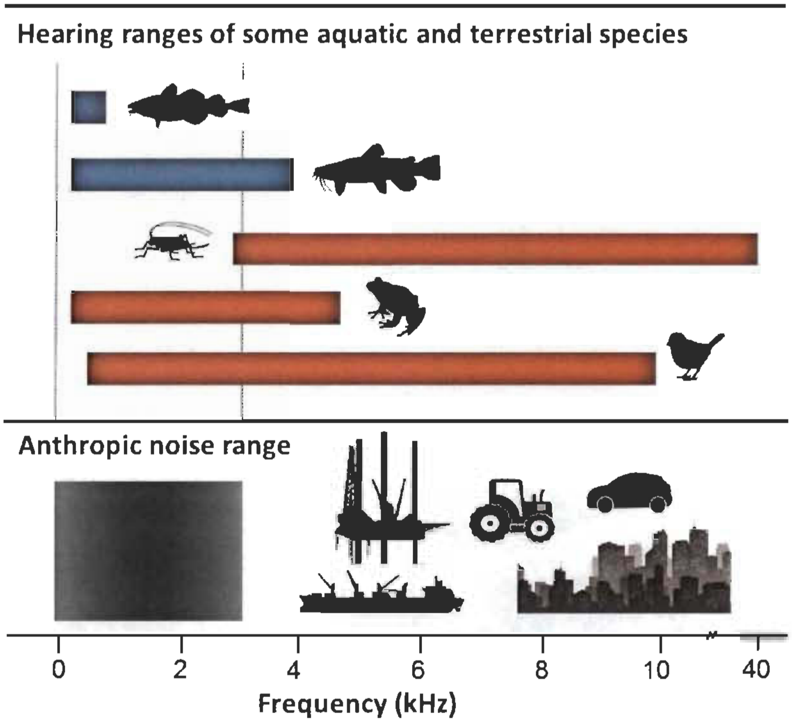

Figure 5. Hearing ranges of some aquatic and terrestrial species and frequency range of anthropic noise. The vertical dashed lines demarcate the anthropic noise range. From top-to-bottom, blue and orange horizontal bars represent Atlantic cod, a marine species representing fish with an average hearing ability (Chapman and Hawkins 1973); channel catfish, a freshwater species representing fish with especially good hearing abilities (Wysocki et al. 2009); bush cricket or katydid, with a very large hearing range that is typical of Tettigoniidae ensiferan species (Hill and Oldfield 1981; Romer et al. 1989); tree frog, with a relatively large hearing range for anurans (Hubl and Schneider 1979); and field sparrow, a passerine bird with average hearing abilities (Dooling et al. 1979). *Figure adapted from Slabbekoorn et al. 2010.*

As mentioned above, ambient noise levels have increased over the last decades in both land and aquatic environments. Noise levels affect not only animal species that use sound to communicate, but also species that hear sound and use it to navigate, feed, or detect potential threats, as is the case for many fish species (Richard 1968; Tolimieri et al. 2000; Simpson et al. 2005). Sound transmits well in aquatic environments – it travels faster and farther (Bradbury and Veherencamp 2011). Transient and very loud noises, such as pile driving and seismic gun surveys, can cause fish to became temporarily deaf if they are close to the source (Popper et al. 2003; 2009). However, noise introduced by human-related activities, like public or freight transport vessels or recreational boating, may contribute to the rise in the general ambient noise, event at long distances, but at moderate levels. This rise of noise in natural ecosystems from diverse and transient sources, which may sometimes be below the level of perception but above the detection threshold, may also increase the difficulty of signal detection (Braun 2015).

Hearing thresholds have been measured in more than 100 fish species using electrophysiological and/or behavioural methods (Ladich and Fay 2013). While controversy exists regarding the use of one method or another, and little theory is available to evaluate how results from the methods relate to one another, behavioural methods have been shown to produce lower hearing thresholds at lower frequencies than electrophysiological methods (Ladich and Fay 2013). It is contradictory, though, that most fish HT have been measured in terms of sound pressure level while fish seem to be sensitive to particle motion, and only some anatomical specializations seem to allow sound pressure detection (see Popper and Fay 2011; Nedelec et al. 2016).

The interactions and effects of a moderate level of ambient noise on fish community structure and dynamics, including species distribution, abundance, and predator-prey interactions, remain to be studied (Slabbekoorn et al. 2010). Recent studies have reported that behavioural changes and habitat-use responses of free-swimming fish to boat noise is species-specific (Jacobsen et al. 2014). Biotic interactions, particularly predator-prey interactions, seemed to be altered by higher ambient noise levels. Some evidence exists that the addition of underwater noise increased food-handling errors and decreased foraging efficiency in captive prey (Purser and Radford 2011). Similarly, prey were more susceptible to predation when exposed to high levels of motorboat noise on experimental coral reef patches (Simpson et al., 2016). However, research is still needed to develop theoretical bases to support these few observations with more general hypotheses and consistent empirical results.

Context and thesis objectives

Since soundscape ecology is a novel discipline in ecology, there are many unresolved questions related to understanding how the acoustic properties of the ecosystem interact with organisms, geophysical dynamics, and human activities. Our work in this thesis falls into two of the main themes within soundscape ecology: 1) the development of standard measurements and theoretical bases to identify and quantify the processes within the soundscape as well as the soundscape's interactions with natural or human systems, and 2) the assessment of interactions between the soundscape and the structure and dynamics of animal communities.

First, we aim to contribute to the development of standard measurements and quantification of soundscapes. For this, we will evaluate the use of acoustic metrics to carry out rapid biodiversity assessments and to systematically differentiate between soundscape contexts in aquatic and terrestrial ecosystems. Second, we aim to evaluate how the environment modulates acoustic (niche) partitioning and acoustic masking principles in animal communities, using a combination of theoretical models and field experiments.

In chapter one, our specific objectives are to evaluate the performance of acoustic metrics compared to the signal power spectrum to discriminate between aquatic and terrestrial soundscape contexts. To this end, we recorded several acoustic events within 14 terrestrial and aquatic soundscape contexts and we used two separate random forests to determine the accuracy of discriminations made using the acoustic metrics and the power spectrum. The power spectrum represents the complete (non-degraded) acoustic information of each soundscape event, while acoustic metrics provide a single ecologically interpretable value. In addition, we propose a new acoustic metric which is based on the compression size of the acoustic digitalized signals.

In chapter two, our specific objective is to assess the effect of the soundscape as an acoustic resource affecting animal community assemblage patterns. For this purpose, we recorded several ensiferan communities from temperate ecosystems and developed a theoretical framework based on a combination of null and empirical models. We tested the hypothesis that acoustic heterogeneity increases with the number of species stridulating in the recordings of the natural ensiferan communities and that the acoustic heterogeneity of naturally assembled ensiferan communities is higher than that of randomly assembled ones. We simulated ensiferan communities to construct the random assemblage model and we compared the slope of the acoustic-heterogeneity-species-richness relationship in naturally assembled communities to the randomly assembled ones. To simulate acoustic communities, we used recordings obtained from the Macaulay Acoustic Library, which is an open-access online library that contains over 250,000 digital audio and video recordings of birds, mammals, amphibians, reptiles, fishes, and insects from around the world.

In chapter three, our specific objective is to evaluate the effect of underwater ambient noise on predator-prey interactions. To do so, we developed a mathematical framework based on a three-species system that explicitly links fish captures to hearing sensitivities and ambient noise levels. We assessed the potential effect of ambient noise masking on fish behaviour in a system where visual detection is limited. We then applied our framework to a particular case study: that of the interaction between northern pike and yellow perch in a temperate shallow lake whose surface is frozen during the winter; this creates a system where light limitations may force fish to rely on acoustic cues to hunt. In the recent literature, ambient noise has been proposed as a masking factor favouring the hunting success of predators. We evaluate here whether prey may also benefit from acoustic masking, depending on ambient noise conditions and the hearing thresholds of the different species.

CHAPTER I

ACOUSTIC METRICS TO DISCRIMINATE SOUNDSCAPE CONTEXTS

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Abstract

Acoustic metrics assist our interpretation of soundscapes by aggregating a complex signal into a unique number. Numerous acoustic metrics have been developed for several purposes, including performing rapid biodiversity assessments, evaluating the effect of human-induced noise on animal behaviour, and characterizing the spatial heterogeneity of aquatic and terrestrial ecosystems. In this study, we evaluated the potential of six acoustic metrics compared to the signal frequency spectrum to discriminate between acoustic events in 14 soundscape contexts. To this end, we computed two separate random forests and used the mean decrease in Gini index and the out-of-bag error estimates as indicators of the relative importance and performance of the metrics in soundscape discrimination. Both the acoustic metrics and the frequency spectrum did well in discriminating soundscape contexts. The full frequency spectrum and the four best acoustic metrics achieved correct reclassifications of 80% and 60%, respectively. While the spectral signature is still the most accurate measure to characterize acoustic events, acoustic metrics acheived also a reasonable classification accuracy. Furthermore, due to their predetermined structure, their values provide a more intuitive ecological interpretation. In addition, we propose a new friendly use acoustic metric which is based on the compression size of the acoustic digitalized signals.

Keywords: Soundscape, acoustic metrics, acoustic heterogeneity, soundscape context.

Introduction

Soundscape ecology is the science of understanding how the acoustic structure of the landscape affects the abundance and distribution of organisms. Over the last decade, several metrics have been proposed to describe the variety of acoustic structures produced by both biotic and abiotic sounds, each metric with its advantages and drawbacks. So far, acoustic metrics have been successfully used for different purposes, ranging from performing rapid biodiversity assessments (e.g., Sueur et al. 2008b, Pieretti et al. 2011, Depraetere et al. 2012, Parks et al. 2014a, Roca and Proulx 2016) to evaluating the effect of human-induced noise on animal behaviour (e.g., Joo et al. 2011, Kasten et al. 2012).

Some studies have investigated how acoustic metrics correlate with habitat features and in which context they should be used. Different metrics have been shown to be more sensitive to the spatial heterogeneity of aquatic (McWilliam and Hawkins 2013, Lillis et al. 2014) or terrestrial (Bormpoudakis et al. 2013) ecosystems, or to the hydraulic and geomorphic conditions in freshwater systems (Tonolla et al. 2011). However, the disadvantage of all acoustic metrics is that they attempt to put a single number on a complex phenomenon by degrading the information in the acoustic signal, and not all acoustic metrics are easy to grasp, compute, and/or interpret.

An alternative to existing acoustic metrics is to use standard data-compression algorithms (e.g., JPEG or PNG for images, FLAC or MP3 for audio) as a means of measuring the complexity (or incompressibility) of information in the digital signal. Due to their widespread use and popularity, compression ratios are easy to implement by non-specialists. For example, Proulx et al. (Proulx et al. 2014) used a combination of landscape metrics for measuring the structural heterogeneity of digital photographs. These authors noted that structural heterogeneity values were tightly and linearly correlated to the compression ratio of JPEG images (Joint Photographic Experts Group). The correlation arises from the fact that spatially heterogeneous digital images are less efficiently compressed than images showing coarser spatial patterns (Proulx et al. 2014). Using the same reasoning, the compression ratio of the FLAC audio format (Free

Lossless Audio Codec) could be used as a rapid, simple, and intuitive measure of soundscape heterogeneity.

We herein define an acoustic event as the spectral and temporal signature of the acoustic signal, including different (biotic and abiotic) sources, recorded at a given location, on a given day, and over a given period within a given landscape. All acoustic events within the same landscape form a soundscape context. The objectives of this study were to assess 1) how good heterogeneity metrics are for discriminating between acoustic events in different soundscape contexts, and 2) which of the six-selected metrics perform the best. The complete (non-degraded) information in the signal's frequency spectrum of the acoustic events is used a baseline for comparison. Finally, we test the hypothesis that the FLAC compression ratio correlates with other existing metrics of the soundscape heterogeneity.

Material and Methods

Study sites

Through three consecutive years (2014-2016), we recorded acoustic events from 14 soundscape contexts (Table 1). Bird recordings were taken in June between 03:00 and 09:00, and orthopteran recordings were made in September between 21:00 and 03:00. We selected 20 recording positions within each soundscape context. Recording positions were separated by at least 500 m to minimize pseudo-replication. We used an omni-directional digital sound recorder (H2n Handy Recorder, Zoom, Tokyo, Japan) mounted on a tripod at 50 cm above the ground. We took recordings in 16-bit WAV format at a sampling rate of 44.1 kHz. In addition, we sampled 100 randomly selected points in a small natural stream in late July and early August (Table 1). We recorded underwater sounds by connecting to the H2n recorder a hydrophone (H1a hydrophone, Aquarian scientific, Anacortes, USA) and a powered amplifier (PA4 Hydrophone buffer/preamp, Aquarian scientific, Anacortes, USA).

Acoustic metrics

Of all the metrics, the acoustic entropy index (*H*; Sueur et al. 2008b) is the most frequently used (e.g., Parks et al. 2014b, Lillis et al. 2014, Roca and Proulx 2016), and it integrates both the spectral and temporal components of an acoustic signal. *H* varies between 0 and 1, where 1 indicates a highly heterogeneous signal. More sophisticated metrics were subsequently derived, including the acoustic complexity index (*ACI*; Pieretti et al. 2011), the acoustic diversity index (*ADI*; Pekin et al. 2012) and the number of peaks in the frequency spectrum (*NP*; Gasc et al. 2013). The normalized difference soundscape index (*NDSI*; Kasten et al. 2012) was developed to compare the acoustic signal of soundscapes with different relative contributions of anthrophony and biophony. *NDSI* is the normalized difference in the absolute amplitude of the frequency bands considered typical of biophony (2-8 kHz) minus those typical of anthrophony (1-2 kHz). *NDSI* varies between -1 and +1, where +1 indicates a signal dominated by biophony.

Processing sound recordings

We extracted 100 20-second audio subsamples from each acoustic event in each soundscape context, for a total of 1400 subsamples: 800 for birds, 500 for orthopterans, and 100 from aquatic systems. We converted the WAV original audio subsamples into the FLAC format using the function **wav2flac** from the {seewave} package (Sueur et al. 2008a) in R (R version 3.1.3; R Development Core Team 2015) and extracted the file bit-size from both WAV and FLAC audio files. We divided the FLAC size by the WAV size for each subsample and obtained a ratio (hereafter called *FW*). *FW* will tend towards 0 if the FLAC size is much smaller than the WAV size, and towards 1 if FLAC size and WAV size are nearly equal. We used the function **meanspec** from the {seewave} package in R to extract the mean frequency spectrum of the digital signal. We used a short-term Fourier transform with a 50% window overlap and 512 window length. The frequency spectrum was composed of 256 frequency bands between 0 and 22000 Hz. We used this same package to compute the *H*, *NP*, *ADI*, *ACI*, and *NDSI* acoustic heterogeneity metrics on each subsample.

Statistical analysis

To test the hypothesis that acoustically heterogeneous digital audio files are less efficiently compressed than files showing simpler acoustic patterns, we computed the Spearman correlation between the acoustic heterogeneity metrics and the *FW* ratio.

To compare the ability of the acoustic metrics or the full frequency spectrum to discriminate between soundscape contexts (i.e., signaling animal group in a given ecosystem type; Table 1), we developed two separate random forests (RF) models. For each RF model, we grew 4000 trees and tested *sqrt(p)* predictor variables at each split (where p is either the number of metrics or frequency bands). For each tree constructed in the random forest, a 2/3 of the data are subsampled to train the classification model and 1/3 of the data are left out to test the model (i.e., OOB cases). The misclassification error is then averaged across all OOB cases and trees, providing a general out-of the bag (OOB) error estimate for the model. We used the Gini index as a measure to determine variable importance. It measures the reduction in classification error when including an additional predictor variable (either an acoustic metric, or a frequency band) in the model. We implemented the RF algorithm using the function **randomForest** in R {randomForest} (Breiman 2001).

Results

The *FW* ratio showed a strong, positive, linear correlation with *ADI* and *H* (Figure 1). The random forest results showed that the full frequency spectrum achieved a better discrimination between soundscape contexts than the acoustic metrics ($\text{OOB}_{\text{ac. metrics}}$ misclassification of 38%; $\text{OOB}_{\text{f. spectrum}}$ misclassification of 20%). According to the Gini index, *H* was the most important metric in the RF classification followed by *NDSI* (Figure 2). Adding acoustic metrics to the RF increased discrimination accuracy up to about four metrics, at which point a plateau was reached (Figure 2).

Discussion

This study is the first to propose the use of compression ratios (FW) as a tool to estimate the heterogeneity of an acoustic signal. Both the acoustic metrics and the frequency spectrum did well in discriminating soundscape contexts. The combination of four acoustic metrics allowed for a better discrimination (60% correct reclassification) than the best single metric (20%). However, the frequency spectrum achieved the highest correct reclassification (80%), suggesting that information is lost when using acoustic metrics.

Computation of acoustic metrics is not easy for non-specialists. Most of them are coded as functions in software environments like MATLAB or R. Meanwhile, FLAC compression is achieved through free, user-friendly, online or downloadable audio converters. In this study, we showed that the size of a compressed FLAC audio file was a good indicator of the acoustic heterogeneity of different soundscape contexts. The *FW* ratio correlated positively with *ADI* and *H*; that is, sound files of higher acoustic heterogeneity were less easily compressed than homogenous ones. This method provides a simple and accessible way to estimate the acoustic heterogeneity of an acoustic signal.

FW was more tightly correlated with *ADI* ($\rho = 0.82$) than with *H* ($\rho = 0.66$). Technically, the only difference between *H* and *ADI* is that the latter is a sophisticated version of the *H* index. The frequency resolution of the average spectra of ADI is reduced to 1 kHz and it considers only the spectral heterogeneity of the acoustic signal (Pekin et al. 2012). Thus, the sensitivity of *ADI* to background noise is diminished to some extent. The fact that *FW* shows a stronger correlation with *ADI* than *H,* suggests that *FW* may also be less sensitive to background noise. This point is supported by the broad range of *H* values observed among the acoustic events characterized by high *FW* values (Figure 1).

When using the full frequency spectrum in RF models, only 20% of the out-of-bag acoustic events were incorrectly reclassified. This result highlights the advantage of not degrading the information present in the audio files. However, classification models fitted on so many variable (i.e., 256 frequency bands) may be difficult to interpret. Conversely, acoustic metrics have a predetermined structure, such that they are a more intuitive to interpret and relate to ecological processes. Besides, acoustic metrics acheived reasonable reclassification accuracy in the RF classification (60% accuracy).

H and *NDSI* were the most important metrics in the RF classification. *H* has been shown to be sensitive to background noise (Depraetere et al. 2012). *NDSI* is an estimator of the relative contribution of the anthrophony compared to the biophony. Since we did not apply a high-pass filter to the audio files, the implication is that low-frequency sounds were present in all recordings but at varying intensity levels. Such background noise is commonly dominated by sounds of geophysical or anthropic origin, which main energy resides on the low frequency bands (Brumm and Slabbekoorn 2005). We conclude then, that background noise was a key discriminating feature among our 14 soundscape contexts.

Our results indicated that H and NDSI are complementing metrics in the classification of soundscape contexts. Other acoustic metrics less sensitive to background noise, such as ADI and FW, may be more useful for biodiversity assessment and acoustic signaling species monitoring instead. Yet, the combination of many acoustic metrics, rather than a single one, yielded a better discrimination of acoustic events. Towsey et al. 2014 sought to optimize a methodology to estimate avian species richness from acoustic recordings. In line with our results, they also concluded that a weighted combination of a few metrics provided a more accurate discrimination of species groups.

We herein defined the soundscape context as a collection of acoustic events, each capturing the spectral and temporal signature of the acoustic signal, including different (biotic and abiotic) sources at a given location, on a given day, over a given period, within a given landscape. Soundscape contexts provide fundamental information about the environment to listening species, such as the presence of cohabiting con- and hetero-specifics, potential dangers (e.g., Magrath et al. 2015), habitat breeding suitability (e.g., Pupin et al. 2007), as well as competition for the acoustic resource (e.g., Schmidt and

Balakrishnan 2014, Roca and Proulx 2016). Since the soundscape captures the heterogeneity of the acoustic environment both within and between ecological contexts, it may have unforeseen implications to the fitness and behavior of signaling species. In this context, the accuracy and precision of the metrics or methods that allow an automatized characterization of soundscape contexts, acquire a particular relevance in ecology.

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Tables

Table 1. The 14 soundscape contexts used in the analyses. Each soundscape is defined by a geographic position, date, and ecosystem type as well as the presence/absence of a dominant signaling animal group (DSAG). The geographic coordinates represent the average latitude and longitude of all recording positions within a given soundscape context.

Ecosystem type	**Locality**	**Lat.**	**Long.**	**Date**	**DSAG**
Boreal forest	Chibougamau	49.790784	-74.063275	25/06/2014	Birds
Mature mixed forest	La Mauricie National Park	46.749848	-72.933071	25/06/2015	Birds
Mixed forest	Sutton Natural Environment Park	45.096466	-72.549190	11/06/2015	Birds
Young mixed forest	Bic National Park	48.341669	-68.804407	03/07/2015	Birds
Wetlands	Chibougamau	49.790784	-74.063275	26/06/2014	Birds
Fluvial marshes	Parc écologique Godefroy	46.301477	-72.533145	06/06/2014	Birds
Farmlands	Mauricie region	46.415907	-72.714403	06/06/2014	Birds
Urban areas	Mauricie region	46.330851	-72.563802	08/06/2014	Birds
Bog	Bog Lac-à-la-Tortue	46.548384	-72.675131	19/08/2015	Orthopterans
Fluvial marshes	Northern shore, Lake St. Pierre	46.194391	-72.999654	01/09/2015	Orthopterans
Farmlands	SCIRBI*	46.079886	-73.146324	17/08/2015	Orthopterans
Farmlands	St. Lawrence River lowlands	46.222196	-72.515575	16/08/2013	Orthopterans
Urban areas	Mauricie region	46.343504	-72.583342	28/08/2014	Orthopterans
Stream	La Mauricie National Park	46.741174	-72884029	29/07/2016 17/08/2016	–

* SCIRBI: Société de Conservation, d'Interprétation et de Recherche de Berthier et ses Îles.

Figure legends

Figure 1: Bivariate relationships between the FLAC-WAV compression size ratio and other acoustic metrics. FW: FLAC-WAV ratio, H: acoustic entropy index, ADI: acoustic diversity index, NP: number of peaks, NDSI: normalized difference soundscape index, ACI: acoustic complexity index.

Figure 2: Relative importance of acoustic metrics in random forest models. A) Mean decrease in the Gini index for each acoustic metric. Higher values correspond to acoustic metrics that better discriminated between soundscape contexts. B) Joint contribution of the acoustic metrics, added in importance order, to the RF model cross-validation accuracy.

Figures

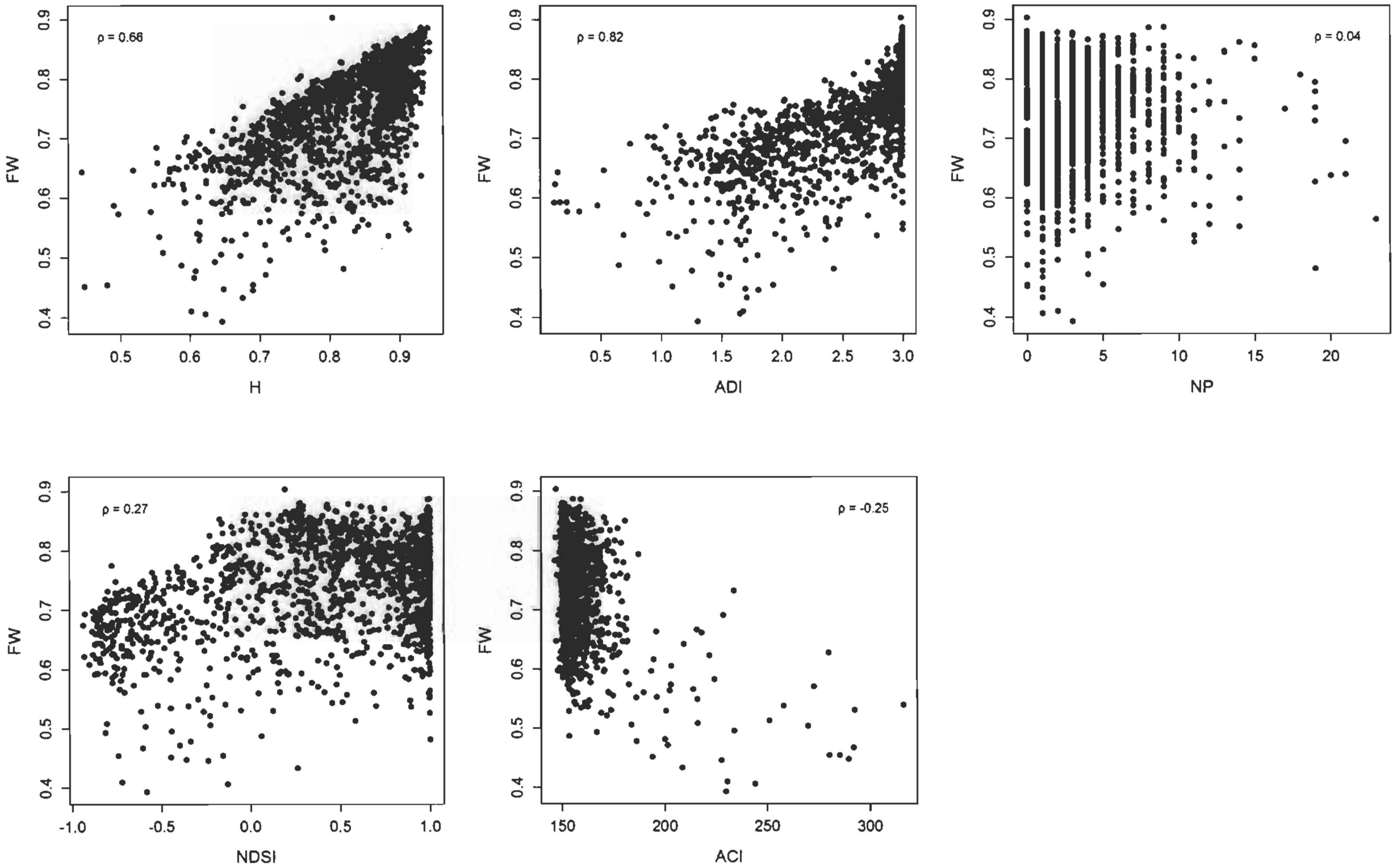

Figure 1.

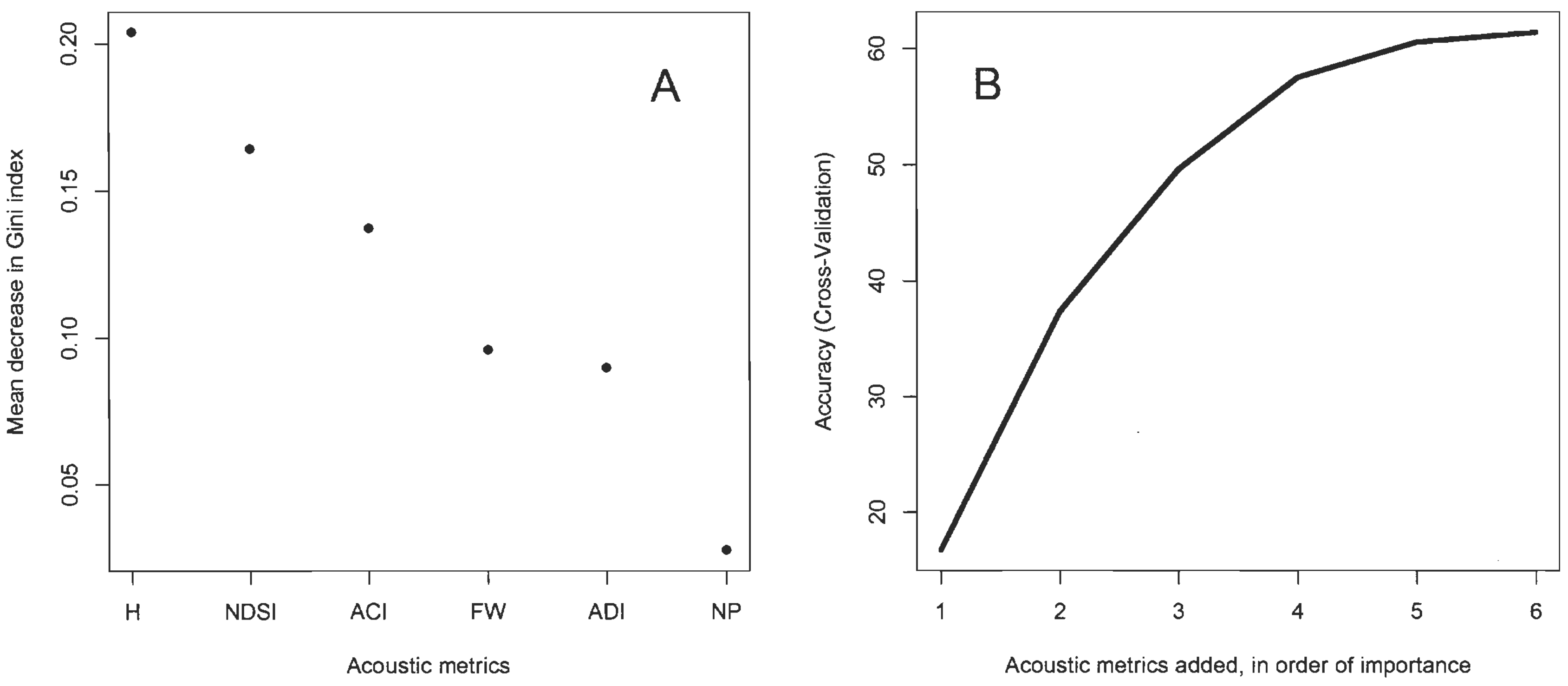
A
Mean decrease in Gini index
0.20
0.15
0.10
0.05
H
NDSI
ACI
FW
ADI
NP
Acoustic metrics
B
Accuracy (Cross-Validation)
60
50
40
30
20
1
2
3
4
5
6
Acoustic metrics added, in order of importance

Figure 2.

CHAPTER II

ACOUSTIC ASSESSMENT OF SPECIES RICHNESS AND ASSEMBLY RULES IN ENSIFERAN COMMUNITIES FROM TEMPERATE ECOSYSTEMS

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Abstract

Vocalizing animals are known to produce a wide range of species-specific spectral and temporal communication patterns. As a consequence, the acoustic heterogeneity of insect communities is expected to increase with the number of vocalizing species. Using a combination of simulation models and field surveys, we tested the hypotheses that i) acoustic heterogeneity increases with the number of cricket and katydid species in ensiferan communities and ii) acoustic heterogeneity of naturally assembled ensiferan communities is higher than that of randomly assembled ones. The slope of the acoustic heterogeneity - species richness relationship in naturally assembled communities was positive but did not differ from that of randomly assembled communities, suggesting a rather weak competition for the acoustic space. Comparing the species richness-acoustic heterogeneity relationship of naturally and randomly assembled communities, our study provides a novel approach for understanding species assembly rules in animal groups that rely on acoustic communication.

Keywords: Soundscape ecology, acoustic heterogeneity, rapid biodiversity assessment, crickets, katydids, bioacoustics, biodiversity.

Introduction

The acoustic space can be represented as a resource that is shared by singing, calling or stridulating animals (Krause 1987). Vocalizing animals produce species-specific spectral and temporal communication patterns (e.g., Lüddecke et al. 2000, Sueur 2002) that may have evolved to minimize acoustic interference amongst one another (Römer et al. 1989, Römer 1993, Schmidt and Balakrishnan 2014). A consequence of this specialization is that the acoustic heterogeneity of a community is predicted to increase with the number of vocalizing species within it. To illustrate this point, Sueur et al. (2008b) calculated the acoustic entropy (i.e. a measure of how evenly filled is the spectral and temporal acoustic space) of simulated assemblages by randomly mixing communication patterns of bird, amphibian and insect species from Western Europe. The acoustic heterogeneity of either simulated or natural communities was since reported to increase with species richness in other ecosystems (Sueur et al. 2008b, Depraetere et al. 2012, Gasc et al. 2013).

Recent work on stridulating insect communities showed an inter-specific differentiation in the spectral communication patterns of cohabiting species, supporting the premise that acoustic heterogeneity is structured by competition (Diwakar and Balakrishnan 2007, Schmidt et al. 2013). For example, among tropical cricket communities, 144 of 153 unique species combinations (94%) showed little overlap in emitted frequencies and represented species assemblages in nature that were more dissimilar than if assembled at random (Schmidt et al. 2013). Comparable results were obtained for cricket and katydid assemblages in a rainforest ecosystem (Jain et al. 2014).

Acoustic heterogeneity indices would carry benefits over more conventional insect surveys, which are needed by stakeholders and landowners for assessing environmental impacts and improving land-use management (Fartmann et al. 2012). Rapid biodiversity assessment programs monitoring biodiversity proxies, or so-called recognizable taxonomic units (RTUs), can circumvent many of the logistical hurdles of conventional species surveys (Kerr et al. 2000, Obrist and Duelli 2010). Given their global distribution and key role in decomposition and recycling processes (Gangwere 1961), cricket and katydid species of the Ensifera suborder are well suited to biodiversity assessment programs since their stridulating patterns can be categorized into RTUs.

In the rapidly progressing fields of soundscape ecology and ecoacoustics, the potential of acoustic heterogeneity indices as biodiversity proxies has not been fully demonstrated (Sueur et al. 2014). Furthermore, such indices can be compared against simulation models to disentangle the relative importance of community assembly rules with respect to spectral, spatial and temporal communication patterns in the acoustic space. Here, using a combination of simulation models and field surveys, we test the hypotheses that i) acoustic heterogeneity increases with the number of species in recordings of natural ensiferan communities and ii) acoustic heterogeneity of naturally assembled ensiferan communities is higher than that of randomly assembled ones. The confirmation of the later would, thus, indicate a competition for the acoustic space.

Material and Methods

Randomly assembled communities

We consulted specialized guides (Pelletier 1995, Elliott and Hershberger 2007, Himmelman 2009) to identify the stridulating ensiferan species most commonly found in Northeastern North-America. For each of these thirty-three species, we retrieved all available recordings covering the regions of Québec (Canada) and New Jersey, New York, and Ohio (USA) from the Macaulay Library (Cornell University, Ithaca, NY; Table 1). We selected one recording per species and region according to global quality criteria; i.e. absence of background noise or signal interference. An example of the regional species pool for Québec is given in Table 2. We subsequently clipped each recording to a 10-second duration, starting at the first instance of a stridulating call. Our search procedure yielded 48 files of 33 different species belonging to the Gryllidae and Tettigoniidae families (Table A1 in Supplemental Material). All audio files came as a mono-channel 16-bit WAV format at a sampling rate of 44.1 kHz.

For each of the four regions, we simulated the sounds produced by ensiferan communities given an increasing gradient of species richness (*SR*) from 1 to 8 species. Within a given *SR* level, we randomly sampled recordings from the regional species pool and assembled acoustic communities using the formula: $M = WA$; where A is a matrix of *SR* columns by 4,410,000 rows (i.e. 10 seconds recording at 44.1 kHz) and M is the matrix of assembled acoustic communities. W is a square matrix of size *SR* with weighting factors on the diagonal and ones elsewhere. W allowed us to obtain different amplitudes for each species to mimic natural conditions. We ran the assembly process 30 times for each *SR* level (1-8 species), for a total of 240 acoustic communities per region. The signal of one species was randomly up-weighted in each simulation run by setting the diagonal factors of the W matrix to a value randomly sampled between 1.0 and 1.5. Since species were randomly positioned in the A matrix, we extracted only the first vector of the M matrix for subsequent analyses. Additional simulations showed that our results did not depend on the above choice of parameters.

Naturally assembled communities

On August 16-17th, 2013, we recorded stridulating ensiferan communities in farmlands of the St-Lawrence River lowlands, near the city of Trois-Rivières (Québec, Canada). We selected a total of ten farms with large buffer strips of herbaceous vegetation and cornfields not subjected to insecticide treatments. In each farm, we placed a digital sound recorder (H2n Handy Recorder, Zoom, Tokyo, Japan) at 200 m from the field border inside one cornfield and recorded for 24 hours simultaneously at all ten field sites. On the following day, we moved each recorder to a nearby herbaceous strip and recorded there for an additional 24 hours. We recorded under optimal weather conditions *sensu* Walker and Cade (2003) (i.e. clear sky, wind speed below 10km h^{-1} and air temperature around 25°C) and at the peak of the reproduction period for cricket and katydid species in this region (Pelletier 1995). Microphones were mounted on tripods at a height of 1.5 m above the ground. Recordings were taken in 16-bit WAV format at a sampling rate of 44.1 kHz.

Signal processing

We performed a stratified random sampling and retained twenty 20-second audio clips within each 24h recording for a grand total of 400 clips. The 20-second clip length was chosen in order to allow a balanced representation of different stridulating species in the natural communities. Audio clips were selected to ensure an even repartition of into *SR* levels. We applied a high pass filter at a cutoff frequency of 2 kHz and a roll-off of 12 dB to remove background noise associated with nearby roads. The lowest carrying frequency of the studied species is 3 kHz and, hence, filtering below 2 kHz did not affect the information content of the signal. Sampling, clipping and filtering were achieved using the cross-platform editor Audacity®.

We calculated the acoustic heterogeneity of simulated and natural acoustic communities using the acoustic entropy *H* index in the Seewave R package (Sueur et al. 2008a). The index measures the normalized Shannon-Rényi entropy of the signal's spectral and temporal components. The *H* index is reported to increase when (low intensity) background noise prevails over biological sounds (Depraetere et al. 2012). Thus, *H* can be high if the recording consists of faint background noise. To account for this "intensity effect" in our statistical model, we included the mean absolute amplitude of audio clips as a predictor variable. Absolute amplitudes were extracted using the "env" function in the Seewave R package. We expected *H* to increase with increasing *SR,* independent of an intensity effect.

We compared results obtained with the *H* index to those obtained with another acoustic heterogeneity index. The Number of Peaks (*NP*) counts frequency maxima above a given threshold in the rescaled frequency spectrum. *NP* is linked to the number of different song types in the recording and should be less sensitive than *H* to background noise (Gasc et al. 2013). We calculated the *NP* index of the audio clips representing natural (ensiferan) acoustic communities using the Seewave R package and parameter settings suggested by Gasc et al. (2013).

Statistical analysis

To model the acoustic heterogeneity of the simulated communities, we fitted a generalized linear model with the "glm" R function (R version 3.1.0, Development Core Team 2014), using a Gaussian error distribution and a logit link. The logit link was used to account for the fact that the *H* index is mathematically bounded between 0 and 1. The model included two predictor variables: region (Québec, New Jersey, New York, Ohio) and *SR* (1-8 species).

We fitted a generalized linear mixed-effects model to the *H* index of natural acoustic communities with the "glmer" R function in the lme4 package (version 1.1.7; Bates et al. 2014), using a Gaussian error distribution and a logit link. We included the following three predictor variables as fixed effects: *SR* (1-4 species), log-transformed mean absolute amplitude, and habitat type (cornfield; buffer strip). We modeled the recording site, nested within farm, as a random effect. We fitted the same model structure to the *NP* index calculated on natural acoustic communities. Model selection was conducted on the basis of the Akaike Information Criterion (AIC; Burnham and Anderson 2002). Figures were drawn in R using the ggplot2 package (Wickham, H. 2009).

We also evaluated whether the acoustic heterogeneity of naturally assembled ensiferan communities differed from that of randomly assembled ones. For the *SR* levels of 1 to 4 species, we overlaid the *H* index of natural acoustic communities on the 95% confidence interval of acoustic communities simulated using Québec's regional species pool. We conducted a bootstrap procedure to evaluate if the acoustic heterogeneity-species richness (*H-SR*) relationship of natural communities differed from those calculated with the simulated communities. To do so, we randomly sampled with replacement the *H* and *SR* values of 120 simulated communities and calculated the least-square intercept and slope of the *H-SR* relationship. We iterated this process 10,000 times. We compared the *H-SR* intercept and slope for Québec's natural communities against the bootstrap distributions obtained using the iteration procedure. We concluded that a significant difference between the natural and simulated communities was found if the intercept, or slope, fell outside the range of bootstrapped values (Figure 1).

Results

The *H* index of simulated acoustic communities increased with increasing *SR* levels (β_{SR} slope = 0.12) and differed among regions (β_{region} = 0.21; i.e. higher in New-Jersey and lower in Québec), indicating a dependence of *H* on the regional species pool (Figure 2). Comparisons of model AIC values also lead to this result: $AIC_{SR + REGION}$ = -2802.6; AIC_{SR} = -2777.2; AIC_{REGION} = -2418.2.

The *H* index of natural acoustic communities was positively associated to *SR* levels (β_{SR} slope = 0.080) and was higher in herbaceous buffer strips relative to cornfields ($\beta_{habitat}$ = 0.19) (Figure 3). Species' relative occurrences also differed between the two acoustic habitats (Table 2). *H* was negatively associated to the (log) absolute amplitude of the audio clip ($\beta_{amplitude}$= - 0.47; Figure A1 in Supplemental Material). Adding the *SR* variable in a model already including absolute amplitude and habitat type improved the model fit: $AIC_{AMPLITUDE + HABITAT + SR}$ = -1524.5; $AIC_{AMPLITUDE + HABITAT}$ = -1485.1. Similar results were obtained for the *NP* index of acoustic heterogeneity (Figure B2). *NP* was positively associated to *SR* levels (β_{SR} slope = 0.18), was higher in herbaceous buffer strips ($\beta_{habitat}$ = 0.14), and was negatively associated to the (log) absolute amplitude of the audio clip ($\beta_{amplitude}$= - 0.16). Thus, only the results obtained for the *H* index are discussed hereafter without loss of generality.

Model intercepts for cornfield and herbaceous buffer habitats fell outside the bootstrap distribution range of simulated *H-SR* relationships (10,000 iterations; Min intercept = 0.300, Max intercept = 1.106). In contrast, both slope estimates fell within the bootstrap distribution range (10,000 iterations; Min slope = 0.056, Max slope = 0.333). Observed *H-SR* intercept and slope on the logit scale were respectively 1.413 and 0.087 in the herbaceous buffers habitat, and 1.257 and 0.081 in the cornfield habitat (Figure 3).

Discussion

This study provides the first example of a positive relationship between acoustic heterogeneity and ensiferan species richness within natural communities. However, the slopes of the acoustic heterogeneity-species richness relationships did not differ significantly between naturally and randomly assembled communities. Such negligible difference in slopes would suggest that the acoustic space is not structured by direct competitive interactions among stridulating species, at least not for ensiferan communities in the temperate agro-ecosystems of Québec.

Randomly assembled communities

The *H* index discriminated acoustic communities with lower *SR* (1- and 2-species) from those with higher *SR* (3- and 4-species). Our simulations also showed that *H* saturates rapidly for temperate communities of more than four species; a result similar to the findings of Sueur et al. (2008b). We note that the vast majority of our ensiferan communities comprised less than five species stridulating at the same time and place. Nevertheless, our results would suggest that in species rich ecosystems, the *H* index may saturate at relatively low levels of species richness and, thus, compromise its accuracy as a high-resolution proxy measure. While *H* represents a global measure of acoustic heterogeneity, other measures can be used to quantify acoustic partitioning and complementarity in insect communities (e.g., Schmidt and Balakrishnan 2014).

As the number of stridulating species increases the acoustic space gets filled more consistently over time and more evenly across audio frequencies, yielding less *H* variation at higher *SR* levels. In contrast, *H* varied greatly both within and between regions at low *SR* levels; hence the intercept of the simulated *H-SR* relationship reflects the average *H* index of individual species in the regional pool. Considering that nearly half of the species in our dataset were exclusive to either one of the regions, acoustic differences in the identity of species stridulating alone (that is when $SR = 1$) translated into intercept differences in *H* within and between regions. The regional pool of ensiferan species is, on one hand, largely determined by environmental factors, such as air temperature and dispersal barriers, all of which condition their geographic distribution (Vickery and Kevan 1985, Masaki 1996). On the other hand, ensiferan species distribution at the local scale is a product of selection for particular vegetation structures (e.g., grasses, herbs, litters, woodlands, wetlands, etc.) and micro-climatic environments (Poniatowski and Fartmann 2008, Wünsch et al. 2012).

Naturally assembled communities

As already observed for simulated acoustic communities, the intercept of the *H-SR* relationship derived from natural communities depends on the interplay between the acoustic identities of ensiferan species and their relative occurrences. Farmland habitats investigated in the present study differed in their average *H*, with herbaceous buffer strips having a higher intercept than cornfields. This difference can, in part, be explained by the fact that not all species were found singing alone and that their relative occurrences differed between the two habitats (see Table 2). Furthermore, not all species from the regional pool were heard singing in the field. Out of 15 candidate species in the regional pool, we identified 6 species stridulating in cornfields (i.e. with percent occurrence > 1%) and 9 species in vegetation buffers. The two habitat types displayed distinct acoustic signatures despite being less than 1 km apart and were surveyed under comparable climatic conditions, thus emphasizing the sensitivity of our approach.

Our findings revealed that the acoustic heterogeneity of ensiferan communities in temperate agro-ecosystems did not differ from that of randomly assembled communities once species pool intercept differences (i.e., H_{local} vs. $H_{regional}$) were taken into account. This result is in apparent contradiction with the conclusion of recent studies on species-rich ensiferan communities, wherein pairwise comparisons of spectral communication patterns revealed little acoustic overlap between species (Schmidt et al. 2013, Jain et al. 2014). While our results suggest that competition for the acoustic resource is weak at the local community level, the aforementioned experiments emphasized the importance of acoustic competition on a much broader evolutionary timescale. In other words, competition for the acoustic resource within ensiferan communities may be weak only because species have evolved markedly different communication patterns and adaptations that prevent acoustic interference nowadays (Schmidt and Balakrishnan 2014). Alternatively, ensiferan species in managed agro-ecosystems may not have evolved together for a long time and competition for the acoustic space might still be at work. Crop fields and herbaceous buffer strips are relatively recent habitats that may have attracted opportunistic ensiferan species in a random-like fashion.

Conclusion

The acoustic heterogeneity concept is rooted in niche theory, which means that species vocalizing in the same habitat share and, thus, partition the same acoustic resource. In this context, the incredible variety of animal communication patterns could be interpreted as distinct traits that species have evolved for exploiting different acoustic resources. Measuring acoustic heterogeneity in field recordings of vocalizing animal communities provides a simple way of assessing how much of this resource is exploited along the spectral, spatial and temporal dimensions of the acoustic space.

Sound libraries already provide recordings for numerous vocalizing species from around the world and the number of such easily accessible audio files is rising (see Table A1). As we illustrated here, these recordings allow reconstructing the regional species pool of stridulating insects to simulate acoustic communities at different levels of species richness. The same approach could also be used on other animal groups such as birds and anurans. Simulated acoustic communities can be used as the "null models" against which field recordings are compared. Our study presents the first application of this framework and provides a fresh look on the question of how interspecific competition for the acoustic space constrains species assembly in animal groups that rely on acoustic communication.

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Tables

Table 1: Stridulating ensiferan species in the regions of Québec, New Jersey, New York, and Ohio for which audio recordings could be retrieved from the Macaulay Library (Cornell University, Ithaca, NY).

Quebec	**New Jersey**	**New York**	**Ohio**
Allonemobius allardi	*Amblycorypha carinata*	*Acheta domesticus*	*Amblycorypha alexanderi*
Allonemobius fascitus	*Amblycorypha oblongifolia*	*Amblycorypha rotundifolia*	*Amblycorypha oblongifolia*
Allonemobius griseus	*Amblycorypha rotundifolia*	*Conocephalus nigropleurum*	*Amblycorypha rotundifolia*
Amblycorypha oblongifolia	*Gryllus pennsylvanicus*	*Gryllus veletis*	*Atlanticus testaceus*
Conocephalus fasciatus	*Neoconocephalus robustus*	*Oecanthus nigricornis*	*Eunemobius carolinus*
Eunemobius carolinus	*Oecanthus latipennis*	*Oecanthus pini*	*Gryllus pennsilvanicus*
Gryllus pennsylvanicus	*Orchelimum pulchellum*	*Oecanthus quadripunctatus*	*Gryllus veletis*
Metrioptera roeselii	*Orchelimum vulgare*	*Orchelimum gladiator*	*Neoconocephalus nebracensis*
Neoconocephalus ensiger	*Orocharis saltator*	*Scudderia pistillata*	*Oecanthus nigricornis*
Oecanthus fultoni	*Pterophylla camellifolia*	*Scudderia texensis*	*Orchelimum nigripes*
Oecanthus nigricornis	*Scudderia curvicauda*		*Orchelimum vulgare*
Oecanthus quadripunctatus			*Orocharis saltator*
Orchelimum gladiator			
Scudderia curvicauda			
Scudderia pistillata			

Table 2: Regional pool of 15 cricket and katydid species found in open fields of southern Québec. Percent occurrences were calculated from the presence/absence of species in 400 audio clips of stridulating ensiferan communities in farmlands of the St-Lawrence River lowlands (Québec, Canada).

Ensiferan subfamily	**Species**	**Percent occurrence**	
		Cornfields	**Herbaceous buffers**
Gryllinae	*Gryllus pennsylvanicus*	16%	16%
Nemobiinae	*Allonemobius allardi*	10%	7%
	Allonemobius fascitus	8%	13%
	Allonemobius griseus	0%	0%
	Eunemobius carolinus	50%	33%
Oecanthinae	*Oecanthus nigricornis*	<1%	6%
	Oecanthus quadripunctatus	10%	3%
	Oecanthus fultoni	0%	0%
Phaneropterinae	*Amblycorypha oblongifolia*	4%	17%
	Scudderia pistillata	<1%	0%
	Scudderia curvicauda	0%	0%
Tettigoniinae	*Metrioptera roeselii*	0%	3%
Conocephalinae	*Neoconocephalus ensiger*	0%	0%
	Orchelimum gladiator	0%	0%
	Conocephalus fasciatus	0%	2%

Figure legends

Figure 1: Conceptual framework comparing the species richness – acoustic heterogeneity relationship of naturally and randomly assembled communities. Randomly assembled acoustic communities (black dashed line ± 95% confidence interval in grey) at different species richness (*SR*) levels are simulated by sampling species from a regional species pool. Each simulated acoustic community forms a local species pool within the regional pool. Naturally assembled acoustic communities (black solid line) are obtained from direct field recordings. The acoustic heterogeneity (*H*) index is calculated on both natural and simulated communities. Panels illustrate how to interpret differences in the intercept (row panels) and slope (column panels) of the *SR* - *H* relationship. Firstly, the acoustic heterogeneity of natural acoustic communities can be higher (H local > H regional) or smaller (H local < H regional) than the average acoustic heterogeneity of simulated communities. This would reflect environmental constraints associated to local habitats within a region. Secondly, if *H* increases faster with increasing *SR* in natural than in simulated communities, the steeper slope would indicate acoustic complementarity among species. Conversely, a flat slope would indicate acoustic overlap.

Figure 2: Relationship between ensiferan species richness and acoustic heterogeneity of randomly assembled communities. The assembly process was repeated 30 times at each level of species richness (*SR*), for a total of 240 acoustic communities simulated in each of the four regions. Boxplot hinges represent first and third quartiles.

Figure 3: Species richness – acoustic heterogeneity relationships for both natural and simulated communities of stridulating ensiferan species in Québec. The shaded area encompasses 95% of the simulated acoustic heterogeneity values along the species richness gradient. Ecological interpretation of intercept and slope differences is found in Figure 1.

Figures

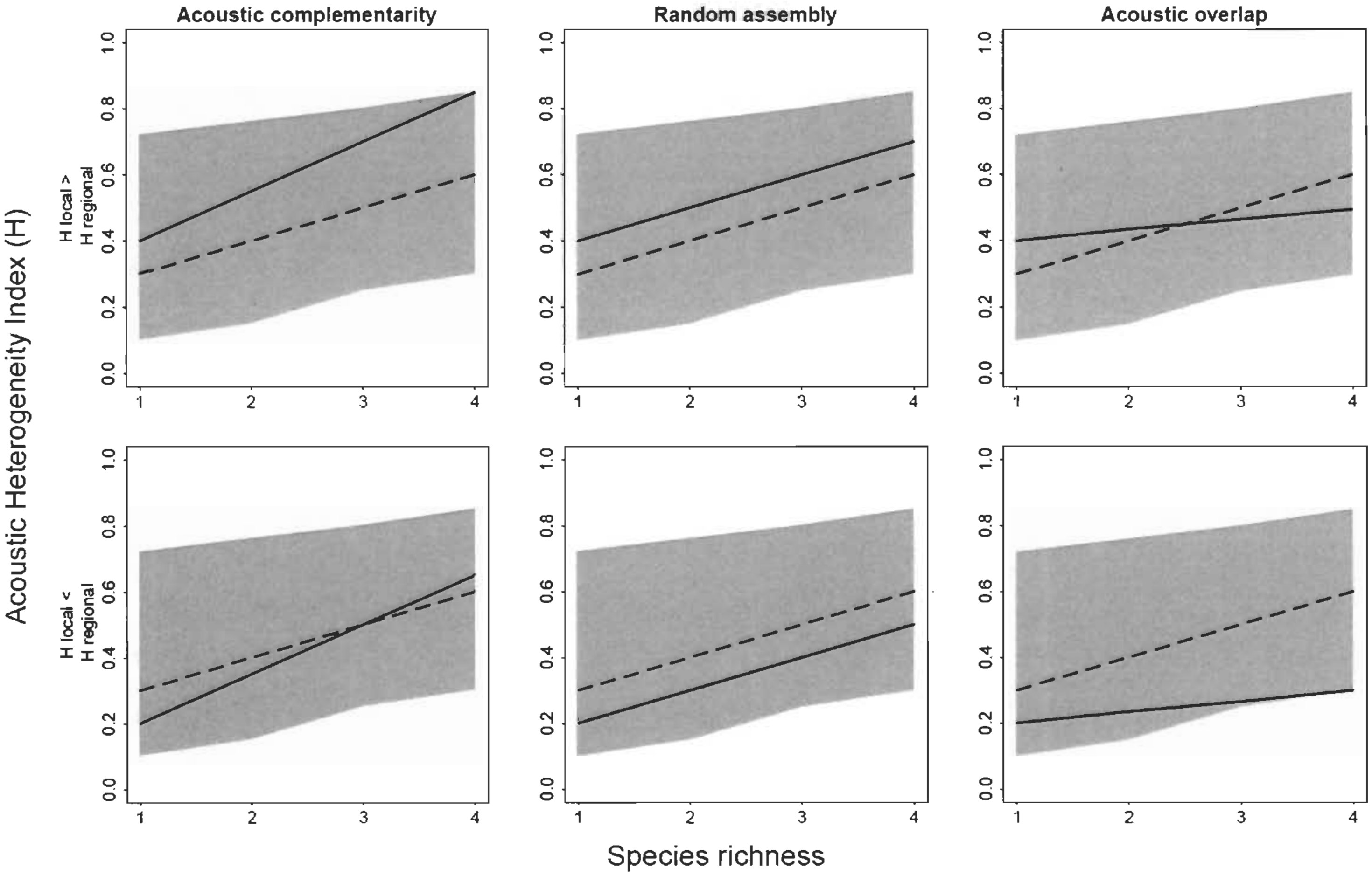


Figure 1.

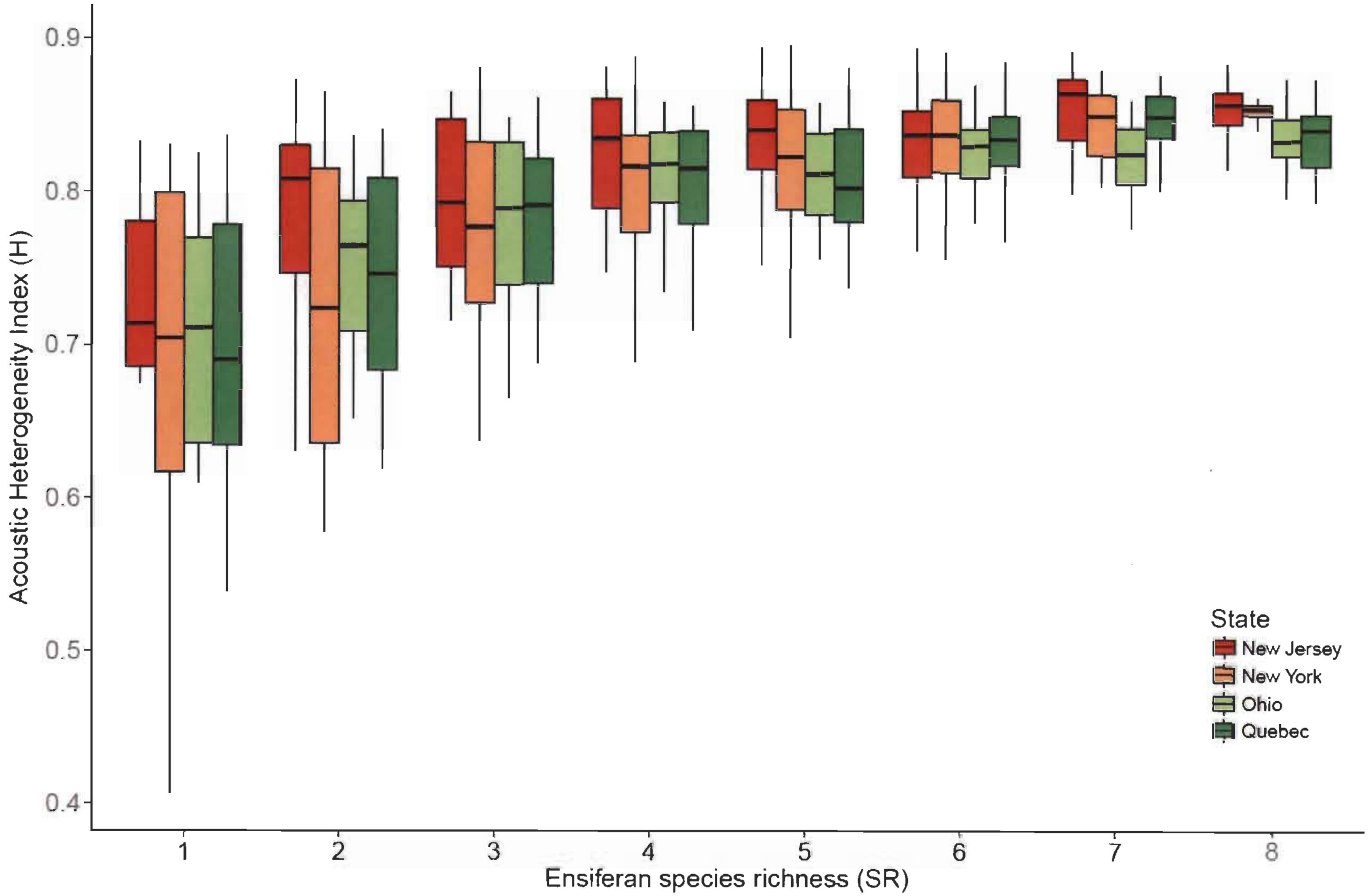
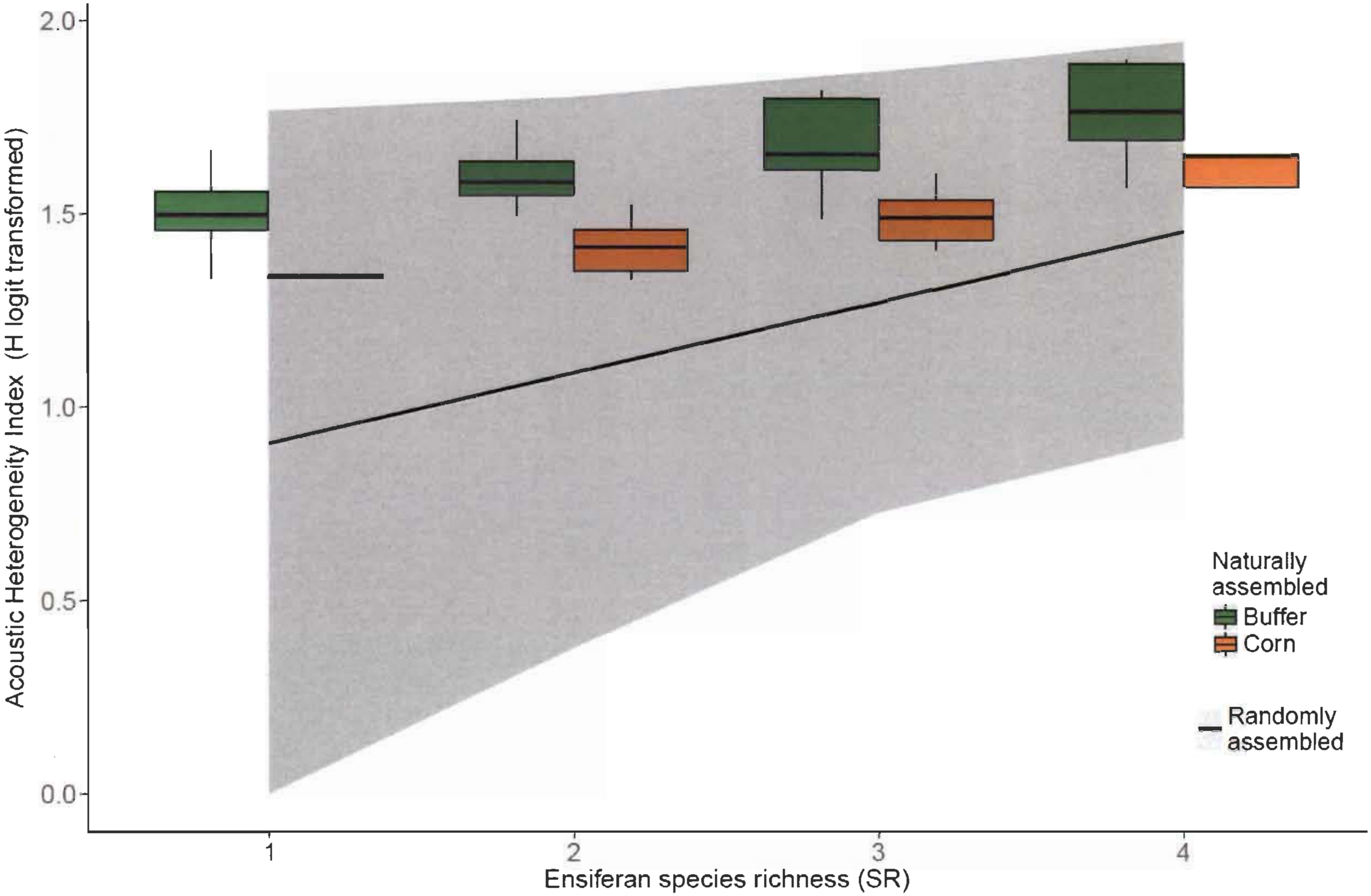

Acoustic Heterogeneity Index (H)
0.9
0.8
0.7
0.6
0.5
0.4
1
2
3
4
5
6
7
8
Ensiferan species richness (SR)
State
New Jersey
New York
Ohio
Quebec

Figure 2.



Acoustic Heterogeneity Index (H logit transformed)
2.0
1.5
1.0
0.5
0.0
1
2
3
4
Ensiferan species richness (SR)
Naturally assembled
Buffer
Corn
Randomly assembled

Figure 3.

Ecological Archives Material

Appendix

Table A1: Public repositories of audio recordings for species and soundscapes from around the world.

Figure A1: Relationship between acoustic heterogeneity (*H*) and mean absolute amplitude (*A*) of ensiferan communities from farmlands of the St-Lawrence River lowlands (Québec, Canada). H-A relationship is expressed at different species richness levels (*SR*).

Figure A2: Species richness-NP index of acoustic heterogeneity relationship for natural communities of stridulating ensiferan species in Québec.

Table A1: Public repositories of audio recordings for species and soundscapes from around the world.

Library name	Coverage	Taxa	File access	Format	Who can contribute
		United States			
Macaulay Library of Natural Sounds (Cornell University)	Worldwide	175,000 recordings of birds, insect, fish, frog, and mammals	Online access to listen	Mono; WAV and .MP3; 44.1 kHz; 16 bit	Everyone
Borror Laboratory of Bioacoustics (BLB)	USA and worldwide	40,000 recordings of birds, mammals, reptilians, amphibians, fish, arachnids and insects	* Free-online access	Mono; MP3; 22 kHz; 16 bit	Everyone
Florida Museum of Natural History Bioacoustic archives	USA, Neotropics	20,500 recordings of birds	* Free-online access to 190 recordings	Mono; WAV; 44.1 kHz; 16 bit	Everyone
Singing Insects of North America	America and north of Mexico	433 recordings of cricket, katydid, and cicada	* Free-online access	Mono; WAV; 44.1 kHz; 16 bit	Everyone
Wisconsin Audio Library (Wisconsin breeding bird atlas)	Wisconsin	191 recordings of birds, reptilians and mammals	* Free-online access	Mono; MP3; 44.1 kHz; 16 bit	–
The California Library of Natural Sounds (CLNS)	California	32 recordings of bird, insect, and amphibians	Online access to listen	–	Everyone
Discovery of Sound in the Sea, Rhode Island	Worldwide	Acoustics in the ocean: whales, fish, invertebrates, other sounds	* Free-online access	Stereo; MP3; 11 kHz; 16 bit	–
Fishbase.org (Fishbase Consortium)	Worldwide	90 recordings of fish	* Free-online access	Mono; MP3; 44.1 kHz; 16 bit	–

Library name	Coverage	Taxa	File access	Format	Who can contribute
Europe					
Xeno-canto (Netherlands)	Worldwide	142,398 recordings of birds	* Free-online access	Mono; MP3; 44.1 kHz; 16 bit	Everyone
British Library (Environment and nature Public collections)	Worldwide	2,156 recordings of birds, mammals, amphibians, reptilians and insects > 1,000 soundscapes	Online access to listen	Stereo; MP3; 44.1 kHz; 16 bit	Everyone
Animal Sound Archive at the Museum für Naturkunde in Berlin	Worldwide	120,000 recordings of birds, mammals, invertebrates, fish, amphibians and reptilians	Online access to listen	Mono; .MP3; 44.1 kHz; 16 bit	Everyone
FonoZoo (Museo Nacional de Ciencias Naturales of Madrid, Spain (CSIC))	Worldwide	43,605 recordings of mammals, birds, reptilians, amphibians and fish	Restricted access, requests to FZ	Mono; .MP3; 44.1 kHz; 16 bit	Everyone
Alosa	Spain	Small archive of birds, mammals, amphibians and landscapes recordings	Online listening (purchase for 1-2 € / file)	Stereo; .MP3; 44.1 kHz; 16bit	–
"Suonie e Canti delgi Uccelli d'Eurapa" Italy	Europe	413 recording of birds	* Free-online access	Mono; .WAV; 22 kHz; 8 bit	–
South America					
"Colección de Sonidos Ambientales" Alexander von Humboldt Institut	Eastern Colombian mountains	20000 recordings of birds, mammals, amphibians, insects, and natural environments	Restricted access, previous CSA contact is required	–	Everyone

Library name	Coverage	Taxa	File access	Format	Who can contribute
"Biblioteca de Sonidos de Aves de México"	Mexico	1076 recordings of birds	* Free-online access	Stereo; .MP3; 44.1 kHz; 16 bit	Everyone
"Fonoteca neotropical Jacques Vieilliard" (FNJV)	Brazil	11000 recordings of birds, mammals, fish, amphibians, reptilians, insects and arachnids.	Restricted access, contact FNJV required	WAV; 48 kHz; 24 bit	Everyone
		Australia			
Australian National Wildlife Collection Sound Archive	Australia	60,000 recordings of birds, mammals, amphibians and invertebrates	* Free-online access to 40 bird species recordings	Stereo; .MP3; 44.1 kHz; 16 bit	Everyone
South-eastern Australian bat call library	South-eastern Australia	Bat calls	* Free-online access (files stored in ANABAT2 format)	–	Everyone

* Data use licence required.

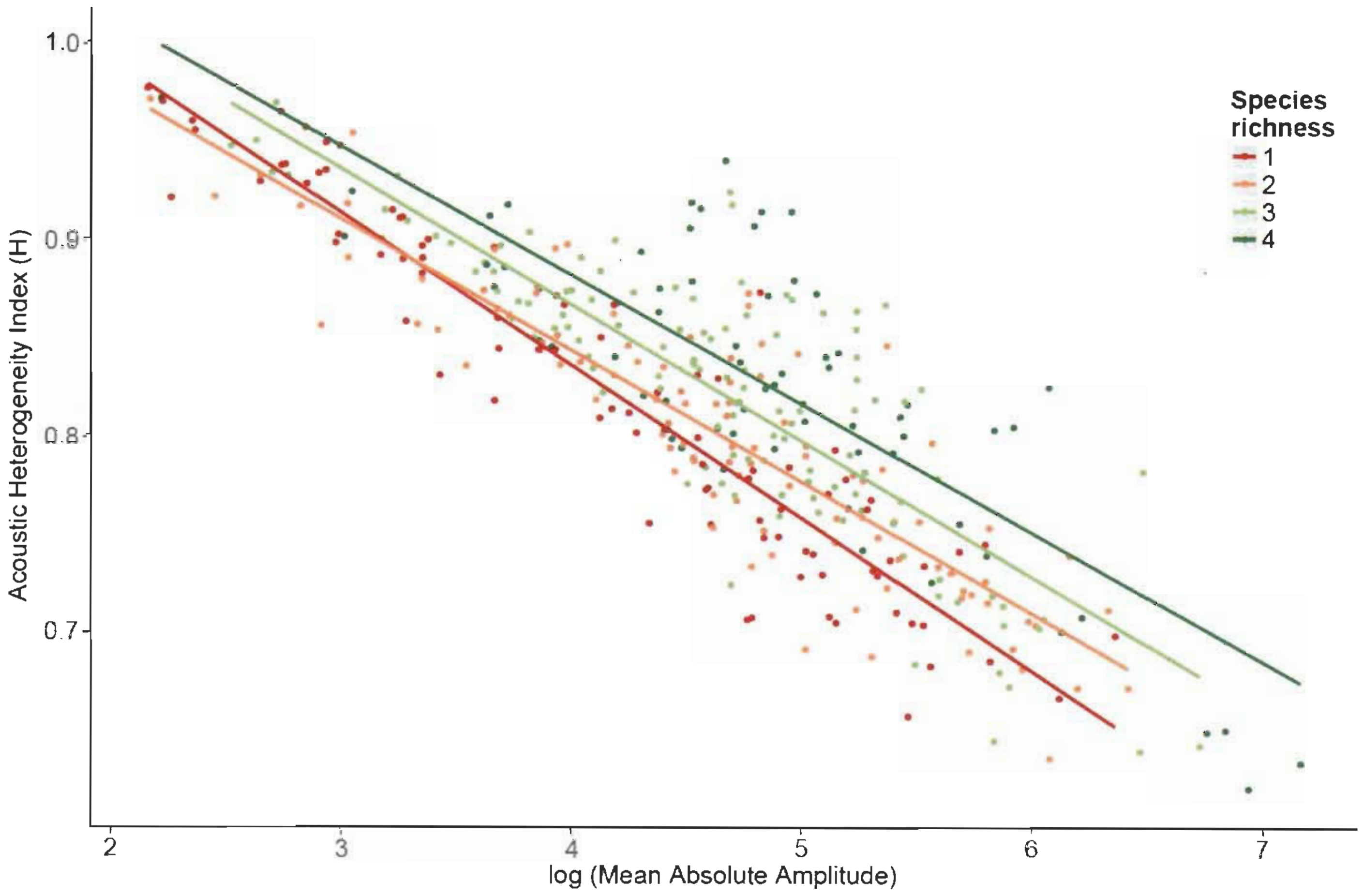

Acoustic Heterogeneity Index (H)
1.0
0.9
0.8
0.7
log (Mean Absolute Amplitude)
2
3
4
5
6
7
Species richness
1
2
3
4

Figure A1.

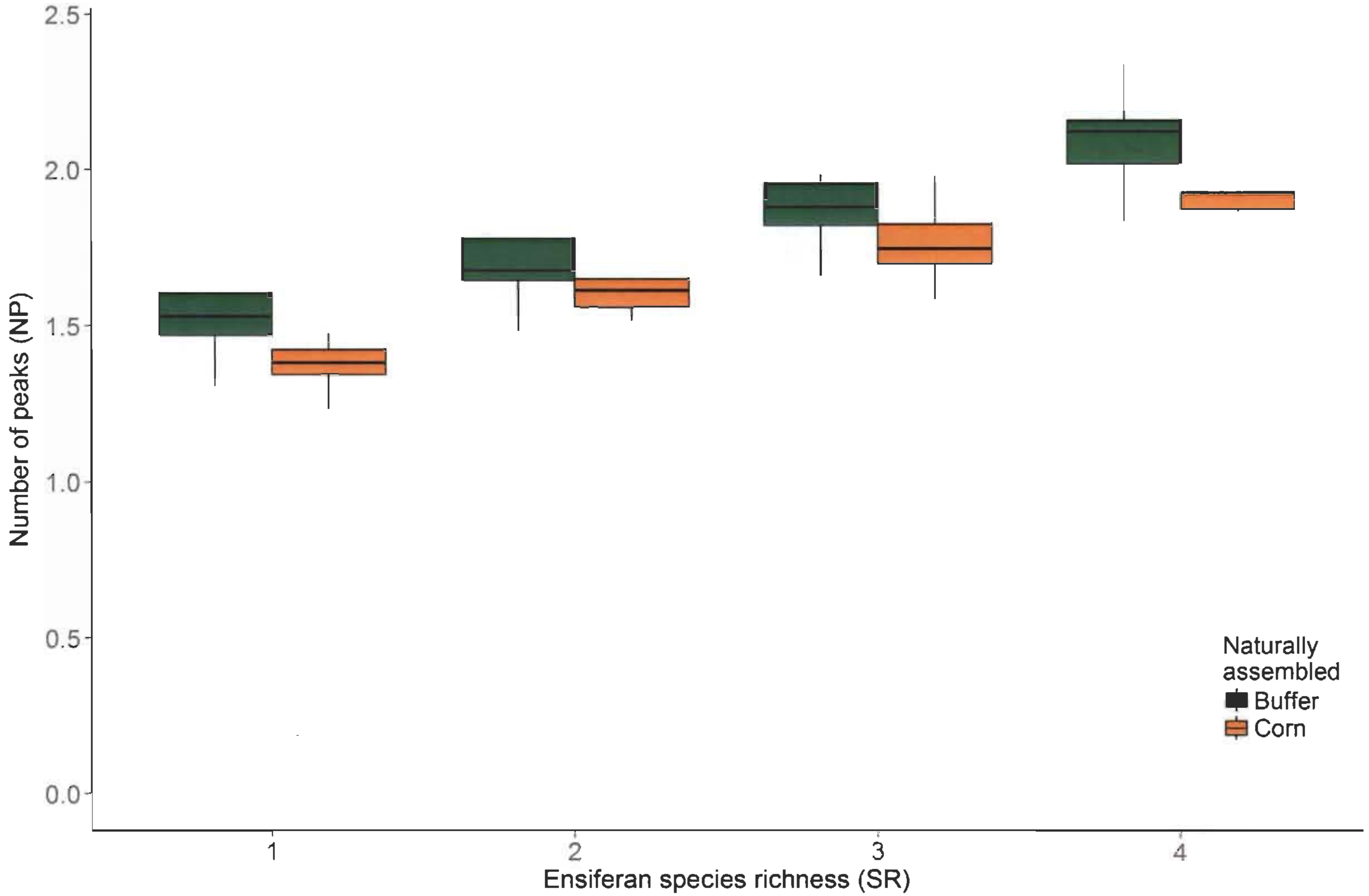

2.5
2.0
1.5
1.0
0.5
0.0
Number of peaks (NP)
1
2
3
4
Ensiferan species richness (SR)
Naturally assembled
Buffer
Corn

Figure A2.

CHAPTER III

USE OF ACOUSTIC REFUGES BY FRESHWATER FISH: A THEORETICAL FRAMEWORK AND EMPIRICAL SUPPORT

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Abstract

Sounds are more easily transmitted underwater than through air and many freshwater fish species can hear them. Recent studies on freshwater fish evidenced that hearing sensitivities can be limited by the level of ambient noise, a phenomenon also known as acoustic masking. The general objective of the present study is to propose and evaluate a theoretical framework explicitly linking fish captures to species hearing sensitivities and ambient noise levels in freshwater ecosystems. The proposed model shows that the feeding activity of fish prey is conditional on the probability of being acoustically detected by their predators. Model simulations and preliminary field results suggest that yellow perch (*Perca flavescens*) may take advantage of the underwater ambient noise to feed more actively at lower predation risk. Yellow perch catch per unit effort were multiplied by a factor of 2.7 in noisy *versus* quiet days, suggesting increased feeding activity in presence of increased ambient noise. Acoustic monitoring programs for freshwater ecosystems require a fundamental knowledge of underwater noise levels, species hearing sensitivities, and features affecting sound propagation. The approach proposed in this paper is seminal in linking the above descriptors in a coherent mathematical framework to understand the effect of underwater sounds on predator-prey interactions. Such a framework is needed to make testable predictions and generalise to other taxa and ecological contexts.

Key words: Acoustic masking, acoustic refuge, ice fishing, northern pike, theoretical framework, underwater ambient noise, yellow perch.

Introduction

Over the last century, sounds produced by human activities have contributed to an increase in the noise level of many terrestrial and aquatic environments, including freshwater ecosystems. Addressing the myth of a silent underwater world, Slabbekoorn *et al.* (2010) identified one of four major research gaps in soundscape ecology as follows: "Does the presence of masking noise affect the ability of fish to find prey (get food) or detect the presence of predators (become food)". Although the majority of freshwater fish species do not vocalize *per se*, they can hear and discriminate sounds (Ladich and Schulz-Mirbach 2016, Lugli 2015). Yet, almost all fish species produce incidental sounds by attacking and manipulating food items. As an example, stridulation sounds are emitted by rubbing the teeth, bones of the skull, jaw apparatus, branchial apparatus, fin rays and vertebrae (Ladich and Bass, 2003, Rice and Lobel, 2003). More generally, feeding sounds originate from a combination of cavitation and stridulation. Interception of such sounds, could be a major advantage to hunting fish, but a disadvantage to the sender (Scholtz and Ladich, 2006).

Earlier attempts to evaluate the impact of ambient noise on predator-prey interactions in freshwater fish have so far yielded contradictory results. An experimental study of captive three-spined sticklebacks (*Gasterosteus aculeatus*) found evidence that the addition of underwater noise increased food-handling errors and decreased foraging efficiency (Purser and Radford, 2011). A field study of three fish species exposed to motorboat noise revealed no behavioural change in the predator (pike; *Esox lucius*), but increased the swimming activity of two prey species, which the authors interpreted as a noise deterrence effect (Jacobsen *et al.* 2014). Most recently, Simpson *et al.,* (2016) showed that ambon damselfish (*Pomacentrus amboinensis*) were more susceptible to predation when exposed to high levels of motorboat noise on experimental coral reef patches. These authors noted that the winners and losers in other predator-prey systems will depend on the species' relative hearing sensitivities, as well as the level of ambient noise.

Previous experiments on freshwater fish showed that hearing is limited by the level of ambient noise, a phenomenon also known as acoustic masking (reviewed in Ladich and

Fay, 2013). Ambient noise is a combination of various sounds from transient sources that are below perceptual recognition, but above detection threshold (Braun 2015). In aquatic systems, ambient noise rises naturally from remote surf, waves, wind and rain, as well as current passing over rough substrates (Amoser and Ladich, 2010). Underwater levels of ambient noise vary considerably among freshwater ecosystems, ranging from approximately 60-80 dB in still water up to 120-140 dB (re 1 μPa) in whitewater (reviewed in Ladich, 2013). In ecosystems subjected to boating activity, underwater ambient noise can be augmented by nearly 40 dB above baseline levels (e.g., Vasconcelos et al., 2007; Picciulin et al., 2010). Under the ice sheet of frozen lakes, the ambient noise is influenced by ice cracking events (124 dB in the 200-300 Hz frequency range), as well as human related activities such as snowmobile use (Mann et al. 2009).

A theoretical framework is required if one is to make predictions on the direction and magnitude of underwater masking noise effects on a predator-prey system. The general objective of the present study is to develop and propose a simple mathematical model explicitly linking fish captures to hearing sensitivities and ambient noise levels in a system where visual detection is limited. More specifically, we studied a three-species system under the ice sheet of a temperate shallow lake, where fish must rely on acoustic cues in absence of light. Our findings suggest that, when cut from their visual cues, some fish species may use the ambient noise as a refuge to hide from predators and forage more actively.

Methods

In this section, we present a mathematical model describing the feeding behavior of a fish prey and how ambient noise levels influence its acoustic detection by a fish predator. Input parameters to the model are the ambient noise level, the predator's hearing threshold, and the feeding sounds of the prey. Acoustic parameters to the model are all expressed in dB units of sound pressure level (SPL; re. 1 μPa) over a narrow frequency band of fish hearing (e.g., 200-400 Hz). Even though many freshwater fish use their inner ear as an "accelerometer" to detect particle velocity rather than pressure differences, most fish audiograms are available in SLP units only. For this reason, the model is based on SPL units, but the generality of predictions is unaffected by this choice.

Theoretical framework

We consider an underwater environment composed of two main acoustic components. First, the ambient noise, which consists of a mixture of background sounds coming from distant sources. Second, incidental feeding sounds, which are emitted by a prey fish attacking, manipulating or crunching food items (i.e. its "resource"). While ambient noise is constant and undefined (De Coensel, Botteldooren and De Muer, 2003; Yang *et al.,* 2015), feeding sounds are punctual and have a more distinctive acoustic signature (Scholz and Ladich, 2006).

The ideal gas model is commonly applied to estimate encounter rates between mobile organisms (Gerristen and Strickler 1977; Olson 1964; Kiltie 1980). The encounter rate (*ER*; i.e. the number of encounters per unit time and area) of a predator with its prey is modeled using the general equation (Hutchinson and Waser, 2007):

$$ER_{pred} = p_{pred} \cdot p_{prey} \cdot d_{pred} \cdot \sqrt{\bar{v}_{pred}{}^2 + \bar{v}_{prey}{}^2}\ , \qquad \text{Eq. 1}$$

where p is the fish density per unit area, d_{pred} the predator's detection distance of its prey, and $\sqrt{\bar{v}_{pred}{}^2 + \bar{v}_{prey}{}^2}$ the relative swimming speed calculated from the mean cruising velocity $\bar{v}$ of both the predator and its prey.

Eq. 1 translates to an attack rate (*AR*; i.e., the number of attacks per unit time and area) if ER_{pred} is multiplied by β_{pred} [0-1], a parameter capturing the probability that the predator will successfully attack its prey if an encounter occurs:

$$AR_{pred} = \beta_{pred} \cdot ER_{pred}\ . \qquad \text{Eq. 2}$$

Following the same line of reasoning, the attack rate of the prey (AR_{prey}) on its preferred food resource is given by:

$$AR_{prey} = \beta_{prey} \cdot p_{prey} \cdot p_{resource} \cdot d_{prey} \cdot \sqrt{\bar{v}_{prey}{}^{2} + \bar{v}_{resource}{}^{2}} \quad \text{Eq. 3}$$

Isolating p_{prey} in the above equations and rearranging, we find:

$$\frac{AR_{prey}}{AR_{pred}} = \frac{\beta_{prey}}{\beta_{pred}} \cdot \frac{d_{prey}}{d_{pred}} \cdot k_1 \cdot k_2 \,, \quad \text{Eq. 4}$$

where k_1 and k_2 are assumed constant and represent the relative density ratio $p_{resource}/p_{pred}$ and mean speed ratio $\sqrt{(\bar{v}_{prey}{}^{2} + \bar{v}_{resource}{}^{2})/(\bar{v}_{pred}{}^{2} + \bar{v}_{prey}{}^{2})}$.

We now consider the case of a predator relying mainly on acoustic cues (i.e., incidental sounds) to hunt. A good example would be fish hunting on preys producing incidental feeding sounds by manipulating and crunching food items in conditions of reduced visibility. In principle, the detection distance of the predator d_{pred} could be reduced if acoustic cues are masked by the ambient noise. Eq. 3 predicts two scenarios for the prey under a reduced d_{pred}. First, the prey may directly benefit from a lower encounter rate with the predator. We call this scenario: foraging normally at reduced predation risk. Second, the prey may increase its attack rate, thus producing more feeding sounds, without increasing its predation risk. We call this scenario: foraging more actively at equal predation risk (Figure 1).

The acoustic detection distance of the predator (d_{pred}) on its prey is determined by the transmission loss (TL) equation, which empirically describes underwater sound attenuation (Urick, 1975; Ingenito, 1978; Richardson *et al.*, 1995; Bass and Clark 2002):

$$TL = \lambda \log_{10} d + \alpha d, \quad \text{Eq. 5}$$

where λ is the attenuation coefficient, α is the absorption coefficient (dB m^{-1}) and d the transmission distance. The coefficient λ is predicted to vary between 10 and 20, whether the sound propagates in a free-field (i.e., spherical model) or in a wave-guide (i.e., cylindrical model), respectively (Richardson *et al.*, 1995; Bass and Clark 2002). Sound attenuation due to absorption (αd) in freshwater is negligible (<0.001%) and this term can be ignored. Rearranging Eq. 5, the maximal distance at which the predator will detect its prey in absence of acoustic masking is given by:

$$d_{pred} = 10^{[FS-HT]/\lambda} \quad . \qquad \text{Eq. 6}$$

In presence of acoustic masking, detection is limited by the ambient noise and Eq. 6 becomes $d_{pred} = 10^{(FS-AN)/\lambda}$ (Figure 2). The prey's feeding sound (*FS*), the predator's hearing threshold (*HT*) and the ambient noise (*AN*) in the above equations are all expressed in dB (re 1 µPa). The multiplicative factor of d_{pred} under acoustic masking is given by the ratio between the maximal distance at which the predator will deterct its prey in absence of acoustic masking and the detection distance in presence of acoustic masking: $\frac{10^{(FS-AN)/\lambda}}{10^{(FS-HT)/\lambda}}$, which simplifies to $1/10^{(AN-HT)/\lambda}$. Inserting this factor in Eq. 4 yields:

$$\frac{AR_{prey}}{AR_{pred}} = \frac{\beta_{prey}}{\beta_{pred}} \cdot \frac{d_{prey}}{d_{pred} \times \frac{1}{10^{(AN-HT)/\lambda}}} \cdot k_1 \cdot k_2 \ ;$$

$$\frac{AR_{prey}}{AR_{pred}} = 10^{(AN-HT)/\lambda} \cdot \frac{\beta_{prey}}{\beta_{pred}} \cdot \frac{d_{prey}}{d_{pred}} \cdot k_1 \cdot k_2 \qquad \text{Eq. 7}$$

Assuming everything else constant, Eq. 7 tells us that for each additional dB of *AN* above the predator's *HT*, the ratio AR_{prey} / AR_{pred} increases exponentially by a factor of: $10^{(AN-HT)/\lambda}$ (Figure 1). We assumed that the detection distance of the prey d_{prey} was unaffected by *AN* because its food resource does not itself produce sounds. The model can be modified to account for an ambush predator ($\bar{v}_{pred} = 0$), a sessile prey

($\bar{v}_{prey} = 0$), other types of incidental sounds produced by the prey, as well as behavioural adaptations of the predator (e.g., increasing β_{pred} with increasing *AN*).

Case study

The objective of this section is to provide empirical support to the effect of the ambient noise on predator-prey interactions. For this purpose, we considered a predator-prey system where northern pike (*Esox lucius*) feeds preferentially on the yellow perch (*Perca flavescens*), which in turn feeds preferentially on baitfish minnows, in an environment that is uniformly open (i.e., without refuges), dark and at constant temperature. We analysed ice-fishing data from a study conducted in 2014 and 2015 on the south shore of Lake St. Pierre (46°08′21″N 72°51′37″W). Lake St. Pierre is a large fluvial lake of the St. Lawrence River (Québec, Canada) that is approximately 35 km long and 15 km wide, with a mean depth of 3.1 m at mean discharge. In winter, most of the lake is covered by ice but the navigation channel is freed by icebreakers for commercial shipping. Water temperature is slightly below the freezing point and light intensity under the ice is close to nil (-0.23°C and 0 lux; I. Roca pers. Obs.). Lake St. Pierre's abundant fish stocks and intense activity (e.g., commercial transport, recreational fishing) makes it an ideal system for studying the impact of *AN* on predator-prey interactions.

Ice-fishing is a popular recreational activity on the lake. Fish are captured using tip-up units with lines hanging through holes drilled in the ice. Beside northern pike and yellow perch, other species frequently fished during winter include *Sander canadensis* (sauger), *Sander vitreus* (walleye) and *Lota lota* (burbot). Yellow perch is one of pike's most common prey (e.g., Seaburg and Moyle 1964, Wolfert and Miller 1978) and feeds preferentially on smaller fish (cyprinids) in absence of other food resources (Moffet and Hunt 1945, Diehl 1992). While the perch is a free-swimming (active) forager, the pike is a sit-and-wait (ambush) predator (Nursall 1973, Eklöv 1992).

Experimental ice-fishing sites were located at the confluence of two major tributaries. The area is operated by an outfitter who deploys approximately 150 fishing cabins on the ice each year. Over weekend days, the area is crowded with people walking around, drilling holes, setting-up lines and driving motorized vehicles. In contrast, the area is much quieter during work days (Monday-Friday). In 2014, we sampled six sites over four weekend days (January 18-19 and 25-26). In 2015, we sampled two of those six sites on ten different occasions (four weekend days and six work days) between January 10th and February 19th.

Each sampling site consisted of two parallel rows of four holes drilled though the ice at an interval of two meters, for a total of eight fishing holes. We mounted one tip-up fishing line over each hole and baited it with commercially available minnows. We fished each site for five hours per day between 07:00 and 12:00h. We released all caught fish after identification at the species level. We used catch per unit effort (i.e., number fish caught per species, site and day) as a proxy for attack rates. We categorized each fishing day into "weekend" or "work" days to provide a qualitative scale of ambient noise levels. To investigate the relation between fish captures and ambient noise levels, we fitted two generalized linear mixed-effects models, one for pike captures and one for perch captures. Pike or perch captures were included as dependent variables, human activity (weekend/work) as the independent categorical variable, and site and year as random effects. We used the function **glmer** from the package {lme4} (Bates et al., 2015) within the R platform (R Core Team, 2015, version 3.1.3), with a Poisson error distribution and a log link.

In January 2017, we verified that the level of underwater *AN* at the experimental area was increased during weekend in comparison to work days. We recorded sounds under the ice by connecting a digital recorder (H2n Handy Recorder, Zoom, Tokyo, Japan) to a H1 hydrophone powered by a PA4 amplifier (Aquarian scientific, Anacortes, USA). Over two weekend days, we took 10-minute audio clips (16-bit WAV format at a sampling rate of 44.1 kHz) at 10 randomly chosen positions within the 1.5-2 m isobaths. Recording positions were at least 100 m away from each other. We repeated the above protocol over two work days. We applied a band filter to each audio clip to extract the information in the 200-400 Hz frequency range. We expressed differences between weekend and work days on a relative decibel scale (RDS_{dB}) as follows: $RDS_{dB} = 20\log_{10}\left[\frac{weekend}{working}\right]^2$, where *weekend* and *work* stands for the root-mean-square digital amplitudes averaged across audio clips recorded over either weekend or work days. We used a bootstrap approach to construct the 5-95% confidence interval (CI) around $\mathrm{RDS}_{\mathrm{dB}}$.

Results

The level of human activity on the ice sheet of Lake St. Pierre was an important predictor of yellow perch captures in our statistical model. Perch captures increased during weekends compared to work days ($n = 26$, $z = -3.203$, $p = 0.001$). Northern pike captures did not differ significantly between the two categories (Figure 3). The measured *AN* levels on weekend days were, on average (5-95% CI), 16 dB (13-20), above the levels recorded on work days, supporting our premise that human activities increased the acoustic background under the ice.

Yellow perch captures per unit effort (± 1 SE) averaged 4.1 catches (± 0.66) during weekend days and 1.5 catches (± 0.45) during work days. Thus, the multiplicative factor by which the ratio AR_{perch} / AR_{pike} increased in the presence of acoustic masking was 2.7. If perch used the acoustic refuge to forage more actively at equal predation risk, while assuming an attenuation coefficient $\lambda = 20$, Eq. 7 predicts that underwater *AN* during weekends was 10 dB above Pike's *HT*.

Discussion

Our modelling framework proposes that, when cut from their visual cues, some fish species use the ambient noise to hide from predators and forage more actively. We empirically showed that yellow perch takes advantage of the augmented ambient noise to forage more actively in an environment with low visibility, where food is scarce. Whether fish in other ecological contexts will maximize the probability of detecting food patches, or minimize the predation risk, will depend on many factors, including resource availability, predator abundances and proximity of physical refuges. The mathematical model we are proposing is general and applicable to other freshwater and terrestrial ecosystems.

Previous studies have considered the underwater noise as a potential source of stress to fish (Purser and Radford 2011, Simpson et al. 2015, Simpson et al. 2016, Sabet Van Dooren and Slabbekoorn 2016). Indeed, activities such as pile driving and seismic gunning produce underwater sounds that can cause fish to become temporarily deaf (Pooper, 2003; 2009). Alternatively, opportunistic species may use lower levels of ambient noise to move or feed unnoticed. While anthropic activities contribute to rise underwater ambient noise levels in natural environments, the effect of this ambient noise on fish behaviour may be different to that of pile driving or explosive sounds. In lake Gosmer (Denmark, Europe), Jacobsen et al. (2014) observed that the European perch increased its swimming speed when the noise from a sailing 4hp engine boat was introuduce in the system; yet it did not affect northern pike. Our results suggest that, rather than escaping motorboat sounds, perch may use the augmented underwater ambient noise to hide from predators.

We can draw some parallels between acoustic and physical masking principles. Dense vegetation habitats provide an advantage to prey fish over their predators (Lima and Dill, 1990; East and Magnan, 1991; Lima, 1998; Lopes et al. 2015). In the presence of physical refuges, prey fish face a behavioural choice: i) decreasing their predation risk by hiding or ii) swimming more actively to access patchy resources. Since fish have to continuously weigh predation risk against resource access, a behavioural trade-off ensues (Dupuch et al. 2009a, b; Figueiredo et al. 2015). Whenever prey fish detect the presence of acoustic refuges, our results suggest the existence of a similar behavioural trade-off. The effect of increased ambient noise on predator-prey interactions could be particularly important in habitats with dense vegetation or other vertical structures (e.g., coral reefs). Acoustic masking is also likely in quiet environments where sounds may propagate over long distances, as well as in turbid waters where visibility is limited.

We can find both anecdotal (e.g., sound producing fishing lures) and scientific evidence that underwater sounds have the potential to attract, rather than deter fish. For example, marine juvenile fish were more abundant and species-rich in experimental areas broadcasting reef habitat sounds rather than no sounds (Radford et al. 2011). Hence, in the context of our study, we cannot rule out the possibility that, independently of predation risk, drilling and motor sounds over the ice attracted yellow perch. However, unless northern pike is a less curious species than yellow perch, the number of pike captures should also have increased under augmented ambient noise, especially if prey are abundant. The fact that we did not detect this trend for pike supports an acoustic masking effect in favor of the perch. Semi-experimental studies using underwater noise playback to control noise levels are needed to further test the hypothesis.

Other mechanisms could explain the absence of a sound deterrence effect on the foraging behaviour of yellow perch. For instance, perch fish could increase their foraging activity because they have "learned" that their encounter rate with minnows increases under augmented ambient noise levels. Indeed, the vast majority of minnow fish belong to the Cyprinidae family, which is a group of fish presenting a higher sensitivity to underwater sounds than Percidae (Ladich and Fay 2013). Assuming that minnows would initiate sound deterrence behaviours at lower noise levels than yellow perch (e.g. Jacobsen et al. 2014), then drilling and motor sounds over the ice could increase their swimming speed (e.g., startle responses). In mathematical terms, this would translate into a higher swimming speed for both the perch and its resource (the minnows), therefore increasing the encounter rate in Eq. 3. Considering that minnows were in fixed position in our experimental setup, it is also plausible that they agitated more intensely on noisy days and that it stimulated perch attack rates. Alternatively, yellow perch may expect to encounter more distressed minnow in high ambient noise level conditions and increase its swimming activity to favor encounters. We cannot determine at this point if yellow perch uses the increased ambien noise to hide from predators, as an acoustic cue to go hunting, or both. However, our theretical model and preliminary field results point towards circumstances where some fish species may take advantage of the variation in sound levels.

In the presence of increased underwater noise levels, winners and losers will depend upon species hearing sensitivities and behavioural adaptations. Fish hearing abilities are typically measured using audiograms obtained in closed water tanks and available for a limited number of species (Ladich and Fay 2013). Yet, most fish audiograms are unable to disentangle sensitivity to sound pressure from sensitivity to particle motion (Popper and Fay 2011). Yellow perch and northern pike, the two species considered in our case study, are considered "hearing generalists" on the basis of their audiograms (Ladich and Fay 2013) and because they lack specialised structures such as Weberian ossicles or extended swimbladders (Braun and Grande 2008). However, fish species without hearing adaptations, including many perciforms, respond to sounds emitted at rather large distances (Wahlberg and Westerberg 2005, Dale et al. 2015, Radford et al. 2011). More research will be necessary before we resolve this paradox and understand how hearing generalists perceive sounds far from the sound source.

Our theoretical framework translates information on species hearing sensitivities and ambient noise levels into catch per unit effort. Under the acoustic refuge hypothesis, our preliminary findings suggest that the average level of ambient noise under the ice during the weekends should be 10 dB above the hearing threshold of the predator. For evaluating model predictions, we considered a simplified system where the predator is in a fixed position (i.e., ambush) and depends on acoustic cues to hunt. We assumed that no other factors, such as temperature, resource distribution, or the presence of physical refuges, would affect the swimming activity and foraging behaviour of yellow perch. While these assumptions are defendable in the context of our study, they must be carefully evaluated in other ecological contexts.

Sounds are more easily transmitted underwater than in air, and most freshwater fish species can hear them. Our work is seminal in proposing a mathematical framework that simulates the effects of masking noise on a predator-prey system. In contrast with the recent literature, we herein explored the possibility that moderate and sustained levels of noise may allow prey (or predators) to take advantage of the acoustic mask to feed or move unnoticed. How fish perceive their acoustic surrounding and how underwater noise levels affect predator-prey interactions will be important questions to consider in the management of freshwater ecosystems.

Acknowledgments

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Tables

Table 1. Northern pike and yellow perch relative abundances under the ice of Lake St. Pierre (Québec, Canada). Total captures and catch per unit effort (day^{-1} site^{-1}) in 2014 and 2015.

Species	**2014**		**2015**	
	Captures	**Catch per day^{-1}site^{1}**	**Captures**	**Catch per day^{-1}site^{1}**
Northern pike	2	0.33	9	0.45
Yellow perch	27	4.50	40	2.00
Total:	**29**	**4.83**	**49**	**2.45**

Figures legends

Figure 1. Representation of the behavioural trade-off faced by prey fish exposed to increased levels of underwater ambient noise in a simplified predator-prey system. Theory predicts two limiting behaviours for the prey in presence of acoustic masking: i) foraging more actively at equal predation risk (yellow line), ii) foraging normally at decreased predation risk (blue line). In the first case, the probability of prey detection by the predator does not increase (multiplicative factor = 1). In the latter case, the probability of detecting the prey is decreased by a multiplicative factor that depends upon the predator's hearing thresholds (*HT*) and ambient noise (*AN*) levels (see text). The grey area between the two limiting behaviours represents the range of behavioural trade-offs that can be realized under acoustic masking.

Figure 2. Ambient noise effect on predator's detection distance. When ambient noise level is below predator's hearing threshold, the predator can locate the prey, at a particular distance, by the sound produced while the prey handles its resource. However, when ambient noise level is above the predator's hearing threshold, surrounding sounds may be masked and the predator detection distance may decrease. In this condition and at the same initial distance, the prey may handle its resource without being detected by the predator.

Figure 3. Yellow perch and northern pike mean captures per day and site during noisy and quiet days in Lake St. Pierre (Québec, Canada). The "noisy" category represents weekend days when the ice fishing village was very active (many fishermen and motorized vehicles) and is used as a proxy for high ambient noise levels. The "quiet" category represents work days when the fishing village was calm and is used as a proxy for low ambient noise levels. Bars and whiskers represent mean captures per unit effort and standard errors, respectively. Samples sizes are reported in the parentheses.

Figures

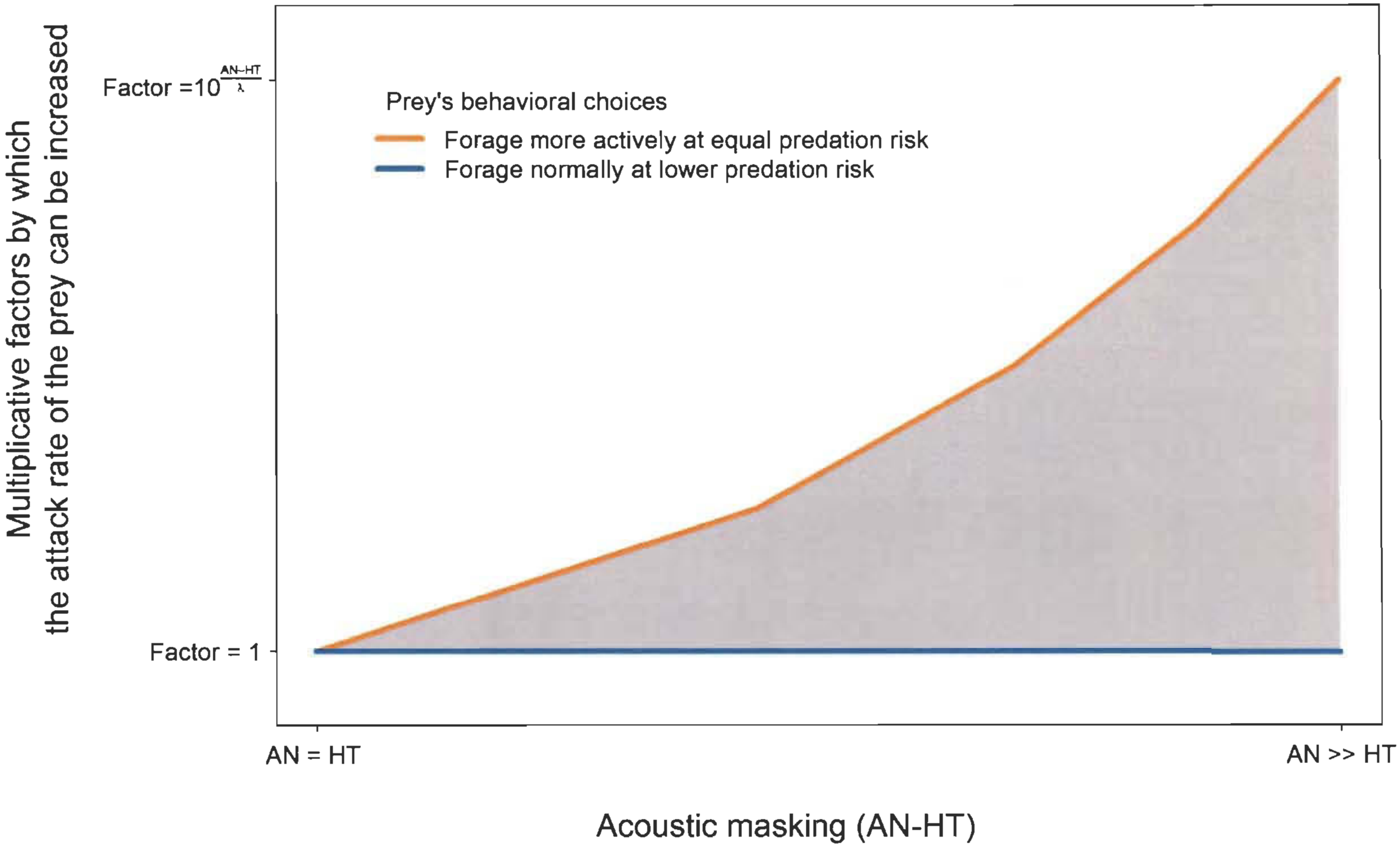

Figure 1.

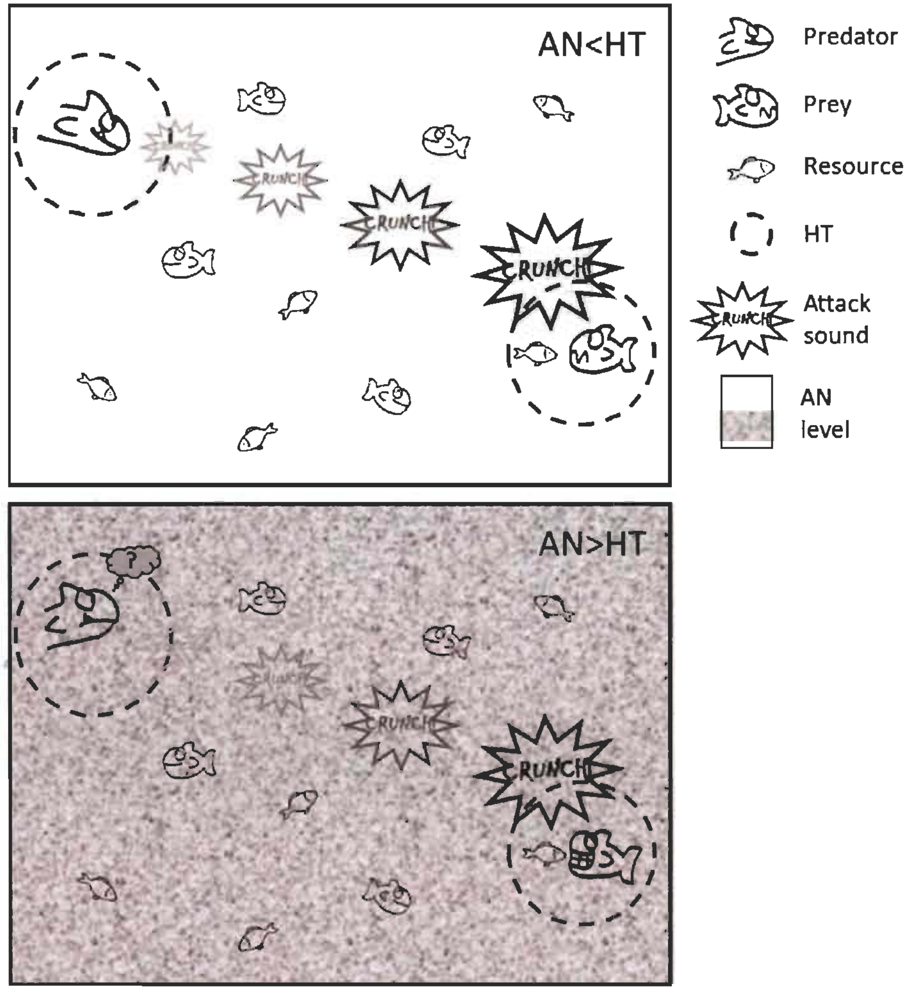
AN<HT
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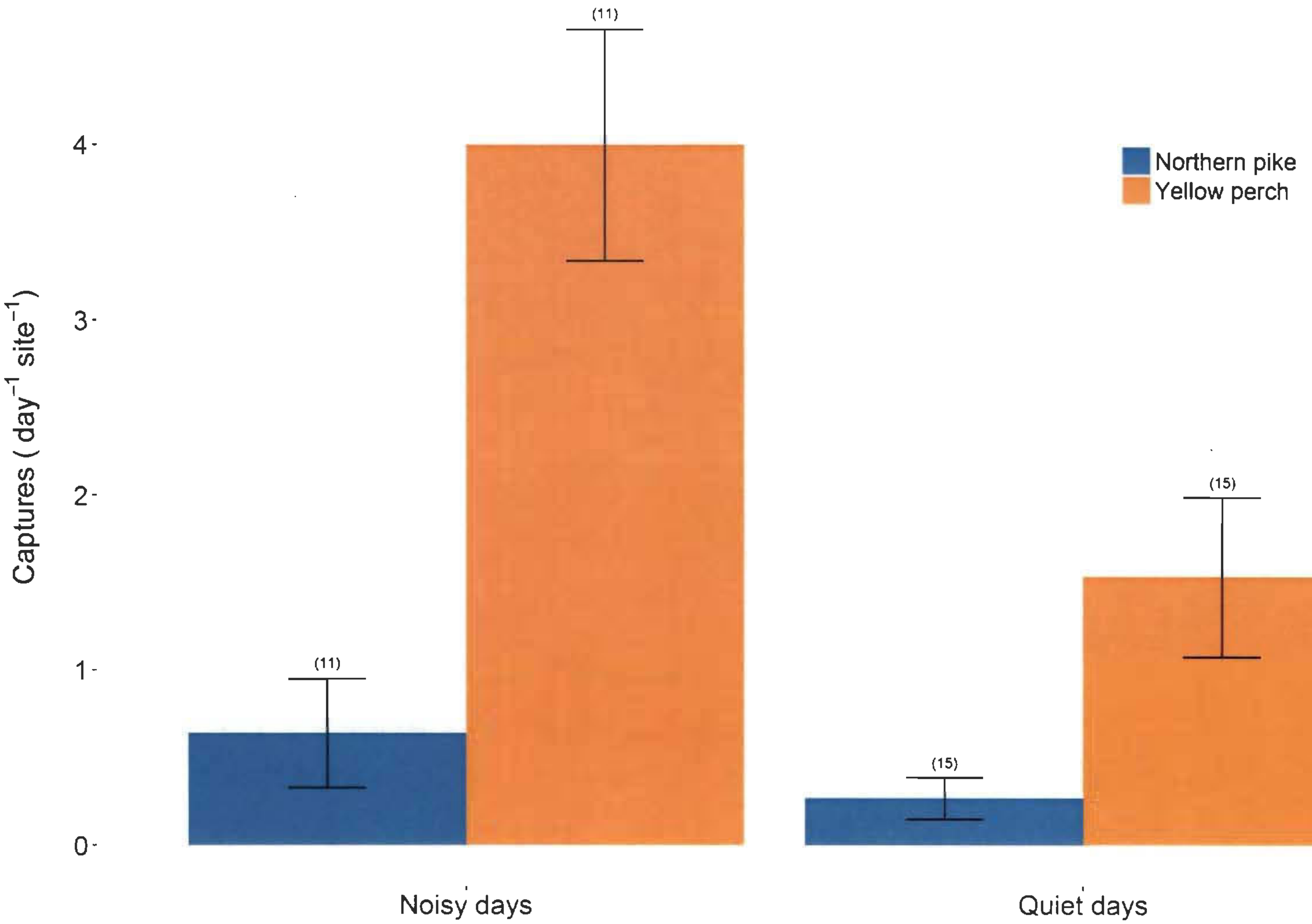
Figure 2.


Captures (day^{-1} site^{-1})
4
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Noisy days
Quiet days
🟦 Northern pike
🟧 Yellow perch

Figure 3.

GENERAL DISCUSSION, PERSPECTIVES AND CONCLUSION

Synthesis and scientific contributions of the thesis

This dissertation represents the synthesis of our work and research contribution to the field of soundscape ecology. Our general objectives were to assess two of the several themes where research is scarce in soundscape ecology. These two themes are also closely related; they are 1) the development of theoretical bases and standard measurements to identify and quantify processes within the soundscape as well as the soundscape's interactions with natural or human systems, and 2) the assessment of interactions between the soundscape and animal community structure and dynamics. Specifically, we evaluated the use of acoustic metrics to assess acoustic diversity from recordings of ensiferan communities in temperate ecosystems and to differentiate between aquatic and terrestrial soundscape contexts. We also developed two theoretical frameworks that allowed us to assess interactions between the soundscape and community assemblage patterns, and the effects of underwater ambient noise on predator-prey interactions.

In chapter I, we proposed the use of FLAC (Free Lossless Audio Codec) sound file compression size as a user-friendly tool to estimate the acoustic heterogeneity of a sound signal based on the hypothesis that acoustically heterogeneous digital audio files are less efficiently compressed than files showing more homogeneous acoustic patterns. We also assessed the power of acoustic metrics to discriminate between different aquatic and terrestrial soundscape contexts compared to the discriminating power of the complete (non-degraded) information in the signal power spectrum. Both the acoustic metrics and the frequency spectrum did well in discriminating soundscape contexts. While the frequency spectrum achieved the highest correct classification rate (80%), the acoustic metrics also performed well; we found that the combination of four acoustic metrics allowed better discrimination (60% correct reclassification) than the best single metric (*H*; 17%).

In chapter II, we first evaluated the potential to use the Acoustic Heterogeneity Index (H) to estimate the number of species in recordings of natural ensiferan communities. We then compared the acoustic heterogeneity of naturally assembled ensiferan communities to those of randomly assembled simulated communities. To do this, we used a combination of simulation models and field surveys (carried out in farmlands from the St. Lawrence River lowlands in Quebec). We compared the slope of the acoustic-heterogeneity-species-richness relationship of natural and randomly assembled communities.

Our findings revealed that acoustic heterogeneity-species richness relationship slope of ensiferan communities in temperate agroecosystems did not differ from that of randomly assembled communities once the pooled species intercept differences (i.e., H local vs. H regional) were taken into account. Given these results, we propose that competition for the acoustic resource within ensiferan communities may be weak, and that it could be explained because species have already evolved markedly different communication patterns and adaptations that currently prevent acoustic interference.

In chapter III, we assessed the effect of underwater soundscape on fish predator-prey interactions. First, we proposed a simple mathematical framework explicitly linking fish captures to hearing sensitivities and ambient noise (AN) levels in a system where visual detection is limited. Second, we studied a three-species system (predator-prey-resource) under the ice sheet of a temperate shallow lake, where fish are forced to rely on acoustic cues in the absence of light. Our findings suggest that, when cut off from their visual cues, some fish species may take advantage of the ambient noise to hide from predators and forage more actively. Furthermore, our empirical results show that yellow perch (*Perca flavescens*) may forage more actively when ambient noise levels are high (more than twice as many individuals were captured on average at higher AN levels vs lower AN levels), when their foraging activity is masked to potential predators such as pike (*Esox lucius*). However, winners or losers in predator-prey interactions will depend on the species' hearing capacities, noise levels, and environmental conditions.

Research perspectives

Theoretical frameworks and soundscape measurements

Theoretical frameworks will support research questions and allow the formulation of testable predictions that could be easily generalized to different taxa and ecological contexts. They could even provide tools to link fundamental and applied sciences. Our work in chapters two and three are two examples of how a formalized theoretical framework could enhance research in soundscape ecology. In chapter two – through the comparison of null and empirical models– we provided a novel approach for understanding community assembly rules in animal groups that rely on acoustic communication. We were able to draw conclusions about the inter-specific competition for the acoustic resource and discuss its evolutionary implications. In chapter three, our mathematical framework proposes a new perspective in which underwater ambient noise has an impact on fish predator-prey interactions, and ambient noise may benefit the prey depending on the species' hearing abilities and ambient noise levels. Both frameworks could be extrapolated to other systems with different species and environmental conditions.

Working with soundscape measurements has the particular advantage that a great deal of acoustic data can be collected in a relatively short period of time. The equipment used to collect acoustic data can be easily managed by non-expert staff, and many sound files can be obtained from continuous and simultaneous recordings at different locations. These advantages lead to large databases that are often freely and publically available. In the appendix associated with chapter II, we assembled a list of several acoustic libraries hosting thousands of digital audio recordings of animals (birds, mammals, amphibians, reptiles, fishes, and insects) and soundscapes from around the world. Making use of this great amount of acoustic data stored in public libraries within the context of theoretical frameworks could shed light on many questions within soundscape ecology that need to be addressed from a macroscale perspective (Brown 1995). For instance, the disentanglement of general processes and patterns characterizing the interaction between soundscape and animal community structure and dynamics at a global scale (e.g., broad regional and continental scales, long temporal scales) from those determined by local or short-term biotic or environmental conditions (e.g., Towsey et al. 2014a).

Another advantage to working with soundscape measurements is that they allow the study of areas without easy access, such as the forest canopy (Riede 1997), marine and freshwater habitats (Luczkovich et al. 2008), and environments with little or no light (Meyer et al. 2011; Obrist et al. 2004). This non-invasive method also allows the investigation of sensitive zones, such as nature reserves, with minimum impact.

Acoustic metrics produce values that provide summary and intuitive ecological information about the soundscape. Initially, acoustic metrics were conceived as a proxy for biodiversity. One of the first and most popular standard metrics is the acoustic entropy index (*H*; Sueur et al. 2008). It was developed to extract a global heterogeneity measure of the acoustic output of any vocal community. Over the last decade, many other acoustic metrics have been proposed (see Sueur et al. 2014), and they have generally proven to be useful for the rapid development of biodiversity assessments in birds, anurans, and orthopteran communities (Sueur et al. 2008; Pieretti et al. 2011; Depraeterre et al. 2012). Nevertheless, there are also some limits to the use of these metrics. For example, all acoustic metrics have been shown to be sensitive to species identity in addition to species richness, and thus are deficient as perfect proxies of species diversity (Gasc et al. 2015). Some metrics are sensitive to anthropic noise. This fact may cause overestimation of the acoustic diversity in acoustic communities with poor levels of species richness (Depraeterre et al. 2012; Gasc et al. 2015). Some acoustic metrics saturate rapidly with moderate to high levels of species richness, as we have seen in chapter II (e.g., Sueur et al. 2008). Others consider fixed anthropic or biotic frequency bands, where the frequency range of elements in a natural soundscape may vary from one location to the other (Qi et al. 2008; Kasten et al. 2012). In fact, there may not be a single acoustic metric that alone could be considered an absolute reliable proxy for biodiversity. Nevertheless, a combination of several acoustic metrics could be an interesting solution. The combination of particular metrics has been shown to be quite accurate for determining species richness and even for identifying species from acoustic recordings of a natural bird community (Towsey et al. 2014b).

Acoustic metrics could become useful in compiling a complete ecosystem portrait, especially when they are correlated with other indicators; for instance, LIDAR-derived metrics of vertical canopy. Hot spots for vocal species identified through acoustic metrics were found to correlate with patches of forest having large gaps in the upper canopy and dense foliage in the lower canopy (Pekin et al. 2012) providing valuable information about the ecosystem structure and functioning. In our work, we showed that the combination of several acoustic metrics is quite good at discriminating between soundscape contexts in several aquatic and terrestrial ecosystems. Further studies using metric combinations could lead to the systematic and efficient identification of different soundscape types, for instance, those of particular interest for conservation (e.g., Dumyahn and Pijanowski 2011). These metrics could also be used to evaluate the relationship between soundscape contexts and ecosystem productivity, functionality for wildlife requirements, and/or availability as an acoustic resource for vocal or stridulating species. Research is needed to evaluate the potential for sound recordings to eventually shape management decisions by highlighting especially rich habitats or helping explain which features of the landscape support particular animal communities.

Soundscape as an acoustic resource

The soundscape has been shown to provide fundamental information to listening species about the surrounding environment, for instance, information about cohabiting con- and hetero-specifics, potential dangers (e.g., Magrath et al. 2015), habitat breeding suitability (e.g., Pupin et al. 2007), and/or acoustic resource availability (e.g., Schmidt and Balakrishnan 2014). Species seek this information to reduce uncertainty and thus enable adaptive behavioural decisions (Wagner and Danchin 2010). Since the soundscape captures the heterogeneity among habitat types and reflects the spatial and temporal variability of the acoustic resource, the study of soundscapes and their interaction with natural systems may offer new insights on distribution, fitness, and evolution in animal species that use acoustic signals to communicate (Clobert et al. 2009; Maan and Seehausen 2011).

The theoretical framework that we developed in chapter II allowed us to draw interesting conclusions about the role of competition for acoustic space on assemblage patterns of local ensiferan communities. Through our work, we have identified several open and pertinent research questions as well as promising tools. We suggested two different hypotheses to explain our results concerning the observed randomness in assemblage patterns of natural local communities. Below, we provide a short summary of both hypotheses and propose some experiments that could be developed to assess the research perspectives they open up.

Hypothesis one: we proposed that competition for the acoustic space does not currently constitute a strong selective force and that it does not structure the community composition in present-day ensiferan communities in temperate ecosystems. Instead, diverse factors, such as competition for other resources (e.g., food, shelter), predation, or species tolerance to environmental changes, may constitute a stronger selective force at local scales. This hypothesis could be tested further using our theoretical framework. It could be applied to ensiferan communities across different ecosystems within a large regional or continental range. Results showing the same random trend in local communities when compared with their respective random regional model over the whole latitudinal range would support the idea that competition for acoustic space in ensiferan communities is weak at the local scale. Nevertheless, it may reinforce the idea that this competition could have been a strong selective force shaping local and regional populations at one time, such as that any present-day combination of species from the regional pool could cohabit without any mayor risk of interference.

An interesting question related to this reflection would be whether competition for the acoustic resource has or has ever had the same effect in shaping local communities in other animal groups that use sound to communicate. Birds, anurans, and fish have been shown to partition their acoustic space when assembled in vocal communities (e.g., Sueur et al. 2008; Villanueva-Rivera 2014; Ruppé 2015). What is the shape of the acoustic-heterogeneity-species-richness curve in local communities of these animal groups compared to random models? Local bird or anuran communities showing random assemblage patterns – that is, similar to simulated communities extracted from regional pools – would support that the competition for the acoustic resource is weak nowadays. It does not rule out though that this competition might have been a strong selective force in the past. It could have had an effect in shaping the regional pool of stridulating species and other vocal animal groups so that any random combination of present-day species from the regional pool, inside the same animal group, could be assembled in a local community without a major interference risk. On the other hand, results showing a wide segregation of acoustic patterns in the acoustic signal of local communities would indicate the presence of present-day competition for the acoustic space in some animal groups, and thus that the acoustic resource does not influence all vocal or stridulating animal groups in the same way. A feature that is definitely different between vocal and stridulating groups is vocal plasticity. Vocal plasticity allows species to overspread the acoustic patterns of their calls in competition for the acoustic space (Slabbekoorn 2013; Cunnington and Fahrig 2010). Therefore, if present-day competition is found to be occurring, its importance as a selective force should still be evaluated in relation to the species' plastic capacities.

Hypothesis two: the randomness observed in assemblage patterns of local ensiferan communities could be explained as an effect of altered habitat conditions. Assuming that competition for acoustic space is a present-day selective force at local scales, a prediction that could follow from the Acoustic Niche Hypothesis (ANH) is that less-disturbed habitats with unaltered species assemblages will exhibit lower overlap between the signals of the vocal community than more disturbed habitats where species compositions were recently altered. In managed agro-ecosystems, species may not have evolved together over a long period, and competition for the acoustic space might still be underway. This hypothesis could also be evaluated by developing a similar experiment as in our chapter II. Within the same region, one could study the assemblage patterns of local ensiferan communities in both recently altered and unaltered ecosystems. Results that show similar patterns in both ecosystem types would support the hypothesis that present-day community assemblage patterns at the local scale are more dependent on other environmental factors (e.g., nutritional resources) than on the availability of the acoustic resource. The opposite would suggest that random assembly is due to habitat alteration and that the acoustic resource may still be an important selective force at local scales in managed ecosystems.

Invasive species or intrusive noises such as anthropic sounds, may alter the acoustic partitioning of a pre-established acoustic community because they are not part of the "preselected" regional pool. It is then pertinent for future research to evaluate the real impact of these sounds, independently from the impact of habitat loss, on intraspecific competition for acoustic space and its implications in the assemblage of local communities.

Alternatively, it is worthwhile to also consider the hypothesis that competition for acoustic space may have never constituted an important selective force. Instead, the intraspecific sexual selection (i.e., the receiver selection; Guilford and Dawkins 1991), for particular vocal patterns may have shaped species-specific calls. Other variables as climate, nutritional resources, and other biotic interactions may be responsible for the constitution of regional pools and local assemblages.

Underwater soundscape

The underwater environment is filled with biotic and abiotic sounds, many of which can be important for the survival and reproduction of fish. Through our model in chapter III and our empirical results, we show that ambient noise level variation may have an effect on the activity of prey fish. We offer a hypothesis in which the mechanism underlying an increase in attack rate is the active use of acoustic refuges, which the augmented ambient noise levels provide. However, we cannot rule out the possibility of other explanations for the results that we observed in the field. For example, as we already mentioned, drilling and motor sounds over the ice could also have had an attraction effect on fish that was not related to predation risk. Nevertheless, we observed that only yellow perch captures increased under augmented ambient noise even though there were other species fished during our study (i.e., pike).

In our model, we proposed a simple system in which ambient noise increases homogeneously in a particular area. In fact, ambient noise levels in natural ecosystems seem to follow a more variable distribution (Figure 6). Indeed, acoustic refuges (understood as areas of increased ambient noise levels where prey activity is masked to potential predators) may be distributed in a localized and variable pattern in the underwater landscape, creating an acoustic mosaic of intensities. It would be interesting to map ambient noise levels and relate them to fish distributions under the ice cover. This could help evaluate the extent and implications of fish use of acoustic refuges. Our model could be adjusted to take into account this patchiness in ambient noise level.

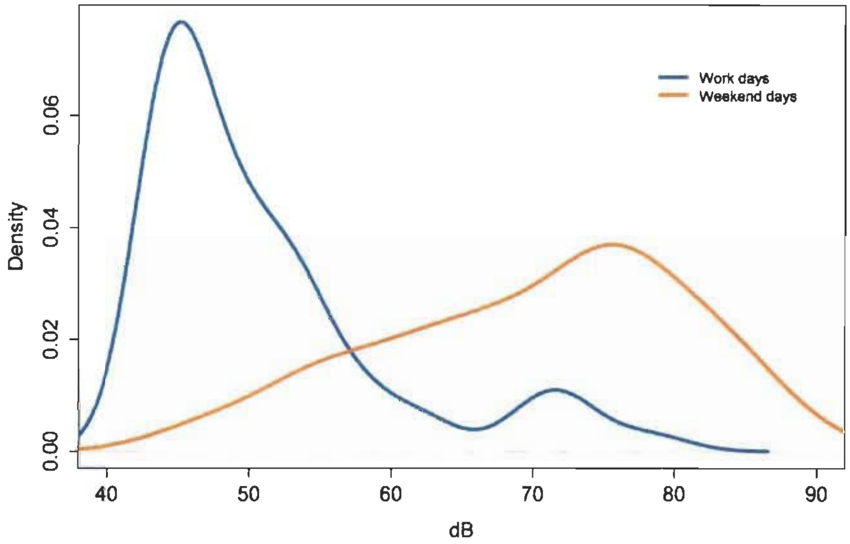

Figure 1. Density distribution of ambient noise intensity levels during work days and weekend days. Noise intensity level is reported as dB (ref 1 μPa). Methods and values are reported in chapter III.

Semi-experimental studies using playback of underwater noise could empirically validate our model. It could test whether, under similar environmental conditions (e.g., climate, water depth, activity on the lake), the attack rate of prey fish increases with playback noise intensity. It could also evaluate the existence of critical points, in terms of acoustic intensity, that would trigger a rise in attack rate. The advantage of using semi-experimental studies in underwater soundscape is that they can easily be developed in different ecosystems with different predator-prey systems. In contrast to laboratory studies, semi-experimental ones allow the evaluation of the effect of a particular sound on the fish community under natural physical and chemical conditions (within a larger spatial range and more natural conditions of substrate, depth, water temperature, oxygen, and so on), while controlling for sound spectral patterns.

If our model proves to be applicable to different systems and ambient noise is shown to hinder fish predators in trophic interactions under conditions where light limits visual detection, predators that use sound for hunting can be hindered under noisy conditions through lower availability of suitable foraging areas and lower catch efficiency. As we said in chapter III, the winners and losers under conditions of increased underwater noise levels will depend on environmental conditions, species' hearing sensitivities, and behavioural adaptations. While this fact highlights the need for anthropic noise to be included in environmental management plans, it also shows the importance of its consideration in studies assessing fish behaviour and community dynamics.

In our view, the knowledge of species' sound production and auditory abilities and masking noise characteristics may yield more consistent results when used in the context of theoretical frameworks. Such a framework is needed to make testable predictions about a particular hypothesis, investigate the mechanisms underling an observed process, and generalize to different taxa and ecological contexts. For instance, many studies done in terrestrial ecosystems have proposed theoretical frameworks to study the effects of masking noise on the communication patterns of birds, anurans, and orthopterans (e.g., Slabbekoorn and Peet 2003; Roca et al. 2016; Dooling et al. 2015; Desrochers and Proulx 2017). In aquatic systems, some studies have already developed theoretical frameworks to assess variations in whale acoustic communication space due to acoustic masking (e.g., Clark et al. 2009). These examples can be used as guidelines to frame research on the relationship of underwater soundscape and fish distribution, abundance, and biotic interactions.

To address ambient noise effects on fish community dynamics, soundscape ecology needs to work closely with the field of bioacoustics research. Accurate measures of fish sound production and auditory abilities are needed to supply theoretical models and draw practical conclusions about the effect of ambient noise on fish. It is paradoxical that the hearing threshold (HT) of most fish species has been measured in terms of sound pressure level whereas fishes seem to be sensitive to particle motion and only some anatomical specializations seem to allow sound pressure detection (Popper and Fay 2011; Nedelec et al. 2016). Sound pressure and particle motion are directly related only under certain conditions that are not generally met in shallow waters (Nedelec et al. 2016). Thus, in shallow-water habitats, HT should be measured in terms of both pressure and particle motion to better understand the contribution of one or the other to the hearing ability of a particular species. Indeed, there is some evidence of fish species with no anatomical specialization that are able to detect both particle motion and sound pressure (Chapman and Hawkins 1973, Jerkø et al. 1989, Wysocki 2009). Due to their apparently restricted sensitivity to sound pressure levels, fish are generally considered to hear poorly at far-field distances. This assumption is inconsistent with behavioural studies, where fish lacking morphological specializations are responsive to sounds emitted far away (even 400 m; Chapman and Hawkins 1973; Wahlberg and Westerberg 2005; Dale et al. 2015; Radfor et al. 2012). We believe there is enough evidence to make it worthwhile to further study fish hearing abilities and related behaviours, especially the ability to detect sounds in the far-field.

Soundscape ecology of freshwater ecosystems will surely become an increasingly active and pertinent area of research for several key reasons. First, the underwater environment is far from being the silent world that it was once thought to be: many fish and invertebrate species produce acoustic signals and almost all are sensitive to sound (Ladich and Schulz-Mirbach 2016; Lugli 2015). Second, sound travels easily and over great distances in most aquatic environments. And third, ambient noise levels have increased over the last several decades due to human-related activities (Slabbekoorn 2010).

To better understand the consequences of human-related noises on the integrity of freshwater ecosystems, we need to improve our knowledge of species' hearing abilities and the role of soundscape on the structure and dynamics of aquatic communities. The recording and playback of sounds in aquatic ecosystems require more sophisticated equipment than in terrestrial systems. Advancements in sensor technologies and the development of user-friendly guidance on the methods, instrumentation, and underlying physics of sound pressure level and particle motion measurements will improve the quality and quantity of research within this area of study.

Conclusion

Soundscape ecology provides a new perspective to study the complex interactions between animal species, geophysical dynamics, and human activities. In this thesis, we used the study of soundscapes of different terrestrial and aquatic ecosystems together with the development of theoretical frameworks to assess the effects of soundscape on community structure and dynamics and to draw conclusions on community assemblage patterns and predator-prey interactions. Our principal contributions include the following: 1) The proposal of novel metrics and methods in soundscape ecology. We show that a combination of acoustic metrics could be useful to differentiate aquatic and terrestrial soundscapes, and we propose a new acoustic metric based on the acoustic signal digital format size, which may serve as a user-friendly index to rapidly assess acoustic diversity; 2) The development of two theoretical frameworks to study community structure and dynamics that can be applied to several taxa in different ecosystems and contexts; 3) The discovery that the assemblage patterns of local ensiferan communities are similar to the random pattern of the simulated regional community. We suggest that competition for acoustic space is not a strong selective force shaping local assemblages of ensiferan communities in temperate ecosystems; and finally, 4) The proposal of a new theory in which ambient underwater noise may be advantageous to fish prey in predator-prey interactions at certain intensity levels and in particular underwater environmental conditions. This thesis provides several tools and theoretical bases that could be used in many research perspectives as well as interesting results about the effects of the soundscape on animal community structure and dynamics, all of which could be used to guide further theoretical and applied research within the field of soundscape ecology.

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