

REVIEW

Anthropogenic noise and the bioacoustics of terrestrial invertebrates

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ABSTRACT

Anthropogenic noise is an important issue of environmental concern owing to its wide-ranging effects on the physiology, behavior and ecology of animals. To date, research has focused on the impacts of far-field airborne noise (i.e. pressure waves) on vertebrates, with few exceptions. However, invertebrates and the other acoustic modalities they rely on, primarily near-field airborne and substrate-borne sound (i.e. particle motion and vibrations, respectively) have received little attention. Here, we review the literature on the impacts of different types of anthropogenic noise (airborne far-field, airborne near-field, substrate-borne) on terrestrial invertebrates. Using literature on invertebrate bioacoustics, we propose a framework for understanding the potential impact of anthropogenic noise on invertebrates and outline predictions of possible constraints and adaptations for invertebrates in responding to anthropogenic noise. We argue that understanding the impacts of anthropogenic noise requires us to consider multiple modalities of sound and to cultivate a broader understanding of invertebrate bioacoustics.

KEY WORDS: Noise pollution, Near-field sound, Far-field sound, Substrate-borne sound, Biotremology, Animal communication, Masking, Plasticity, Constraints, Behavior

Introduction

Anthropogenic acoustic noise (see Glossary) is widely recognized as an issue of environmental concern (Barber et al., 2011; Shannon et al., 2016). Noise created by ever-growing transportation networks and human activities associated with economic development has become so prevalent that it has penetrated some of the quietest places on Earth. For example, 63% of US protected public lands have background noise levels double that of environmental background noise levels (Buxton et al., 2017). Importantly, the acoustic characteristics of anthropogenic noise differ from those of environmental noise (e.g. sound produced by wind, rain, conspecifics, heterospecifics); thus, it represents a novel challenge for animals. For vertebrates, the impact of noise is multifaceted. It has been found to have negative consequences for mating and courtship behavior, predator–prey dynamics, movement, habitat selection and physiology (Shannon et al., 2016).

However, the impact of anthropogenic noise on invertebrates has largely gone unstudied (Morley et al., 2014; Shannon et al., 2016). Although invertebrates comprise 97% of animal species on Earth, and are important in most ecological processes, only 4% of the work on noise and wildlife has been on invertebrates (Shannon et al., 2016). Viewed with an evolutionary history perspective, this skew

becomes even more dramatic. The ability to hear, which requires a specialized organ or organs, evolved from a single ancestor in vertebrates (Manley, 2012), whereas the ability to hear far-field airborne sounds (see Glossary) evolved independently at least 24 times in insects alone (Greenfield, 2016), and likely many more times in invertebrates. Invertebrates send and receive sound in highly diverse ways; thus, the ways in which anthropogenic noise affects invertebrate behavior are likely vast and complicated.

In this Review, we focus on the effects of anthropogenic noise on acoustically mediated behaviors in terrestrial invertebrates. We define acoustics in the broad sense, as any exchange of information that occurs via mechanical waves propagating in a medium (Fig. 1). Acoustics in terrestrial environments are extensive and their simplest configuration includes airborne far-field sound (pressure waves), as well as airborne near-field sound (particle motion; see Glossary) and substrate-borne sound (see Glossary).

For sounds transmitted through air, the power produced via waves is a product of pressure and particle velocity (Kinsler et al., 1999). Close to the sound source (or in the near-field), particle velocity dominates, whereas further from the sound source (or far-field), pressure waves dominate (Kinsler et al., 1999). This physical phenomenon is partially driven by the fact that pressure attenuates less with distance ($1/r$, where r is the distance from the source) than do particle movements ($1/r^2$) (Kinsler et al., 1999; Jacobsen, 2007). In a general sense, the near-field only occurs at a distance of approximately 0.5–1 wavelengths from the source (Kinsler et al., 1999; Jacobsen, 2007), whereas far-field sound waves (pressure waves) can travel many meters, thus dominating long-range airborne communication in animals.

Substrate-borne sounds are waves transmitted through or on the surface of a solid substrate. Solid substrates are an inherently more complex medium for transmission than air or water. Contrary to airborne or waterborne signals (see Glossary) that travel through a single medium, substrate-borne signals often travel through multiple media with differing properties and many articulating surfaces and boundaries (Elias and Mason, 2014). Additionally, substrate-borne waves can take multiple forms beyond longitudinal waves, depending on the material, geometry and/or size of the medium (Elias and Mason, 2014). The nature of a substrate (e.g. plants, rocks, soil, litter, wood) has major implications for the types of waves transmitted (e.g. longitudinal, transverse, bending, Rayleigh), the distance sound travels, the speed at which different frequencies travel and the optimal frequencies for transmission (Brownell, 1977; Michelsen et al., 1982; Aicher and Tautz, 1990; Hill, 2008). The diversity of possible substrates introduces many possibilities regarding distortion in the spectral and temporal domain of signals.

The study of the interplay between the acoustics of terrestrial vertebrates and anthropogenic noise has been dominated by animals using pressure waves in air (airborne far-field) with few, but notable, exceptions (Narins, 1990, 2001; Shier et al., 2012; Mortimer et al., 2018). However, terrestrial invertebrates routinely use all three types

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Glossary

Aerodynamic sound

Sound production mechanism where the flow of fluid over a structure excites resonance properties of the structure.

Airborne far-field sound

Vibration propagating in air at a distance where sound pressure dominates, and sound particle velocity and sound pressure are in phase.

Airborne near-field sound

Vibration propagating in air at a distance where air particle velocity dominates and sound particle velocity and sound pressure are not in phase.

Cue

Act or structure produced by a sender that has information but has not evolved to elicit a response in a receiver.

Fluid compression

Sound-production mechanism where animals produce rapid changes in the local pressure of the medium (e.g. cavitation, 'sonic boom').

Johnston's organ

Sensory organ found in the antennae of insects that can detect vibrations in the air.

Masking

Situation where a signal/cue co-occurs with noise thereby increasing the threshold for detection by the receiver.

Noise

Mechanical waves uncorrelated with any acoustic feature of interest to a receiver. May be anthropogenic (e.g. traffic, industry) or environmental (e.g. heterospecifics, rain, water, wind).

Percussion

Sound-production mechanism whereby animals produce vibrations using transient impacts of an appendage against another appendage or against the substrate.

Signal

Act or structure produced by a sender that has evolved to elicit a response in a receiver.

Spatial release from masking

A phenomenon whereby a signal/cue is more easily detected when spatially separated from noise.

Substrate-borne sound

Vibration propagating in a solid.

Stridulation

Sound-production mechanism whereby animals produce vibrations using two rigid structures that are rubbed against each other. At least one of the structures (the file) is ridged.

Sympathetic vibrations

Phenomenon whereby an airborne sound causes vibrations in a solid that was previously not moving.

Tremulation

Sound-production mechanism whereby animals produce vibrations using oscillations of a body part.

Tymbalation

Sound-production mechanism whereby animals produce vibrations using a tymbal, a corrugated structure on the exoskeleton.

Vibration

Mechanical waves propagating in a solid or fluid medium.

understandings) about the mechanisms of invertebrate bioacoustics, the characteristics of anthropogenic noise and the ways in which animals adapt to noise, we have come up with a framework for investigating and understanding the potential impact of anthropogenic noise on invertebrates.

We have organized our discussion into three main categories that correspond to three interrelated types of sound: far-field pressure waves, near-field particle motion and substrate-borne waves. For each category, we present what little information is known about the impact of anthropogenic noise on invertebrates. In addition, we make predictions about the ways in which noise can affect communication, including detection, by focusing on the mechanisms invertebrates use for sending and receiving acoustic information. We also discuss how invertebrates might adapt to anthropogenic noise in each acoustic modality and the various constraints inherent to each sound type. In Fig. 2, we lay out hypotheses on how invertebrates may adjust signal characteristics in order to avoid the impacts of anthropogenic noise if there is substantial overlap between noise and communication signals (masking; see Glossary). Finally, with the goal of more broadly understanding anthropogenic noise as an environmental issue, we outline our thoughts on the most pressing lines of inquiry for research in each modality.

Airborne sound

Far-field

Of the modalities of sound that invertebrates use, airborne sound has by far received the most attention, despite the fact that it is the least common modality for acoustic communication. Seven orders of insects (Coleoptera, Diptera, Hemiptera, Lepidoptera, Mantodea, Neuroptera and Orthoptera; Greenfield, 2016) are known to use far-field sound (600 to >130,000 Hz; Schmidt and Balakrishnan, 2015). Their calls can contain information about species identity (Hoy et al., 1982), the caller's location (Cade, 1975; Doherty, 1985) and different aspects of mate quality (Tuckerman et al., 1993; Wagner and Reiser, 2000), as well as fighting ability (Brown et al., 2006). In addition, some species of flies eavesdrop on calling Orthoptera to locate and parasitize them (Cade, 1975). Finally, many species use far-field sounds to detect, avoid or deter predators. For example, some species rely on far-field ultrasound to detect and avoid echolocating bat predators when they are being pursued, whereas others produce defensive acoustic signals to ward off predators (Ter Hofstede and Ratcliffe, 2016).

Thanks to a great effort to understand the impact of specific noise sources on vertebrates that use far-field sounds (Shannon et al., 2016), we have a good understanding of the noise sources likely to impact invertebrates that communicate in the far-field. Anthropogenic noise sources such as traffic on roads and railways (10–10,000 Hz up to 50,000 Hz; Hayek, 1990; Talotte et al., 2003), oil, gas and wind development (compressor noise <20–5000 Hz, wind turbines <50,000 Hz; Barber et al., 2011; Bunkley et al., 2017; Long et al., 2011), military activities (Larkin et al., 1996) and general urban environments (0–22,000 Hz; Wood and Yezerinac, 2006) create noise that overlaps with the frequency ranges of signals and cues (see Glossary) used by invertebrates. Anthropogenic noise sources either produce intermittent noise (traffic on roads and railways, military activities, oil and gas development) or continuous noise (wind turbines, general urban environments); the constancy of the noise can have implications for masking, as well as other impacts (i.e. distraction; Table 1), and likely has implications for the ability of invertebrates to habituate to particular sources of anthropogenic noise (Barber et al., 2009)

of sound. At the same time, anthropogenic activities are known to produce noise in each modality. Here, we attempt to bridge the gap between two fields of study: invertebrate bioacoustics and anthropogenic noise. By mining known information (or current

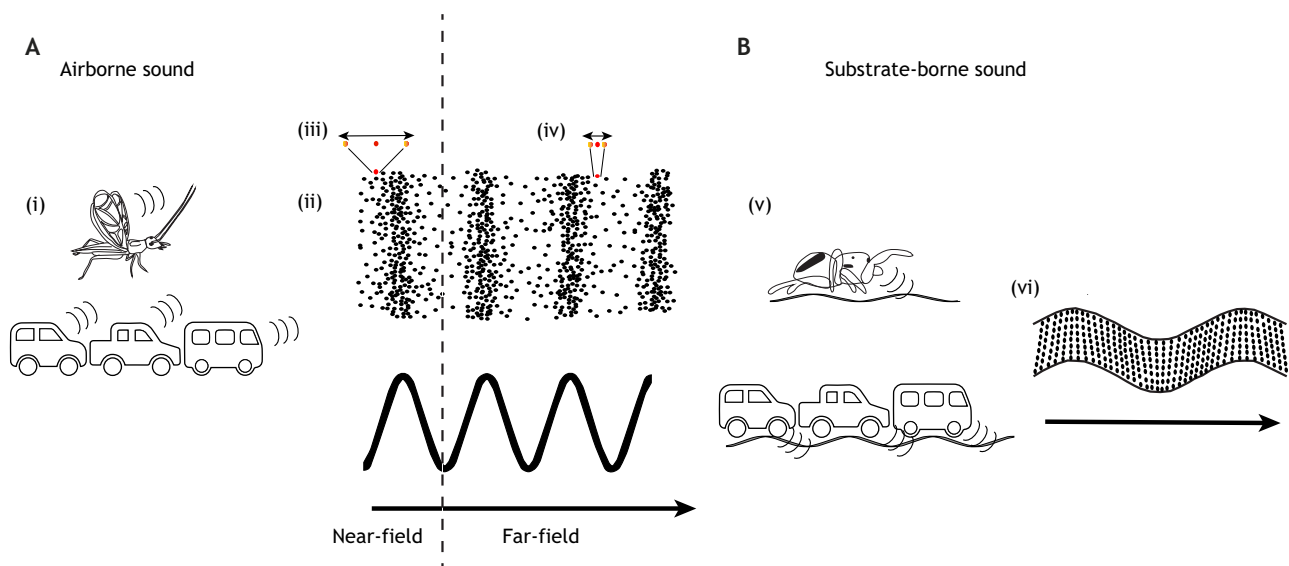


Fig. 1. Acoustic properties of airborne and substrate-borne sound. (A) (i) Both biotic and anthropogenic sources can produce airborne sound. (ii) Airborne sound waves are produced by air particle movements (movement of one air particle highlighted in red with double-headed arrows denoting amplitude of movement), and the resultant changes in air pressure (air pressure amplitude denoted by spacing of air particles shown in black) based on those particle movements are shown. Airborne sound waves can be categorized as either near-field or far-field depending on the distance from the sound source and the relative differences between particle motion or air-pressure amplitude. Arrow denotes the direction of a propagating airborne sound wave (iii). In the near-field, air particle movement dominates relative to air pressure differences. Near-field sound occurs within one wavelength of the sound source. (iv) In the far-field, air pressure differences dominate over air particle movements. Far-field sound occurs at a distance of greater than one wavelength from the sound source. (B) (v) Both biotic and anthropogenic sources can produce substrate-borne sound. (vi) Substrate-borne waves are complex and can occur within or on the surface of a solid substrate (solid lines denote outline of solid surface). Arrow denotes the direction of a propagating substrate-borne sound wave.

Impacts of airborne noise

One of the most common and likely consequences of noise from anthropogenic activities for far-field communication is masking. Masking happens when noise co-occurs with an acoustic signal or cue, thus making it difficult or impossible for animals to assess the information encoded therein. For invertebrates where males use far-field sounds to call to females, such as field crickets and katydids, masking by road noise renders females unable to detect or locate males for mating (Schmidt et al., 2014; Bent et al., 2018; Bailey and Morris, 1986). Similarly, male grasshoppers that locate females by their calls are less responsive to calling females in the presence of noise but are nonetheless accurate when turning in their direction (Reichert, 2015). Masking noise also decreases the ability of the parasitoid fly *Ormea ochracea* to localize calls of their host cricket (Lee and Mason, 2017). For some animals, masking of courtship songs may change the preference functions of choosers. For example, in the grasshopper *Chorthippus biguttulus*, masking noise significantly increases female preference for some traits and decreases it for others, leading to a decreased overall responsiveness of females to male signals (Reichert and Ronacher, 2015). However, masking noise does not always change a chooser's preference. For example, Einhüpl et al. (2011) found that individual male songs preferred by female grasshoppers (*C. biguttulus*) without noise present also elicited responses by females at higher amplitudes of white noise than songs that were not preferred. Finally, rather than suffering the consequences of their signals being masked in the presence of noise, some invertebrates put less energy into calling by shortening calls (which likely diminishes their effectiveness) (Orci et al., 2016) or by stopping calls altogether (Costello and Symes, 2014).

Masking by anthropogenic noise might impact invertebrate predator-prey dynamics, especially between some invertebrate species and their bat predators. Recent studies have found that

some bat species alter their foraging patterns (Schaub et al., 2008; Bunkley et al., 2015) or are less efficient foragers in the presence of anthropogenic noise (Siemers and Schaub, 2011). Although this evidence suggests invertebrates experience predation relief when noise is present, the signals and cues used by invertebrates to hear and flee approaching predators may also be masked. For example, most flying insects use acoustic cues to detect predators, and some produce defensive signals to avoid or deter predators (ter Hofstede and Ratcliffe, 2016). Masking of these signals and cues might increase predation pressure on invertebrates where noise is present; however, these dynamics have yet to be tested.

Strategies to avoid masking

Invertebrates that transmit far-field sounds in noisy environments have multiple ways of overcoming the challenges associated with anthropogenic noise. First, they can avoid noise spatially by moving away from areas heavily impacted by human activities. Although there is no direct evidence of this in invertebrates, Bunkley et al. (2017) found that grasshoppers and camel crickets were less abundant at gas drilling sites with noise than those without. Second, animals may avoid anthropogenic noise temporally, by calling at times when noise is absent or reduced. However, one source of noise, road traffic, is predictably most intense during dawn and dusk (rush hour), times when many invertebrates concentrate their calling activity (Luther and Gentry, 2013). Researchers have suggested that it is unlikely that invertebrates will be able to temporally shift calling because there are increased costs to calling at other times of day, owing to suboptimal atmospheric conditions, particularly at sunset (Van Staaden and Römer, 1997). In addition, short-term temporal activities for some invertebrates might be constrained by phylogenetic history (Shieh et al., 2015). Third, like some vertebrates, invertebrates could increase the amplitude of their calls (Lombard effect) (Nemeth and Brumm, 2010). However, to



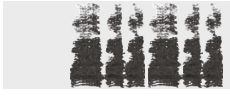


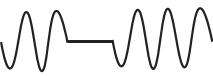






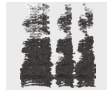

Signal characteristic	Potential for conveying information in noise	
	Weak	Strong
	Quiet	Loud
Amplitude		
	Broadband	Narrowband
Bandwidth		
	Continuous	Intermittent
Temporal structure		
	Constant	Modulated
Modulation		
	No repetition	Repetition
Repetition		
	Unidimensional	Multidimensional
Dimensionality		
	Unimodal	Multimodal
Multimodality		

Fig. 2. Signal characteristics and their hypothesized robustness to masking noise. Column 1: signal information can be conveyed across multiple acoustic characteristics. Column 2: certain variations of each characteristic are predicted to be better at conveying information in the presence of masking noise than others (right to left, respectively). Information can be conveyed using temporal, amplitudinal (white box–wave form) and spectral (grey box–spectrogram) properties.

date, there is no evidence that this occurs. Finally, animals can alter their signals to avoid calling in masked frequencies or, alternatively, increase the intensity of masked frequencies. This has been found to be the case for some invertebrate species. For example, male grasshoppers and cicadas shift their songs to higher frequencies in the presence of noise (Lampe et al., 2012a,b; Shieh et al., 2012).

On the receiving end, listening animals may be able to overcome masking by anthropogenic noise using a variety of neurological mechanisms, including frequency tuning, where receivers are most sensitive to the call frequencies that contain the most energy (Schmidt and Römer, 2011). Receivers might also use spatial release from masking (see Glossary) and/or active amplification mechanisms (Romer, 2013; Mhatre and Robert, 2013; Morley and Mason, 2015; Schmidt and Balakrishnan, 2015). All of these strategies have been demonstrated in invertebrates that contend with environmental noise, but they have yet to be found in response to anthropogenic noise. It is critical that future work seeks to understand neurological strategies for avoiding or compensating for anthropogenic noise.

Constraints to plasticity

Most invertebrates produce far-field sound with hardened sclerotized structures. For example, many invertebrates produce calls by rubbing together structures on their forewings, or tegminal stridulation (see Glossary), coupled with a resonating structure. This sound-production mechanism requires a hardened file of teeth and a scraper that is dragged across the teeth to produce vibrations (see Glossary; Koch et al., 1988; Bennet-Clark, 1999; Montealegre-Z and Mason, 2005). For species that use this mechanism, the frequencies they can produce are driven by the shape of the hardened structures as well as the speed of the scraper movement (Koch et al., 1988; Bennet-Clark, 1999; Chivers et al., 2017). Song frequency is also highly dependent on resonator geometry, with some tree crickets able to produce different frequencies using multiple resonant modes of their wings (Mhatre et al., 2012). Regardless, it is likely that most invertebrate species are constrained in their ability to plastically adjust the spectral properties of signals. Interestingly, Lampe et al. (2014) found developmental plasticity in response to anthropogenic noise, whereby grasshoppers raised

Table 1. Summary of literature examining the consequences of anthropogenic noise beyond masking for invertebrates

Consequence	Invertebrate	Sound modality	Source
Distraction	Caribbean hermit crab (<i>Coenobita clypeatus</i>)	Airborne far-field	Chan et al., 2010; Walsh et al., 2017
Processing errors	Earthworm	Substrate-borne	Darwin, 1892; Mitra et al., 2009
Increased stress	Monarch butterfly larvae (<i>Danaus plexippus</i>)	Unclear, likely substrate-borne	Davis et al., 2018
Developmental changes	Indian meal moth larvae (<i>Plodia interpunctella</i>)	Airborne far-field	Huang et al., 2003; Gurule-Small and Tingnitella, 2018, 2019
Decreased life span	Field cricket (<i>Teleogryllus oceanicus</i>)	Airborne far-field	Gurule-Small and Tingnitella, 2019

under noisy conditions produce higher-frequency songs as adults. Similar predictions can also be made for invertebrates that use other sound-producing mechanisms such as tymbalation, percussion, fluid compression and aerodynamic sound, as these also use sclerotized structures to produce sound (Chapman, 1998).

Across and within invertebrate species that produce far-field sound, active plasticity in response to noise may be partly limited by constraints resulting from their small body sizes. The frequency and intensity of far-field calls that insects can produce is highly correlated with size (Simmons, 1995; Bennet-Clark, 1998). In general, larger individuals can produce louder, lower-frequency sounds and receive lower-frequency sounds than smaller invertebrates (Bennet-Clark, 1998); thus, call frequency is often an honest signal of size in insects (Simmons, 1995). These dynamics will likely limit the use of frequency-shift mechanisms in response to anthropogenic noise by some insects.

Finally, it is important to consider the environment and ecological community in which invertebrates are calling when evaluating the potential impacts of, and adaptations to, masking by anthropogenic noise. Invertebrates face constraints to the frequencies and timing of their calling brought on by habitat structure (attenuation and distortion), masking by other calling animals and predation (Romer, 2013; Schmidt and Balakrishnan, 2015). For example, many crickets and katydids live in assemblages where they are already partitioning the spectral or temporal aspects of their calls so that they do not overlap with one another (Gogala and Riede, 1995; Schmidt et al., 2011; Jain et al., 2014). In these communities, it is unlikely that all species will be able to avoid masking by anthropogenic noise while maintaining their spectral or temporal partitioning.

Near-field

Near-field sound attenuates quickly relative to far-field sound, and conventional thought has been that its detection by terrestrial invertebrates is physiologically limited to less than a wavelength from the source (Kinsler et al., 1999). Thus, research on near-field communication among terrestrial invertebrates has primarily focused on a limited number of animals that communicate at close range and detect near-field sound via the Johnston's organ (see Glossary; flies, mosquitoes, bees; Göpfert and Robert, 2002; Gibson and Russell, 2006; Tsujiuchi et al., 2007) or filiform hairs (e.g. trichobothria) sensitive to particle motion (crickets, spiders; Kämper and Kleindienst, 1990; Barth, 2000). However, many terrestrial invertebrates are covered in innervated hairs, and particle motion is a rich source of information; therefore, many invertebrates are likely to have some capacity for detecting particle motion that has been underappreciated. This hypothesis, however, needs to be assessed further.

Near-field receptors are exquisitely sensitive, with deflections as small as 1 Å triggering neural responses (Shimozawa and Kanou, 1984; Humphrey and Barth, 2008). These receptors are generally tuned to low frequencies (<500 Hz) (Wang et al., 2000; Shamble et al., 2016). The tuning of each receptor depends

primarily on its length, diameter and mass (Barth et al., 1993). Invertebrates use near-field receptors in mating interactions (Tauber and Eberl, 2003; Lapshin and Vorontsov, 2017), to forage (Kirchner, 1994; Barth and Höller, 1999), to detect incoming predators (Tautz and Markl, 1978) and during antagonistic interactions (Santer and Hebets, 2008).

Near-field anthropogenic noise has been overlooked in the literature thus far. However, all sources of airborne anthropogenic noise produce particle motion, as it is inherent to the production of airborne sound (Kinsler et al., 1999). Thus, in the presence of noise, invertebrates that communicate with near-field sound may be subject to a host of consequences, from masking to injury. Noise sources that have a large amount of energy in frequencies below 500 Hz, such as noise from roads (Hayek, 1990), railways (Talotte et al., 2003), and oil and gas development (Barber et al., 2011), are the most likely candidates to produce near-field noise relevant to invertebrates.

At present, no direct evidence exists to support the idea that anthropogenic noise impacts near-field communication. However, one study by Samarra et al. (2009) found that near-field white noise hinders the ability of female *Drosophila montana* to detect and recognize male courtship song when it falls within the same frequency bands. In addition, a host of studies contain new information that expands our understanding of near-field communication in ways that suggest invertebrates may be less robust to the effects of anthropogenic near-field noise than previously thought.

First, near-field communication may take place at much longer distances than once suspected. Previous physical modeling and measurements suggested that near-field communication could only occur across small distances (1–70 cm), such as when animals are flying next to each other in a swarm (Aldersley et al., 2017) or interacting at close distances (Tauber and Eberl, 2003; Santer and Hebets, 2008). However, Shamble et al. (2016) demonstrated with behavioral and physiological data that jumping spiders can detect acoustic energy at distances of at least 3 m using near-field receptors. Similarly, Menda et al. (2019) demonstrated that mosquitoes can detect sound up to 10 m away using their antennae. Furthermore, Zhou and Miles (2017) presented models showing that small fibers (>1 µm), such as those used as near-field receptors, move with the surrounding medium. This scenario suggests that thin hairs will move in response to a large range of stimuli, even those produced at long distances. Additionally, some invertebrates, such as mosquitoes and flies, employ near-field receptor organs that actively amplify quiet signals and provide directional sensitivity (Göpfert and Robert, 2001; Göpfert et al., 2005; Morley et al., 2018). Together, these pieces of evidence extend the effective range of anthropogenic near-field noise to at least 10 m and potentially much further.

Second, invertebrate near-field receptors are likely able to detect a much wider range of frequencies than previously thought. In the past, research mainly focused on the detection of low-frequency

particle motion, because it was thought that biologically relevant cues such as wind and predator/prey movements are also dominated by low frequencies (Barth and Höller, 1999). More recent work, however, has demonstrated that near-field receptors can respond to a wider range of frequencies than previously thought (Bathellier et al., 2012; Zhou and Miles, 2017), and that biologically relevant stimuli also likely contain a broad range of frequencies (Casas et al., 2008). Zhou and Miles (2017), for example, suggested that thin fibers move in response to a large range of frequencies. For example, spider silk, an important near-field detector for many spiders, could measurably capture airflow over frequency ranges spanning infrasound to ultrasound (1–50,000 Hz) (Zhou and Miles, 2017). In another study, Bathellier et al. (2012) used particle image velocimetry (PIV) to demonstrate that spider and cricket filiform hairs are extremely sensitive at much higher frequencies than previously suspected.

Strategies to avoid masking

Although more research is needed, new understandings of near-field sound and receptors suggest that terrestrial invertebrates are likely to be vulnerable to near-field noise in very fundamental ways. Nevertheless, invertebrates that experience negative impacts of anthropogenic noise have a few important tools for avoiding or mitigating these impacts. First, relative to avoiding other types of acoustic noise, it could be especially effective for invertebrates to move a few meters away from the sound source when possible. Second, some species have shown the physical ability to adjust the frequencies of their signals. For example, male and female mosquitoes modulate near-field flight frequencies during courtship (Gibson and Russell, 2006; Cator et al., 2009). Third, some invertebrates use behavioral strategies, such as clustering flight tones in swarms during mating, to reduce acoustic interference to near-field signals (Aldersley et al., 2017). And fourth, near-field receptors of some invertebrates may have the capacity to avoid harmful effects of noise. For example, some invertebrates have near-field receptors with active, non-linear tuning, where the tuning of receptors is amplitude dependent (Göpfert and Robert, 2002; Albert and Kozlov, 2016). In these cases, animals may use non-linear tuning to avoid injury to their receptors when noise is loud. Additionally, there is some evidence that this mechanism may be useful for spatial release from masking (see Glossary; Morley et al., 2018). These examples likely represent just a small sample of the potential strategies available to invertebrates for avoiding near-field noise. Much more research is needed to understand the prevalence of near-field communication and how it is affected by anthropogenic noise.

Substrate-borne sound

Substrate-borne acoustics have largely been left out of the study of anthropogenic noise and its impacts on animals. This is despite the fact that anthropogenic sources create substrate-borne noise (Dowding, 1996; Heckl et al., 1996; Forman, 2000), and over 90% of all animals use some type of substrate-borne sound (Cocroft and Rodriguez, 2005). Invertebrates rely on substrate-borne sounds for many important aspects of their lives, including as a way to collect information about their environment (Evans et al., 2005), to communicate with conspecifics during courtship (Ota and Čokl, 1991; Elias et al., 2003), in competition (Yack et al., 2001; Elias et al., 2008; De Souza et al., 2011) and cooperation (Michelsen et al., 1986; Baroni-Urbani et al., 1988; Endo et al., 2019), to detect prey during foraging (Klärner and Barth, 1982; Pfannenstiel et al., 1995; Fertin and Casas, 2007), to avoid predators (Rohrig et al.,

1999; Castellanos and Barbosa, 2006) and to facilitate symbiotic relationships (DeVries, 1990).

Invertebrates that communicate with substrate-borne sound most often use frequencies <1000 Hz, because low frequencies experience little attenuation in substrates (Bennet-Clark, 1998; Čokl and Virant-Doberlet, 2003). At the same time, human activities such as airport traffic (Fidell et al., 2002), construction (Dowding, 1996) and use of railroads (Heckl et al., 1996), are known to produce low-frequency vibrations (<1000 Hz). Previous work also suggests that because the majority of spectral energy of road noise is in low frequencies (<2000 Hz), roads are likely to represent significant sources of substrate-borne noise (Forman, 2000). Substrate-borne vibrations do not attenuate quickly, and can be detected up to 3000 m from the source (Mortimer et al., 2018). Given that many animals have such sensitive receptors of substrate-borne sound, they are likely to detect anthropogenic sources from even longer distances (Barth and Geethabali, 1982; Shaw, 1994; Mortimer et al., 2018). Anthropogenic sources can produce substrate-borne noise in two ways. First, sources can directly vibrate the earth, producing waves that travel through or on its surface. Second, sources may produce airborne noise that secondarily induces vibrations in substrates (sympathetic vibrations; see Glossary). In general, the former produces vibrations that are louder and will travel further than the latter, because sound loses energy at any substrate boundary (Caldwell, 2014). However, invertebrate receptors are likely to be sensitive to both types of substrate-borne sound.

Variation in the types and structures of substrates is likely to influence how, or whether, anthropogenic noise affects invertebrates that communicate with substrate-borne sound. First, the material properties and dimensions of a substrate determine the likelihood that airborne noise will produce sympathetic vibrations (Press and Ewing, 1951), the propagation of vibratory noise (Elias and Mason, 2011) and its intensity (Hill, 2008). For instance, substrate-borne vibrations do not propagate as well through materials such as sand as they do through plant material (Elias and Mason, 2011), so invertebrates that live on plants or leaf litter might contend with a noisier signaling environment in the presence of human activities than those that live on sand. Second, material properties and dimensions determine the resonance, attenuation and filtering of a given substrate (Kinsler et al., 1999). Invertebrates often take advantage of substrate properties to enhance the efficacy of their signaling by preferentially signaling with frequencies that transmit well through the substrate (Elias et al., 2004, 2010; Čokl et al., 2005; Cocroft et al., 2010). In some cases, vibratory noise from anthropogenic sources could stimulate the resonant characteristics of substrates and mask the frequencies used by invertebrates for communication. Complicating matters further, some substrates reflect sound waves (i.e. echoes and reverberations). For example, noise propagated through rod-like substrates (e.g. stems) could drive the production of standing and/or reflected waves that would distort the properties of signals (Michelsen et al., 1982; Miklas et al., 2001). Third, the boundary conditions of the substrates in question (i.e. substrate shape, articulating surfaces, heterogeneities in surface) can be complex and affect transmission in important ways (Magal et al., 2000). Finally, an individual's signaling environment can include a diversity of substrates, including combinations of natural or human-made materials, all of which differently influence how sound propagates (Wu and Elias, 2014). Currently, it is difficult to make predictions about the ways in which invertebrates will be affected by anthropogenic noise because little is known about the details of substrate-borne sound

propagation in natural signaling environments (Elias and Mason, 2014).

Impact of substrate-borne noise

For the most part, researchers have investigated the impact of general substrate-borne noise disturbance (rather than anthropogenic noise) on communication by experimentally inducing white noise. Substrate-borne noise has been found to disrupt mating in a variety of contexts. For example, female stink bugs adjust the frequency of their signal in response to noise of similar frequencies but do not adjust temporal aspects of their signal when this is masked by noise (Polajnar and Cokl, 2008). In the presence of temporally disruptive substrate-borne noise, male stink bugs respond less frequently to female signals (Polajnar and Cokl, 2008). Wolf spiders that rely on substrate-borne signals for courtship are less likely to mate in the presence of white noise (Gordon and Uetz, 2012). Finally, male black-faced leafhoppers (which produce substrate-borne courtship signals with three distinct sections) cease signaling when white noise is played during the initial phase but not latter phases (Hunt and Morton, 2001). Interestingly, a handful of studies on substrate-borne noise and mating were motivated by the potential to use noise for pest management in agriculture (Polajnar et al., 2015). For example, researchers found that playing substrate-borne noise to mask the mating calls of leafhoppers results in reduced mating (Mazzoni et al., 2009; Eriksson et al., 2012; Nieri and Mazzoni, 2018). In addition, Hofstetter et al. (2014) reported reduced reproductive success, movement and survival of pine bark beetles in the presence of substrate-borne noise that spectrally overlapped with beetle signals.

Masking by anthropogenic noise is also likely to impact foraging and predator–prey relationships of invertebrates, as many animals use substrate-borne sound for finding prey or avoiding predators (Castellanos and Barbosa, 2006; Fertin and Casas, 2007). To date, no evidence exists that this is the case and only one study has investigated this dynamic. Wu and Elias (2014) experimentally induced vibratory white noise of different intensities in webs of European garden spiders and did not find a consistent decrease in prey-detection sensitivities. By contrast, studies investigating substrate-borne noise induced by wind indicate that some invertebrates exploit substrate-borne noise when hunting prey. The salticid spider (*Portia*) and the assassin bug (*Stenolemus bituberus*) are more likely to successfully hunt web-spiders in the presence of wind (Wilcox et al., 1996; Wignall et al., 2011). In these cases, substrate-borne noise is likely to mask vibrations that the predators produce during their approach.

Strategies to avoid masking

Substrate-borne noise may be especially difficult for invertebrates to spatially avoid owing to the fact that it does not attenuate quickly (Kinsler et al., 1999). However, evidence exists that some species may be able to exploit gaps in noise and temporally avoid masking. Wind produces intermittent substrate-borne noise similar to anthropogenic noise sources such as traffic. Researchers found that male treehoppers (which produce substrate-borne courtship signals) preferentially signal during wind-free gaps rather than during experimentally induced wind gusts; females are less likely to respond to male signals during induced wind gusts, and natural treehopper populations are more likely to signal during times of day with less wind (Mcnett et al., 2010).

Invertebrates produce substrate-borne sound with a diverse array of mechanisms (e.g. percussion, stridulation; see Glossary), and the

mechanism an animal uses is likely to affect the extent to which they will be able to shift their signaling frequency in the presence of noise. For example, Bunkley et al. (2017) found differential impacts of noise on the abundances of arthropod families that communicate with substrate-borne sound, potentially owing to the fact that a range of signaling mechanisms is used across families. Terrestrial arthropods use four major mechanisms to produce substrate-borne sound: percussion, stridulation, tymbalation and tremulation (see Glossary). Percussive sound is produced by collisions between parts of the body or between a part of the body and the substrate. These sounds are broadband at the source and the spectral information that arrives at the receiver is solely a result of filtering properties of the substrate (Elias and Mason, 2011). Thus, it is hypothesized that receivers are more likely to use information contained in the timing and/or amplitude of percussive signals than frequency (Elias and Mason, 2011). In the presence of substrate-borne noise, invertebrates that communicate with percussion are unlikely to be able to use frequency-shift mechanisms, such as narrowing the spectrum of signals, to overcome masking.

By contrast, tremulation mechanisms use simple muscular movements of the body and appendages to produce narrowband signals. The ability to shift the spectral properties of tremulation signals depends solely on muscle properties, suggesting that invertebrates that use tremulation will be able to modify the spectral content of their signals in the presence of noise. For example, female southern green stink bugs change the frequency of their tremulations in the presence of frequency-overlapping noise (Polajnar and Cokl, 2008). As mentioned above, invertebrates can also produce substrate-borne signals with stridulation and tymbalation. These mechanisms require specialized exoskeletal structures; when the individual produces vibrations, these structures concentrate acoustic energy to specific bandwidths. In this way, animals can maximize their signal efficacy in particular substrates. The ability of invertebrates to shift the frequency characteristics of signals when using stridulation and tymbalation is likely constrained by muscular physiology (how fast can muscles twitch) and the particular details of their sclerotized sound-producing structures. We do not yet know the extent to which these animals are able to shift the frequencies of their signals in the presence of noise. However, for all invertebrates that communicate with substrate-borne sound, spectral or temporal components of signals are often species- and plant-host specific (Cokl et al., 2005; Cocroft et al., 2006; McNett and Cocroft, 2008). Thus, even if senders can adjust these components to avoid masking by noise, receivers may not respond to the new signals.

Future directions

Across the different communication modalities discussed in this Review, some common research needs have emerged that will need to be addressed to allow us to understand the potential impacts of anthropogenic noise on invertebrate communication. First, it is vital that noise from anthropogenic sources is adequately quantified. In the past, recording equipment developed to record sound that is audible to humans has been sufficient for recording sound relevant to most vertebrates. In order to record sound that is relevant to a broader taxonomic range, many have argued for recording far-field sound without the use of recording filters designed for human hearing (Francis and Barber, 2013; Morley et al., 2014; Shannon et al., 2016). We echo that suggestion here. In addition, there is presently no straightforward method for measuring near-field anthropogenic noise. Although technologies such as PIV and hot wire anemometers have potential applications in this context

(Bomphrey et al., 2005; Sane and Jacobson, 2006), PIV is expensive and has not been easily adapted for field applications, and hot wire anemometers do not have fine enough resolution to record particle motion relevant to invertebrates. Similarly, the recording of substrate-borne sound currently requires expensive laser-vibrometer technology. This technology has only been employed once for measuring noise from anthropogenic activities (Wu and Elias, 2014), and it is not accessible to many researchers. Accelerometers are potentially low-cost alternatives to measure substrate-borne noise, although they are unsuitable for recording sound through many substrates given their weight (Cocroft et al., 2014). All in all, recording and quantifying near-field and substrate-borne anthropogenic noise is a major challenge, but with increased attention and focused effort, existing technologies could be adapted to fit this purpose.

Second, future research should seek to understand the variety of impacts that anthropogenic noise in each modality has on a diversity of invertebrate species. Studies should make sure to report the noise source, characteristics of the noise, the signaling environment (e.g. substrate type), signaling mechanisms and type of acoustic receivers of the animals of interest. Additionally, research should establish patterns of constraints and adaptations to noise in each modality and should address whether adaptations result in differential reproductive success.

Finally, it is pivotal that research seeks to understand how noise affects invertebrates under natural field conditions, particularly for invertebrates that use near-field and substrate-borne modalities. While laboratory studies are important, especially for isolating and manipulating sounds, it is difficult to extract meaningful information about the ecological implications of noise from their results. So far, the best studies in this regard combine data from field and laboratory settings (Lampe et al., 2012a,b, 2014), or take advantage of heterogeneous noise in the landscape (Bunkley et al., 2017). For example, Bunkley et al. (2017) compared arthropod communities at sites developed for gas extraction that had gas compressors (noise) with those that did not have compressors (no noise). Results from these types of studies are critically important for understanding the impact of anthropogenic noise on invertebrates.

Conclusions

Anthropogenic noise is an issue of critical environmental concern, predicted to become an even greater problem with increasing population growth and land-use change. At the same time, invertebrates are experiencing major declines across ecosystems (Potts et al., 2010; Hallmann et al., 2017). The evidence presented in this Review, although limited, suggests that anthropogenic noise is likely to impact invertebrate communication in significant ways. Over the past decades, researchers have conducted important work to understand how anthropogenic noise affects vertebrate species (for excellent reviews, see Brumm and Slabbekoorn, 2005; Patricelli and Blickley, 2006; Slabbekoorn and Ripmeester, 2008; Barber et al., 2011; Ortega, 2012; Francis and Barber, 2013; Radford et al., 2014; Shannon et al., 2016), but investigation into the ways it affects invertebrate life is incomplete. Vertebrates and invertebrates differ in substantive ways, including in the mechanisms they use for producing and receiving sound; critically, this informs how they can respond to noise and the constraints in doing so.

Throughout this Review, we have discussed the sound-producing mechanisms used by invertebrates and their respective vulnerabilities to anthropogenic noise for three types of sound – far-field, near-field and substrate-borne. For the most part, we have

focused on how anthropogenic noise might affect the individual interactions of animals, but these dynamics are also important to understand for their bearing on communities and ecosystems (Francis et al., 2012). The majority of species on Earth are invertebrates; they are critical parts of ecosystems (Mulder et al., 1999; Yang and Gratton, 2014) and are food for many species (Morse, 1971). They also provide ecosystem services important for human life, such as pollination, nutrient cycling and waste removal (Losey and Vaughan, 2006; Noriega et al., 2018). The ways in which invertebrates are affected by and adapt to anthropogenic noise could have great implications for ecosystems and ecosystem services. We argue for the expansion of the focus of anthropogenic noise to include noise in near-field and substrate-borne modalities. Expanding our definition of anthropogenic noise and our focus of research will create a more holistic understanding of the potential reach of anthropogenic noise as a pollutant, and will potentially lead to effective and efficient mitigation strategies.

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Competing interests

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