



Anthropogenic Landscape Changes and Their Impacts on Terrestrial and Freshwater Soundscapes

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Abstract

Purpose of Review Quantifying the effects of anthropogenic sounds on wildlife at the landscape scale of observation has been notoriously difficult because these sounds are often confounded with the presence of infrastructure and loss of habitat through resource exploitation activities. In this paper, we review how anthropogenic landscape changes affect the power level and propagation of sounds in both terrestrial and freshwater ecosystems, as well as the behavioural response of organisms to novel acoustic habitats.

Recent Findings Resource exploitation and other human activities change soundscapes both directly, by affecting sound production and propagation, and indirectly, by modifying landscape structure and species distribution patterns. Intermittent anthropogenic sounds are concentrated in the lower frequencies, tend to be louder than enduring sounds of the same origin and create more patchy soundscapes. We identified key sensorial traits that are related to the auditory acuity of species in different taxonomic groups, including fish, birds, anurans, stridulating insects and small mammals, and which may help us understand why certain species are more sensitive to anthropogenic changes to soundscapes.

Summary Prioritizing research in an increasingly noisy world requires a proper understanding of the auditory sensitivity of species, the characteristics of anthropogenic sounds (i.e. intermittent or enduring), and how sound production and propagation is affected by landscape structure. Further research on species' sensorial traits would provide a framework with which to scale responses to anthropogenic sounds from individuals to communities and better predict the impact of human activities on terrestrial and freshwater ecosystems.

Keywords Anthropogenic noise · Ecoacoustics · Anthrophony · Biophony · Geophony · Song frequency

Introduction

Conservation biologists are increasingly concerned about the potential effects of anthropogenic sounds on habitats and ecosystems (e.g. [1, 2••, 3••]). Typical anthropogenic sound

sources include roads and other transportation networks, renewable and non-renewable energy infrastructures, resource exploitation and urban activities, all of which have been intensively studied in the context of their contributions to habitat fragmentation and loss. Anthropogenic sounds have been related to changes in species distribution patterns associated with transportation networks [2••, 4] and in the context of petroleum and natural gas extraction [5], wind energy [6] and mining [7] activities in terrestrial environments. Yet, quantifying the effects of anthropogenic sounds on wildlife at the landscape scale of observation has been notoriously challenging because these sounds are often confounded with the presence of infrastructure and loss of habitat through landscape changes.

Anthropogenic sounds from resource exploitation activities can interfere with conspecific communication [8••], predator detection and foraging success [6], vigilance [9] and habitat

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selection [10]. However, these processes operate primarily at the individual level and may not directly lead to community or ecosystem changes at the landscape scale of observation. Landscape-scale effects include the multiplicity of causal mechanisms, such as habitat selection, dispersal and birth/mortality processes, involved in shaping species occurrence, abundance or richness across a given region [11]. Contradictory outcomes could arise because species may behaviourally compensate for noise [8], multiple stressors may interfere with each other [12] and because individual-based processes may not generalize to the community or landscape-scale (see [11]). Simple mechanisms, such as behavioural avoidance of loud anthropogenic sounds, can affect some populations negatively if functional habitat is lost, but other populations positively if a decrease in species richness reduces competition among species that are less sensitive to sounds. Similarly, anthropogenic sounds may affect both prey and predators, resulting in different outcomes depending on the strength of trophic interactions [13, 14]. For example, the probability of avian nests being depredated decreases as anthropogenic sounds from natural gas extraction activities increase, because western scrub jays (*Aphelocoma californica*), a key nest predator, avoid anthropogenic sounds [13]. This has the counterintuitive consequence that productivity can be higher near natural gas infrastructure, even for species that avoid this habitat [13]. Such contrasting responses among species, or even individuals, subjected to the same anthropogenic sounds may explain why local ecological patterns do not necessarily generalize across individuals, species, or spatial scales (e.g. [8 vs. 15; but see, 10 vs 16]).

Somewhat less attention has been paid to the impact of anthropogenic sounds on inland water ecosystems (but see [17]), especially at the scale of riverscapes, in comparison with efforts to understand effects of anthropogenic sounds in terrestrial ecosystems. One explanation for this knowledge gap is that freshwater organisms are believed to be mostly silent, even though review reports have emphasized that sound production is common in fish species [18, 19, 20]. Recent overviews of the effects of sounds on fish identified motorized boats, pile driving, dredging and dragging activities as frequent sources of anthropogenic sounds [21, 22]. Moreover, dam management for hydroelectricity production could have immediate consequences on the underwater soundscape of river ecosystems and associated fauna [23]. Landscape changes associated with the above activities may thus influence not only the power level and propagation of underwater sounds but also the behavioural response of freshwater organisms to novel acoustic habitats.

While landscape ecologists are trained to discriminate environmental gradients using physiognomic patterns (e.g. patches, corridors, edges), soundscape ecologists have turned their attention to acoustic patterns. Pijanowski et al. [24] consider soundscape ecology to be a branch of landscape ecology,

but few other authors have theoretically linked landscape and soundscape ecology, and we argue that there is a strong benefit to building on this perspective. Here, we define the soundscape as the geographic distribution of multisource sound perceptions [25]. In practice, alteration of acoustic and physiognomic patterns can lead to the creation of novel sonic habitats (the landscape is more finely grained than the soundscape) or sonic edges (the soundscape is more finely grained than the landscape) [25]. Species experiencing these changes may respond negatively if the novel sonic habitats are of lower quality or if movement is prevented across sonic edges. Therefore, the links between landscape and soundscape ecology are quite clear: both are spatially explicit, understood at a landscape-scale and emphasize the impacts of habitat quality and structure on species living in these environments.

Without a fundamental understanding of how anthropogenic sounds interact with landscape structure and how species perceive acoustic stimuli, the field of soundscape ecology is at risk of producing results with low applicability and potential for generalization [26]. For example, reviews of acoustic deterrent devices used for wildlife depredation in marine [27] and terrestrial ecosystems [28] concluded that benefits were reduced due to rapid habituation and behavioural compensation mechanisms. Although a few landscape-scale experiments have demonstrated effects of anthropogenic sounds on wildlife (e.g. [5, 13, 29]), they have not been replicated in many habitat types or generalized to many taxonomic groups.

Here, we revisited fundamental concepts in landscape ecology to better understand how resource exploitation and other human activities affect soundscapes, which in turn affect the species that live there. We then addressed the important question of why some species are more sensitive than others to variations in their acoustic environment. Ultimately, this review led us to conclude that impacts of anthropogenic changes on terrestrial and freshwater ecosystems cannot be predicted without integrating landscape ecology with the sensorial sensitivity of focal species. We primarily screened the scientific literature on terrestrial and freshwater (inland water) ecosystems, as both are directly impacted by landscape structure and processes, including resource extraction activities, across similar spatial extents. We note that an extensive body of literature also exists on the soundscape of marine ecosystems; indeed, so much research has been conducted on marine soundscapes that covering this literature is beyond the scope of this review. The interested reader can consult recent references on the topic (e.g. [30–33]).

Sound Production in Anthropogenic Landscapes

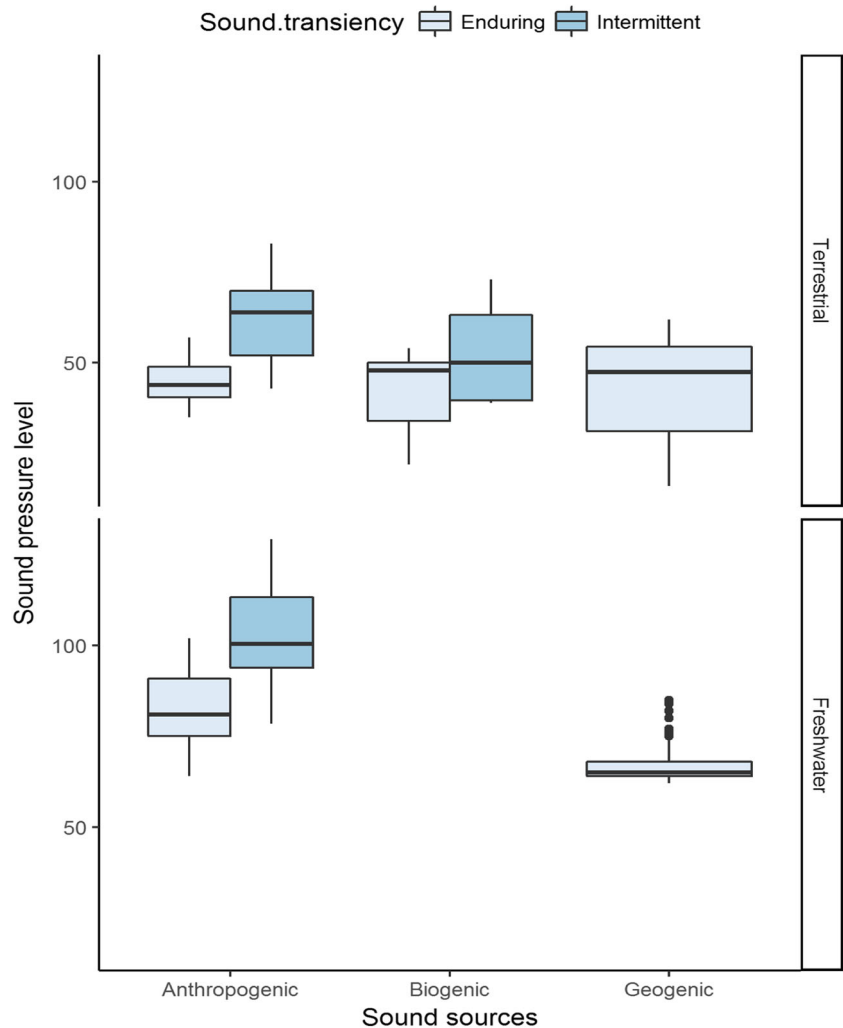
Resource exploitation and human activities have affected the kinds of acoustic stimuli present in natural landscapes. For

example, transportation networks have increased the average power level of sounds in both terrestrial [34] and underwater soundscapes [35]. To illustrate this point in more detail, we retrieved the power level of 65 outdoor sounds recorded in Canada’s National Parks [36], which we then grouped into three sources: anthropogenic (produced by humans or their activities), biogenic (produced by non-human organisms) or geogenic (e.g. wind, rain, ambient background). We also grouped these sounds according to their transiency, as either intermittent or enduring. Intermittent sounds include gas powered devices (e.g. chainsaw, trail bike), human singing and shouting, transient vehicles or dogs barking. Enduring sounds are those likely to be prevalent in the environment for at least 1 h (e.g. windblows, waterfalls, road traffic, bird chorus). These data revealed little difference in sound power across categories for enduring sounds (Fig. 1). However, intermittent anthropogenic sounds were consistently louder than enduring sounds of the same origin, and thus intermittent industrial sounds may have greater impacts on wildlife than continuous sounds. Loud intermittent sounds are also more

likely perceived as threatening [1] and are more difficult to adapt to than predictable sounds [5].

Resource exploitation and human activities have also modified the underwater soundscape of inland waters, for example, by introducing flow control structures (e.g. damming, channel dredging and linearization) and developing recreational and industrial activities on lakes and rivers. In lakes subjected to recreational boating, underwater sounds can be increased up to + 30 dB above baseline levels [39]. Sound power level at source for different classes of ships range between 150 and 180 dB (re. 1 μ Pa) relative to baseline levels of about 90 dB [40]. To illustrate such changes to freshwater soundscapes in the presence and absence of human activities, we revisited data from two Canadian lakes in winter [37, 38], which reported the power level of sounds recorded at arbitrary locations under the ice. Anthropogenic sounds in this context included driving of motorized vehicles (e.g. quads, snowmobiles, trucks and cars), walking of recreational anglers and drilling of holes with gas augers. Both the average and the spatial variation in sound power increased when humans were

Fig. 1 Pressure level (dB) of sounds from different sources recorded in protected lands (Canada’s National Parks; upper panel) and under the ice of two large Canadian freshwater lakes (Lake St-Pierre, QC, and Lake Kennedy, NWT; lower panel). The lists included 65 terrestrial recordings from [36], 40 underwater recordings of ambient (anthropogenic or geogenic) sounds from [37] and 18 underwater recordings of intermittent anthropogenic sounds from [38]. Sound pressure level was referenced to 20 μ Pa in air (terrestrial) and 1 μ Pa in underwater (freshwater) recordings. All terrestrial recordings were A-weighted, whereas all freshwater recordings were Z-weighted in the 100–200 Hz bandwidth



most active, suggesting that the underwater soundscape was not only louder but also acoustically patchier when subjected to anthropogenic sounds (Fig. 1). Consistent with the terrestrial environment, intermittent anthropogenic sounds were typically louder than enduring sounds of the same category.

The most common explanation given for the effect of anthropogenic sounds on wildlife is that those sounds overlap with biogenic signals, resulting in energetic masking [12]. However, a recent study concluded that the likelihood of acoustic overlap is low for a majority of signaling species in three major taxonomic groups, ranging from 5–7% for anurans to 3–4% for birds and less than 1% for ensiferans [41]. This raises the question of whether anthropogenic sounds are a true conservation problem, if biogenic signals of most species do not overlap with anthropogenic sounds. One could argue that 5% of species experiencing direct interference by anthropogenic sounds is already too many, as it adds to the long list of factors that threaten populations. Furthermore, organisms could be distracted, stressed, threatened, or mentally exhausted by anthropogenic sounds regardless of their overlap with biogenic sounds [1, 22], although relatively little attention has been paid to these potential impacts on wild-living species [12]. A comprehensive synthesis of the psycho-acoustic literature of noise effects on humans showed that intermittent sounds have a consistent negative influence on task performance [42]; it remains to be tested whether this pattern also generalizes to wildlife populations.

Sound Propagation in Anthropogenic Landscapes

Landscape structure affects the propagation of sounds in the environment in several ways. As a rule of thumb, the power of sounds, expressed on a decibel scale, attenuates by 6 dB with every doubling of the distance in the free field (i.e. in open air or water). However, physical barriers and vegetation screens will cause sounds to attenuate more rapidly than that a phenomenon called “excess attenuation” (EA ; dB m^{-1}). These impacts can be quantified through models such as Aylor’s equation, which translates in mathematical terms the EA of sounds travelling through a vegetation patch [43]:

$$EA = 3 \left[1 + \exp \left(0.3 - 0.5 \frac{2\pi f}{c_a} LW \right) \right] \left[\sqrt{FL} \right], \quad (1)$$

where f is the sound frequency mode (Hz), c_a the sound speed in air, LW is the mean leaf width (m), F the foliage area per unit volume ($\text{m}^2 \text{m}^{-3}$) and L the vegetation screen width (m). The equation reminds us that EA gets higher (sound is attenuated in excess) by increasing any of the above variables.

Excess attenuation is a highly complex process influenced by a multitude of factors, including source frequency,

meteorological conditions and the presence of obstacles (e.g. ground, vegetation, or topographical features) in the path between the source and the receiver [44]. For example, ground inference may be destructive (i.e. attenuation) or constructive (i.e. enhancement); hard surfaces, often associated with industrial activity, reflect sound waves rather than absorbing them [45]. Conversely, acoustically soft surfaces, which are often naturally occurring (i.e. fresh snow, moss, loose substrates), can lead to decreased noise levels [44]. The vegetation may also affect the propagation of low-frequency sounds because roots and associated litter help maintain soft soil conditions, which promotes attenuation via the ground effects [46]. Larger physiognomic structures like topographic features also strongly influence sound propagation, which in this case is mediated by wind and temperature patterns that covary with altitude and the position of acoustic receivers [see 25]. As such, the propagation of sound is intrinsically linked to the physiognomic structure of landscapes.

Theories associated with landscape ecology were introduced to freshwater systems somewhat later than terrestrial systems but have since become important to freshwater conservation [47, 48]. We argue that soundscape ecology is equally important in terrestrial and freshwater systems; however, similar concepts do not translate easily between these systems because sound propagates differently in water than in air. For instance, sound attenuation of 6 dB for every doubling distance may not apply in shallow waters where a lower attenuation coefficient of 3 dB (cylindrical spreading) is often preferred (e.g. [49]). Furthermore, underwater sounds do not propagate effectively below a cutoff frequency (f_{cutoff} ; Hz) determined by water depth and the specific impedance of the substrate [50]:

$$f_{\text{cutoff}} = \frac{c_w}{4H_c \sqrt{1 - c_w^2/c_s^2}}, \quad (2)$$

where H_c is the height of the water column (m), c_w the sound speed in water (m s^{-1}) and c_s the sound speed in substrate (m s^{-1}). While objects such as leaves and stems rapidly attenuate the high-frequency modes in air, it is the low frequencies that may not propagate in shallow waters. This results in fundamental differences in how land use changes affect terrestrial and freshwater soundscapes. Furthermore, damming and dredging activities in rivers influence water depth, discharge and velocity, with immediate consequences on the underwater soundscape. Indeed, the complex interplay between water depth, velocity and discharge drastically changes the power spectrum of underwater sounds [51, 52]. Freshwaters are, therefore, acoustically patchier than terrestrial landscapes because the power level and dominant frequency of underwater sounds fluctuate rapidly over space, sometimes over only a few meters. Thus, resource exploitation and human activities change not only the source and prevalence of underwater

sounds but also the way they propagate and attenuate in the environment.

Novel Sonic Habitats

Several concepts in landscape ecology can help us better conceptualize impacts of soundscapes on wildlife. The most straightforward of these concepts is that of habitat loss. Habitat loss in landscape ecology is the process of converting existing natural habitats, such as forests, wetlands, or reproduction sites, into inhospitable habitats, typically as a result of human activities. Otherwise, suitable sites may still be avoided if they do not fulfill basic acoustic requirements (e.g. detection of mating calls, absence of non-analog anthropogenic sounds), so modified soundscapes may lead to functional habitat loss or degradation.

Relatively few experiments have effectively quantified the amount of functional habitat loss that is strictly caused by anthropogenic sounds. Sound addition experiments have played anthropogenic sound or “noise” recordings, while assessing behavioural responses of frogs [53], owls [54] and passerines [55] in their natural environment. However, recordings in these experiments are usually played for a limited time, which allow assessment of behavioural plasticity but not sound avoidance per se. Similarly, playback experiments in aquatic tanks have been used to study the effect of motorized boats on fish growth and survival [56–58] but have often yielded inconclusive results that do not generalize easily. In another tank experiment, common sole (*Solea solea*) larvae were exposed to pile driving sounds reaching up to 206 dB (re 1 μ Pa), which did not result in differential mortality between exposure and control groups [59]. Several other studies have attempted to disentangle the effects of traffic sounds from the actual presence of roads using statistical approaches. Two independent meta-analyses on the topic reached to a similar conclusion for birds [60] and anurans [61]; that is, species distribution is typically unaffected by traffic sounds when considered independently of other confounding factors, such as distance to the road, road density and adjacent land cover type.

Despite the above difficulties, it is possible to find conclusive studies on anthropogenic sound avoidance behaviour. Among these is an ongoing sound removal experiment in New Mexico that compares silent natural gas well pads with noisy compressor stations, while controlling for landscape infrastructures. This body of work reported direct negative effects on bird fitness [62] and bat species abundance [29], as well as increasing bird nesting success as an indirect effect of nest predators avoiding the louder compressor stations [13]. In parallel, “phantom road” studies used traffic recordings for landscape-scale sound addition experiments. One particularly influential set of experiments broadcasted road traffic sounds

during the autumn avian migration period at a stopover site in Idaho, USA. Researchers demonstrated avoidance behaviour for many bird species [63], particular among younger individuals [64•], and demonstrated that birds exposed to traffic sounds put on less weight during migration stopover [9]. These experiments successfully demonstrated functional habitat loss and degradation as a result of anthropogenic sounds. However, to the best of our knowledge, the above findings have not been replicated in other systems or taxonomic groups. For instance, a long-term study evaluated the impact of highway construction and playback traffic sounds on endangered golden-cheeked warblers in urban Texas and found no evidence of a negative effect on fly away (avoidance) responses or bird densities [65•]. Another phantom road experiment was conducted on three rainforest mammal species that were known to exhibit road avoidance behaviour [66], which showed that traffic sounds did not act as a barrier to movements across the speaker line for any of the species. Comparable sound removal or sound addition (phantom ship) experiments do not currently exist for assessing the sound avoidance response of whole communities in freshwater ecosystems (but see [4, 67]). Clearly, further research is required to understand the effects of anthropogenic sounds on functional habitat loss.

Sonic Conditions Near Habitat Edges

Habitat edges present another concept in landscape ecology that is strongly linked to acoustic conditions. Habitat edges may be a product of natural processes (e.g. ecotones) or resource exploitation activities that generate abrupt habitat transitions (e.g. [68, 69]). Because of these transitions, microclimatic factors such as solar radiation, temperature and wind may be altered near edges [70], and this can affect the soundscape due to changes in vegetation [71] and forest floor characteristics [72]. Furthermore, when edges are maintained over time, secondary responses of vegetation can entail the growth of a wall of dense vegetation [73]. This so-called edge sealing is expected to change sound attenuation rates by providing fewer gaps between adjacent trees or plants, increasing the likelihood of incident sound waves being scattered or absorbed [74]. Thus, edge sealing can lead to outgoing sounds being trapped inside habitat patches and incoming sounds to attenuate sharply at the boundary [75, 76]. Conversely, changes in forest floor characteristics near edges might result in further propagation of sounds, particularly at higher frequencies [45]. By affecting sound propagation, edges contribute to the acoustic patchiness of the soundscape.

Edges may also have large effects on the composition of sonic communities (e.g. [68, 77]). Production of biogenic sounds may increase at edges if the abundance of particularly vocal species is increased there or if species diversity increases

near edges [24]. In comparable circumstances, competition for the acoustic space may increase between species that do not usually cohabit (e.g. interior vs. edge vs. open-habitat species). Edge species are also more directly exposed to anthropogenic sounds, especially if habitat loss is associated with vegetation clearing and construction of hard reflective surfaces (e.g. pavement, buildings). In particular, changes in wind velocity and shear stress measured at forest patch boundaries are likely to affect the “background noise” environment of birds (and other organisms) in these habitats [25, 78]. Edges may also affect trophic interactions if, for instance, anthropogenic sounds modify the spatial distribution of one species at the advantage of the other or if a predator depends on acoustic signals to detect its prey, or vice versa (e.g. [37]).

Auditory Sensitivity of Species Across Taxonomic Groups

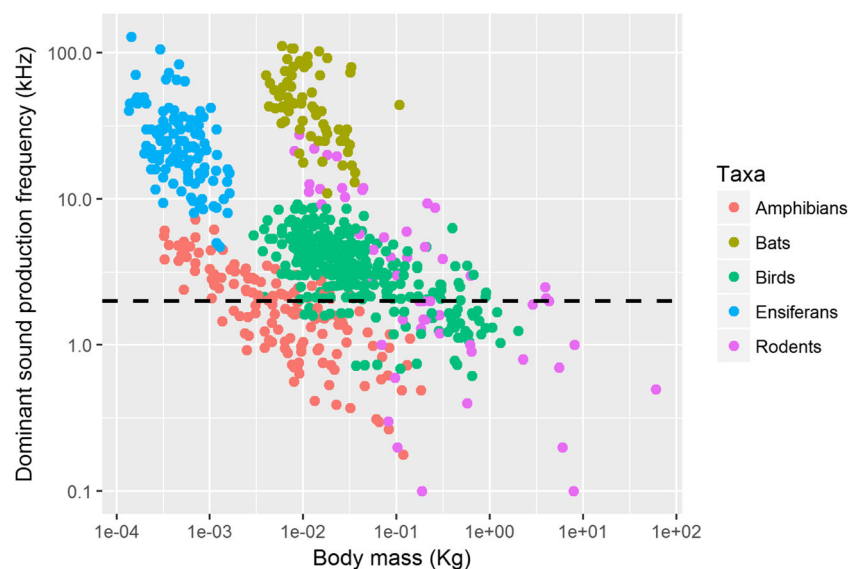
As different organisms perceive sounds differently, some species are likely to be affected by soundscape changes such as those discussed above, while other species are not. Understanding the sensitivity of animals to sounds is thus imperative to identify which species are most likely to be affected by anthropogenic changes to soundscapes, illustrating the importance of evaluating these issues through the lens of sensorial ecology. Sensory drive theory proposes that habitat selection and behavioural adaptation are driven by sensory processes including vision, audition and olfaction [79]. It defines the environment as a combination of sensorial signals (e.g. physiognomic structures, sounds and smells) that are perceived differently among individuals and species. More specifically, comparing organisms based on their visual and auditory acuity may help us predict which ones are most

sensitive to anthropogenic sounds. Auditory acuity in this context is the ability to detect sounds of a given power and frequency in a quiet environment (e.g. audiogram test), while visual acuity is the ability to detect objects of a given size against a contrasted background (e.g. Snellen chart test). Sensorial acuity in animals is in large part attributable to anatomic constraints imposed on the power and frequency of vocalizations [80, 81], the size of eyes [82] and of the inner ears [83].

To understand sensitivity to anthropogenic sounds across a wide range of taxa, we summarized the functional relationship between body size and auditory traits to illustrate the variation that exist among species and taxonomic groups. We queried the following keywords in Google Scholar to find the relevant literature: (fish OR bird OR frog OR anuran OR bat OR rodent OR katydid OR cricket) AND (“dominant frequency” OR “carrier frequency”). Functional relationships derived from 696 terrestrial animal species show that the dominant frequency of biogenic sounds decreases with increasing body size in all taxonomic groups (Fig. 2). Parmentier and Fine [20•] reported similar negative relationships across a range of fish taxa known to produce sounds. Projection of Parmentier and Fine’s values to our trait space would position soniferous fish on the same relationship as amphibians (Fig. 2, not shown).

Functional relationships to auditory and sound production traits are key to understanding how organisms in terrestrial and freshwater ecosystems respond to soundscape changes. Anatomical constraints imposed on sound production suggest that amphibians and rodent species should be more affected by energetic masking, as their dominant frequencies are low, whereas ensiferans, bat and small-sized bird species should be able to effectively transmit sounds at higher frequencies in the presence of anthropogenic sounds (Fig. 2). Consistent with this hypothesis, compensatory responses to anthropogenic

Fig. 2 Body size relationship to the dominant sound production frequency of 696 animal species in five taxonomic groups. Dominant frequencies were extracted from several sources: birds [84–87], amphibians [88, 89], bats [90, 91], rodents [92] and ensiferans (crickets and long-horned grasshoppers) [93, 94]. Similar relationships have been reported for individual fish [20•]. The dashed line marks the 2 kHz upper limit for the dominant frequency of typical anthropogenic sounds [41]



sounds have been observed among large-sized organisms producing sounds at lower frequencies in birds [20, 95•], bats [29] and ensiferans [96, 97]. The above studies emphasized energetic masking as one mechanism that explains the sensitivity of some species to anthropogenic sounds. However, other mechanisms, such as informational masking (e.g. distraction) and threat perception, may also be influential [1, 12, 22].

Additional functional relationships may explain the sensitivity of freshwater fish species to anthropogenic noise. First, it should be noted that two-thirds of the world's fish species inhabiting lakes and rivers bear specialized adaptations connecting the swim bladder to the inner ear, also called the Webber apparatus [98]. The latter adaptations increase the auditory acuity of fish, especially in the higher frequencies [99], and may provide them with an advantage in shallow waters. Second, whenever fish are subjected to incoming sounds, theory and observation tell us that the swim bladder's resonant frequency is inversely proportional to body length [100], suggesting that auditory acuity may vary considerably among fish species, as well as through ontogeny. The influence of swim bladder size on audition is supported by early experiments that measured the auditory acuity of fish with deflated swim bladders [101] or at different stages of ontogenic development [102]. The central role of gas-filled structures on auditory acuity is further emphasized through the great diversity of swim bladder shapes observed in fish, whether or not species possess hearing specializations (reviewed in [103]). Integration of many sensorial traits (e.g. presence of the Webber apparatus, swim bladder size and biogenic sound frequencies) is therefore critical for interpreting fish responses to anthropogenic sounds. Further research is needed to unfold the incredible diversity of auditory traits and adaptations in freshwater fish.

Conclusions

It is clear from the above sections that resource exploitation and other human activities change soundscapes both directly, by affecting sound production and propagation, and indirectly, by modifying landscape structure and species distribution patterns. Intermittent anthropogenic sounds tend to be louder than enduring sounds of the same origin, are concentrated in the lower frequencies, create more patchy soundscapes and are more difficult to adapt to than enduring and predictable sounds. Nonetheless, it is also clear that due to sensorial and behavioural differences among species, negative effects of anthropogenic sounds that have been reported in the literature are unlikely to generalize easily to other taxonomic groups and geographic contexts. These conclusions make it obvious that we need to do far more research to achieve the level of understanding needed to mitigate the effects of anthropogenic

sounds on wildlife. In particular, replicable, long-term, landscape-scale experiments that isolate anthropogenic sounds from other factors are necessary to generalize results in soundscape ecology.

Prioritizing research in an increasingly noisy world requires a proper understanding of the auditory sensitivity of species, the characteristics of anthropogenic sounds (i.e. intermittent or enduring, high- or low-frequency components) and how sound production and propagation is affected by landscape structure. This understanding will allow us to make testable predictions about which species should show avoidance or compensatory behaviours in different environmental contexts. For example, one interpretation of the acoustic adaptation hypothesis (AAH) proposes that, all else being equal, species producing sounds at higher frequencies should be favoured in open habitats [104]. However, the smaller body size of species associated with dense habitats may constrain them to produce sounds at higher frequencies, thus confounding the effects of landscape structure and biogenic sound production. This conundrum might explain why the AAH was not supported in studies on bird, anuran and rodent communities [88, 92, 105]. One promising research avenue in the context of the AAH is to understand the adaptive value of hearing in organisms that have good auditory acuity but do not commonly produce sounds, as in many reptile and fish species.

While animal populations are subjected to a multiplicity of environmental stressors acting in interaction (e.g. habitat loss, edge effects, energetic and informational masking by sounds), their functional response to these stressors is also multi-dimensional. We argued here that body size imposes fundamental constraints on the sensorial abilities of species. Size is also the single best predictor of animal extinction risk, with large-sized species of birds, fishes, mammals and reptiles at increased risk of being listed as “threatened” on the IUCN red list [106]. In many taxonomic groups, body size also correlates strongly with visual acuity [82], brain size [107] and running, swimming or flying speed [108]. However, there is still a large amount of variation in sensorial traits that is not explained by body size or phylogeny. Key sensorial traits, like the inter-aural distance and eye diameter, can be extracted easily from photographs and expressed relative to head or body size. In fish, the swim bladder size can be estimated using echo-sounding techniques. For sonic animals, it is increasingly straightforward to estimate the dominant sound production frequency from digital recordings [41, 109]. Further research on species' sensorial traits would provide a framework with which to scale responses to anthropogenic sounds from individuals to communities and better predict the impact of human activities on terrestrial and freshwater ecosystems.

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Compliance with Ethical Standards

Conflict of Interest The authors have no conflict of interest to declare.

Human and Animal Rights and Informed Consent This article contains no studies with human or animal subjects performed by the authors.

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