How chronic anthropogenic noise can affect communities

Annebelle C.M. Kok[1,2], Boris Berkhout[3], Nora Carlson[4,5], Neil Evans[6], Niki Khan[7], Dominique Potvin[8], Andrew N. Radford[9], Marion Sebire[10], Saeed Shafiei Sabet[11], Graeme Shannon[12], Claudia A.F. Wascher[13]

[1] Marine Biology lab, Groningen Institute of Evolutionary Life Sciences, Rijksuniversiteit Groningen, Groningen, the Netherlands

[2] LAcoustic Ecology lab, Scripps Institution of Oceanography, University of California San Diego, La Jolla, USA

[3] FNWI, University of Amsterdam, Amsterdam, Netherlands

[4] Juanes Lab, School of Biology, University of Victoria, Victoria, BC, Canada

[5] Suzuki Lab, Graduate School of Science Faculty of Science, Kyoto University, Kyoto, Japan

[6] School of Biodiversity One Health and Veterinary Medicine, University of Glasgow, Glasgow, UK

[7] School of Animal, Rural and Environmental Sciences, Nottingham Trent University, Southwell, UK

[8] School of Science, Technology and Engineering, University of the Sunshine Coast, Petrie, Australia

[9] School of Biological Sciences, University of Bristol, Bristol, UK

[10] Cefas Weymouth laboratory, Weymouth, UK

[11] Fisheries Department, Faculty of Natural Resources, University of Guilan, Sowmeh Sara, Iran

[12] School of Natural Sciences, Bangor University, Bangor, UK

[13] Behavioural Ecology Research Group, School of Life Sciences, Anglia Ruskin University, Cambridge, UK

*** Correspondence:**
Corresponding Author
a.c.m.kok@rug.nl

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Abstract

Anthropogenic noise is a major pollutant in terrestrial and aquatic ecosystems. Since the industrial revolution, human activities have become increasingly noisy, leading to both short term and chronic disturbance of a wide variety of animals. Chronic noise exposure can affect animals over their lifespan, leading to changes in species interactions and likely altering communities. However, the community-level impacts of chronic noise are not well understood, which impairs our ability for effective mitigation. In this review, we address the effects of chronic noise exposure on communities and explore possible mechanisms underlying these effects. The limited studies on this topic suggest that noise can affect communities by changing the behavior or physiology of species in a community, which results in direct or knock-on consequences for other communities in the ecosystem. Major knowledge gaps remain due to

the logistically complex and financially expensive nature of the long-term studies needed to address this question. By identifying these gaps and suggesting approaches to address them, we provide a road map toward mitigating the effects of a noisy world.

1 Chronic noise changes communities, but how?

1.1 Introduction

Anthropogenic noise is recognized as a major global pollutant that has considerable implications for human health (Hammer et al., 2014; Matheson et al., 2003; Mohamed et al., 2021) and the behavior, physiology and fitness of wildlife (Barber et al., 2010). Indeed, a substantial body of research has been published over the past two decades that has explored the effects of noise pollution on animals across terrestrial and aquatic ecosystems (Duarte et al., 2021; Jerem & Mathews, 2021; Shannon et al., 2016; Sordello et al., 2020). Anthropogenic noise is a relatively recent global phenomenon that has increased markedly since the industrial revolution both in terms of the level of sound exposure and geographical extent. Research conducted in the US has demonstrated continental-wide changes in the soundscape that extend well beyond the boundaries of urban areas (Mennitt & Fristrup, 2016), with 63% of protected areas experiencing sound exposure double that of the ambient level (Buxton et al., 2017). As such, noise presents a major selective force which has the potential to restructure wildlife communities and even drive evolutionary change (Swaddle et al., 2015). At the same time, noise does not persist in the environment like many other pollutants, as was evidenced during the COVID-19 pandemic when lockdown measures led to sustained global quieting (Lecocq et al., 2020).

Field-based studies and laboratory experiments have provided considerable evidence that exposure to noise can cause a wide range of ecological impacts to wildlife (Jerem & Mathews, 2021; Kunc & Schmidt, 2019; Shannon et al., 2016). These include changing spatial distribution and deterring wildlife from important feeding and breeding areas, or interfering with crucial biological functions such as foraging performance (more food handling errors and discrimination errors), predator avoidance, prey detection and conspecific communication. Furthermore, there are direct physiological costs associated with exposure to noise from increasing stress hormone levels (Troïanowski et al., 2017) to reduced sleep (Grunst et al., 2021). These varied impacts may lead to negative fitness consequences for the individual, population and wider animal community (Francis & Barber, 2013; Slabbekoorn et al., 2010). The effects of noise exposure have been documented across a wide range of taxa and are driven by four key mechanisms that are not necessarily mutually exclusive: 1) Noise masks critical sounds including communication of conspecifics and cues of approaching danger, 2) noise distracts animals from attending to pertinent information in the environment, 3) noise is perceived as a direct threat, thereby altering behavioral responses of the animal, and/or 4) noise initiates chronic stress, leading to long-term behavioral and physiological changes in the animal.

1.2 Definition of chronic noise exposure

Although there have been considerable advances in our understanding of the biological responses associated with anthropogenic noise exposure over the past two decades, most of the research has been conducted using comparatively short-term experiments and observations (Jerem & Mathews, 2021; Shannon et al., 2016). In addition, these studies have predominantly focused on a single species, in either captive or free-ranging environments. However, transport networks, industry and urban environments are major sources of chronic anthropogenic noise that permeate natural and human transformed environments over the long-term. These noise sources are also characterized by acoustic energy mainly being concentrated in the low-frequency spectrum (<2Khz), which travel further than high frequency sounds and potentially impact a wide range of species simultaneously.

To fully understand the impacts of chronic anthropogenic noise exposure on animal communities it is necessary to conduct long-term studies (Jerem & Mathews, 2021). These need to consider the effects of chronic exposure and lasting impacts after exposure has ended. However, a definition of chronic exposure is rarely given (Jerem & Mathews, 2021) and short-term and chronic exposure are on a continuum, making it difficult to classify exposure events in the field. For example, repeated short bursts of exposure (e.g. sonar) over longer periods (a few times a year for years) differ from medium term exposure (continuous for weeks, e.g. construction site) in their effects. Additionally, what is considered chronic will also depend on the life span of the organism. Animal life spans range from weeks to centuries (Austad, 2010). Construction of a pipeline that takes a year would thus be multi generation exposure for some animals, whilst only a brief exposure for others. Finally, the effects of chronic exposure are expected to impact multiple species in the community, and should therefore be long enough to affect species with varying lifespans. Therefore, we suggest the rather vague, but practical chronic exposure definition of: ‘Exposure throughout the lifespan of an animal, at regular enough intervals to have the potential of lasting impacts for the community.’

1.3 State of the knowledge

We conducted a search of peer-reviewed journal articles that have been published since 1970 and have addressed the effects of noise on animal communities. Our article search used the datasets provided in four previous systematic review papers (Duarte et al., 2021; Jerem & Mathews, 2021; Shannon et al., 2016; Sordello et al., 2020), as well as using the Web of Science and Google Scholar search engines to identify any further papers that have been published in the last two years. The search terms we used were “anthropogenic”, “wildlife”, “noise”, and “community”. We specifically focused on studies that explored whether noise exposure affected community-level composition (e.g. changes in abundance and diversity of multiple species) over time. The dataset comprised 48 papers published between 1995-2021 (Table 1, S2). Overall, the most common method to explore the community effects of noise was through direct observation (n=29) followed by playback (n=10) and natural experiment (n=9). Seventy-nine percent of the studies (n=38) reported negative effects of noise exposure in one taxonomic group (decreased abundance/species richness, decreased nesting, decreased offspring survival/hatching success) while only one study documented a positive effect (increased abundance/species richness). The remainder revealed either no effect (n=7) or mixed effects within the same taxonomic group (n=7), with the direction depending upon the species. Birds featured in 38 (79%) of the studies. Seventy nine percent of the studies were conducted in either North America or Europe (n=38). Seventy one percent of the studies (n=34) explored whether noise influenced abundance and/or species diversity.

The early research on community-level effects of noise was conducted by observing the abundance and diversity of bird species as a function of distance from a chronic noise source, such as a busy roadway. This proved an effective method for understanding the effects of noise with clear evidence that species composition, density and abundance were negatively impacted the louder the noise levels (Reijnen et al., 1995, 1996; Reijnen & Foppen, 1995). Later studies provided further evidence and highlighted how species with low frequency calls that overlapped considerably with traffic noise were likely to be impacted to a much greater extent than species with higher frequency calls (e.g. lower occupancy; Goodwin & Shriver, 2011). However, there were challenges associated with this observational approach such as accounting for confounding variables, including habitat fragmentation, chemical pollution, elevated human activity and increased mortality (e.g. vehicle strike), that also occur to a greater extent in close proximity to roads (Summers et al., 2011).

The expansion of gas extraction across North America led to the development of natural experiments where noise-generating compressor stations could be compared with quiet well pads. These natural experiments largely controlled for the confounding variables associated with other forms of disturbance (such as habitat transformation) and explicitly investigated the effects of noise on the abundance and diversity of bird species in an otherwise natural environment (Bayne et al., 2008). These studies demonstrated that occupancy, diversity and abundance of avian species was negatively impacted by anthropogenic noise (Bayne et al., 2008), while also revealing that species exhibited varying levels of sensitivity to noise exposure depending upon the extent of vocal communication masking that they experienced (Francis et al., 2009; Francis, Ortega, et al., 2011). Larger bodied birds with lower frequency calls were found to use noisy areas considerably less than smaller bodied species with higher frequency vocalizations, which presents a strong selective force shaping avian community structure and species interactions such as predator-prey relationships (Francis et al., 2009; Francis, Ortega, et al., 2011). However, researchers working in grassland prairies documented that noise had less of an effect on bird community compared with the presence of gas extraction infrastructure (Nenninger & Koper, 2018). The physiological costs of noise have also been documented using this natural study system demonstrating impacts to glucocorticoid-signaling and reduced fitness across bird species (Kleist et al., 2018), while truly long-term cascading impacts of noise exposure were recently documented in a study that revealed chronic noise exposure (15 years) impacted seedling recruitment and woody plant community structure (Phillips et al., 2021). Interestingly, these effects were still in evidence following the removal of noise.

Scientists have also employed playback experiments across the landscape to experimentally assess the effects of introduced noise on wildlife communities. The advantages of the playback approach include the ability to control the specific location and duration of noise exposure, as well as the noise source sound level. Furthermore, the playback approach allows for the effects of noise to be investigated in isolation of confounding variables that are generally associated with noise disturbance. The first of these landscape-level studies broadcast traffic noise along a 500 m ‘phantom road’ in habitat favored by migratory birds, with the researchers documenting a 25% reduction in bird abundance during playback periods (McClure et al., 2013). Further work by this research group from Boise University revealed that 31% of the bird community avoided the phantom road, while those individuals that remained experienced a reduction in body condition that was associated with an altered trade-off in foraging and vigilance (Ware et al., 2015). There were also age effects with younger birds being impacted by noise to a greater extent than adults (McClure et al., 2017). Subsequent research from Japan has demonstrated similar effects of introduced traffic noise on invertebrates, particularly species that rely on acoustic signals in the environment (Senzaki et al., 2020), while breeding birds in North American grassland prairies declined in abundance when

exposed to playbacks of noise associated with energy extraction at the landscape scale (Cinto Mejia et al., 2019; Rosa & Koper, 2022).

2 Why do we see differences in community composition due to noise?

Noise can have a profound effect on community composition through a variety of mechanisms (Fig. 1). It can directly impact local abundance of different species due to avoidance, increased mortality, and decreased recruitment, while indirectly impacting predator/prey and parasite/host interactions, competitor interactions, and species-driven ecosystem structure. Noise can have such a broad impact because different species within a community respond differently to noise, and these differences in species responses (e.g., declines, altered predator-prey relationships, etc.) alter the community composition and structure, resulting in wide-reaching changes in the community as a result of introduced or increasing anthropogenic noise (fig. S1).

2.1 Noise avoidance

One of the direct influences of noise on an individual's or species' presence in an area is avoidance; many species will temporarily (Bunkley et al., 2017; Carral-Murrieta et al., 2020; McClure et al., 2013; Slotte et al., 2004; Ware et al., 2015) or permanently (Ciach & Fröhlich, 2017; Francis et al., 2009; Herrera-Montes & Aide, 2011; Morton & Symonds, 2002; Nicholson et al., 1992; Pearson et al., 1992; Thompson et al., 2010) avoid noisy areas. A variety of migrating bird species, for example, avoided stopping over in noisy areas, even though they used the same areas in non-noisy conditions (McClure et al., 2013; Ware et al., 2015), while many insects demonstrate reduced abundance in noisy areas (Francis et al., 2009). Those responses varied between species. Different species respond differently to noise (Bunkley et al., 2017; Shafiei Sabet et al., 2016; Voellmy et al., 2016), and while some species may disappear entirely from a noisy area (Voellmy et al., 2016), others may not have as drastic a decline (Bunkley et al., 2017; Voellmy et al., 2016), or, in some cases, may even increase (Bunkley et al., 2017; Voellmy et al., 2016), altering the composition and interactions of the species remaining.

Changes in one species' local presence can have indirect consequences across trophic and taxonomic lines, especially if those relocating are predators or parasites. For example, while bird abundance and diversity decreased near chronic playback of traffic noise, grasshoppers and odonates decreased in areas far from the traffic noise, likely because their predators relocated to those places (Senzaki et al., 2020). Changes in the predator assemblage can alter both the communities they move to (increased/different predation pressure) or those they move from (lower/different predation pressure). They may alter the predator/prey relationships with third parties as predators may be forced to switch to uncommonly eaten prey or start eating prey they have never hunted before. Indirect effects of noise can also fundamentally alter the habitat entire species communities live in, for example, if important species like seed dispersers are impacted. By altering the presence of both pollinators and seed predators/dispersers, noise has been shown to alter both the tree and flower communities that make up ecosystems (Francis et al., 2012; Phillips et al., 2021).

2.2 Increased mortality

While avoidance is a common strategy many species employ that results in changes in community composition, chronic noise can alter species abundance through a number of other mechanisms, including increased mortality. Noise can directly lead to individual mortality through noise-induced permanent injury (excluding hearing loss) or reduction of predator detection. To our knowledge, no examples of noise induced injury have been demonstrated in terrestrial systems; however, they are unfortunately common in marine and other aquatic systems. Noise can kill by causing injuries such as swim bladder and kidney rupture in fish (Halvorsen et al., 2012; Jenkins et al., 2022; National Academies of Sciences, 2011), or through alterations in behavior that can lead to death (e.g., diving behavior (Fernández et al., 2005), strandings (Bernaldo de Quirós et al., 2019)). Though this intensity of noise (e.g., pile driving, sonar, etc.) tends to be less chronic in one specific location, it continues throughout the ocean, and could potentially cause alterations in population distributions or biogeography as these types of activities may cause short-term but drastic extreme local extinction at the site of noise which may echo into the wider ecosystem.

Noise can also increase mortality via predation by impacting a prey-species’ ability to detect or respond to acoustic predator cues. For example, noise can mask important anti-predator calls (e.g., mobbing calls; Jung et al., 2020), distract from alarm signals (e.g., chemical alarm signals in fathead minnows; Hasan et al., 2018), or reduce response to predation (Simpson et al., 2015, 2016), all of which may explain the overall higher mortality due to predation that has been shown in some noisy areas (Simpson et al., 2016). This specific effect of chronic noise can alter predator-prey relationships if predators preferentially switch to new or less commonly hunted prey as they become easier prey in noisy areas, exacerbating that prey’s local decline, while less drastically affected species may then be temporarily released from predation pressure if their anti-predator behavior remains intact or even increased (Neo et al., 2014; van der Knaap et al., 2022; Voellmy et al., 2014). Similarly, noise can affect parasite species’ ability to find their hosts. Both frog-biting midges (Corethrella spp.) who parasitize túngara frog (Engystomops pustulosus; McMahon et al., 2017) and Ormia ochracea which parasitize variable field cricket (Gryllus lineaticeps; Phillips et al., 2019), were less abundant in noisy areas, likely as a result of being unable to localize their prey, which alters the threat of parasitism to their hosts.

2.3 Stress and body condition

Though not as immediately fatal, noise can lead to stress and poorer body condition. Poorer body condition can be a result of increased glucocorticoid concentrations, decreased foraging success, and changes in social relationships and behavior. Noise can result in activation of the hypothalamic–pituitary–adrenocortical (HPA) axis. If the animal is unable to escape the source of stress, the HPA system remains activated (Pravosudov et al., 2001), and the short-term physiological or behavioral changes that ameliorate stress and promote survival can become deleterious. Extended bouts of stress events not only deplete energy reserves, but also impair growth and immune function, accelerate aging, and negatively impact cognitive ability and atrophy of nerve cells in the brain (Ellenberg et al., 2007; Pravosudov et al., 2001; Sims & Holberton, 2000; Wingfield et al., 1998; Wingfield & Kitaysky, 2002). Species in noisy conditions often show altered levels of stress hormones and might show increased stress-responsiveness (Leshyk et al., 2013). For several bird species, higher levels of stress hormones have been reported (Injaian et al., 2018; Kleist et al., 2018; Wasser et al., 1997), which have been shown to make individuals susceptible to increased rates of disease (Anderson et al., 2011; Tu et al., 2022), shorter lives (MacDougall-Shackleton et al., 2009; Tu et al., 2022), and, in the case of young, poorer growth and development (Injaian et al., 2018) and lower hatching success (Kleist et al., 2018).

Studies on short-term noise exposure show that noise can cause changes in foraging success through changes in an individual’s foraging behavior (e.g., lower foraging intensity during noise; Payne et al., 2015, increased vigilance while foraging, thereby decreasing total foraging time, Shannon et al., 2014), decreasing foraging efficiency via increasing food handling errors (Shafiei Sabet et al., 2015) and food discrimination error (Purser & Radford, 2011), an alteration of prey behavior (e.g., increased anti-predator behaviors (Neo et al., 2014; van der Knaap et al., 2022; Voellmy et al., 2014)), masking important prey cues (Mason et al., 2016; Senzaki et al., 2016; Siemers & Schaub, 2011)), or damage to a predator’s hearing (e.g. Kastelein et al., 2016; Ladich, 2013; Wysocki & Ladich, 2005) removing the ability to detect prey sounds. This decreased foraging success in noisy areas may account for species that show decreased body condition in noisy areas (Ware et al., 2015). However, the studies on this topic investigated short-term noise exposure, which leaves the possibility that animals recover by increased foraging after the noise exposure has ended. The effects of chronic noise exposure on long-term foraging success are still unknown.

2.4 Decreased reproductive success

Aside from causing avoidance and increased mortality, noise can alter local populations by impacting reproductive fitness. This can occur through several mechanisms including decreased breeding rates and decreased juvenile recruitment, as well as altered resource allocation. Noise, for example, can reduce breeding rates though disrupting detection of potential mates (e.g., greater sage grouse (Blickley et al., 2012), ovenbirds, Seiurus aurocapilla (Habib et al., 2007)) and alter or reduce mating behavior (e.g., decreasing display, de Jong et al., 2018). In a similar fashion to causing direct mortality and poor condition, noise can result in lower clutch size (Halfwerk et al., 2011), hatching success (Kleist et al., 2018), juvenile growth/condition (Kight et al., 2012; Lagardère, 1982), and juvenal survival (de Jong, Amorim, Fonseca, Fox, et al., 2018; de Soto et al., 2013; Nedelec et al., 2017). Many of these effects are thought to be either a result of changes in parental behavior (e.g., increase aggression and decreased attention to young, Nedelec et al., 2017), increases in larval/juvenile mutation [54], and/or via direct or indirect interactions with elevated stress hormones resulting in higher mortality or poorer condition (e.g. Injaian et al., 2018; Silverin, 1986). In combination, this is especially damaging as populations under chronic stress are less likely to recover, due to increased mortality and decreased fitness of remaining adults. Fitness costs can fundamentally influence population dynamics; for instance, changes in breeding success can drastically alter population size and range by decreasing the numbers of new individuals coming into the population, and in dispersing species, potentially alter population range as a result of fewer individuals to disperse or poorer survival whilst dispersing.

By altering the abundance and/or presence of each species in a community differently, chronic noise has the ability to drastically change community structure and function via individual and population level changes that compound and amplify one another across the variety of species interactions that make up communities and entire ecosystems. This differential response across species is, possibly, one of the most important factors that causes chronic noise to have far reaching effects. By impacting species relationships, noise does not affect any one species in isolation, but through any species, affects an entire ecosystem.

3 Future directions

The impact of chronic noise on animals affects the composition of communities. Direct effects of chronic noise exposure on one species, such as population declines and long-term alterations in behavior, can lead to knock-on consequences for other species in the community. Although the growing body of work on this topic is commendable, given the expensive and logistically complex nature of long-term studies, some key knowledge gaps remain. Below, we discuss the main gaps that we see, and suggest possible approaches to fill these.

To properly understand community impacts of noise, we must compare the responses of different species in the community to noise. Species of the same community can show a variety of responses to chronic noise. For instance, birds with lower frequency vocalizations were affected more strongly by chronic compressor noise than birds with higher frequency vocalizations that did not overlap with the noise (Francis et al., 2009; Francis, Ortega, et al., 2011). However, the differences in response can follow unknown mechanisms. Changes in anti-predator behavior in response to noise exposure, for instance, can vary from diminished responses to faster responses (Kok et al., 2021; McCormick et al., 2018; Simpson et al., 2015, 2016; Voellmy et al., 2014). Furthermore, behavioral responses of animals to human-induced environmental change are not consistent between species (Gunn et al., 2022). Getting a better grip on the mechanisms that underlie these species differences in response is important, because species differences in response to noise can be a strong driver for changes in community composition.

Besides species differences in response, changing species interactions are likely to be an important influence on community change. Parasites that cannot locate their hosts (McMahon et al., 2017; Phillips et al., 2019), predators that leave an area (Fröhlich & Ciach, 2019), seed dispersers that decline in abundance (Francis et al., 2012), all will directly impact the species that they are interacting with, whether or not that species is sensitive to noise itself. Because these interactions lead to indirect effects of noise on the community, the outcome may be difficult to predict. When a predator leaves, does that always lead to a release of predation pressure for the prey, or do other predators fill up the gap? Conversely, when the prey leaves, does the predator switch prey type, or does it follow the prey to the new area? Current studies focus mostly on short-term changes due to noise exposure, while long-term changes in species interactions are likely to have a more profound effect on the community. These long-term changes may be quite different from changes on a short time scale.

Understanding the mechanisms behind community changes to chronic noise exposure will require long-term experimental studies. While a lot of the effects of chronic noise on communities have been uncovered with observational studies, understanding the mechanisms behind these effects will require long-term experimental studies. The changes in behavior that occur under short-term exposure to noise are likely to be different from long-term changes (Kok et al., 2021). A decrease in foraging behavior, for example, might not persist over time, but might be compensated for when the noise stops. While long-term experimental exposure studies are expensive and logistically challenging, the recent developments in citizen science and technology have opened up possibilities that were previously unheard of, such as continental-scale analysis of acoustic niche partitioning in frogs (Allen-Ankins & Schwarzkopf, 2022) or biodiversity monitoring of insect communities for which many species are undescribed (van Klink et al., 2022). Additionally, existing differences in chronic noise exposure in natural settings can be exploited to study community effects, as has been done for the gas compressor stations in North America (Bunkley et al., 2017; Francis et al., 2009, 2012; Francis, Ortega, et al., 2011; Francis, Paritsis, et al., 2011; Phillips et al., 2021).

Finally, to effectively mitigate effects of chronic noise pollution, we need to know what happens when the noise stops. In contrast to other forms of pollution, noise pollution does not leave traces in the environment once removed. However, does the community immediately change back to pre-noise conditions once noise is removed, or are the changes that occurred due to the noise exposure permanent? The few studies that investigated this have shown mixed results. While white-crowned sparrows reverted back to low frequency songs (Derryberry et al., 2020) and spiny chromis larvae had increased survival rates (Nedelec et al., 2022) in quieted conditions, juniper and pinyon seedling recruitment did not recover following the removal of noise (Phillips et al., 2021). The persistence of effects might depend on the time it takes for the effect to reverse, as well as the behavioral plasticity of the affected species. While the COVID-19 pandemic inadvertently created a natural experiment to test the effects of global quieting (Montgomery et al., 2021), we should also start experimentally removing noise from communities, to see if the effects of noise can truly be removed by noise mitigation. Those data will be vital in developing effective conservation strategies for the future.

4 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

5 Author Contributions

All authors conceived the idea behind the manuscript. ACMK, GS, MS, SSS, NK, NC, CAFW wrote the manuscript. GS, MS, SSS performed the literature research. NC made the figures. ACMK revised the manuscript. All authors critically reviewed the manuscript.

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8 Tables and figure headings

Table 1: Number of studies that investigated the effects of noise on communities separated by taxonomic group. N = natural experiment, O = observational, P = playback experiment. Note that studies focusing on more than one taxonomic group are featured multiple times, once per taxonomic group. Mixed effects = effects differed between or within species within the same taxonomic group.

	Taxonomic group							
	Amphibians	Arthropods	Birds	Fish	Mammals	Plants	Reptiles	Worms

Effect	N	O	P	N	O	P	N	O	P	N	O	P	N	O	P	N	O	P	N	O	P	N	O	P
Negative			1	1		1	3	18	7		2		1				1	1	1			1		
Positive								1																
Neutral		1					1	4		1														
Mixed					1	1	2	1	1		1													

Figure 1. Theoretical knock-on consequences as a result of changes in local population of one species directly affected by noise. This example shows decline in recruitment as a result of lower fecundity in female great tits and lower nestling survival. The lowered overall local population could affect a number of other species though a variety of mechanisms including: a) removing hosts for parasites (e.g., blowfly larvae), b) altering predator-prey relationships resulting in prey switching, causing declines in sympatric species due to increased predation pressure, c) removing anti-predator information resulting in higher mortality due to predation, or altering spatial use within a mixed-species community by d) opening a niche previously used by the declining species (Cimprich & Grubb Jnr, 1994), e) removing information/presence that allowed species to broaden their own microhabitat use when the declining species were present (Dolby & Grubb, 1998), or e) removing information/perceived safety that allowed different species to cross barriers such as open spaces (e.g., roads, man-made fields, etc.) (Sieving et al., 2004).