



Invading the soundscape: exploring the effects of invasive species' calls on acoustic signals of native wildlife

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Abstract The transmission and reception of sound, both between conspecifics and among individuals of different species, play a crucial role in individual fitness, because correct interpretation of meaning encoded in acoustic signals enables important context-appropriate behaviours, such as predator avoidance, foraging, and mate location and identification. Novel noise introduced into a soundscape can disrupt the processes of receiving and recognising sounds. When species persist in the presence of novel noise, it may mask the production and reception of sounds important to fitness, and can reduce population size, species richness, or relative abundances, and thus influence community structure. In the past, most investigations into the effects of novel noise have focused on noises generated by anthropogenic sources. The few studies that have explored the effects of calls from invasive species suggest native species alter behaviours (particularly their vocal behaviour) in the presence of noise generated by invasive species. These effects may differ from responses to anthropogenic noises, because noises made by invasive species are biotic in origin, and may therefore be more spectrally similar to the calls of native species, and occur at similar times. Thus, in some cases, negative fitness consequences for native species,

associated with noises generated by invasive species, may constitute interspecific competition. Possible negative consequences of invasive species calls represent an overlooked, and underappreciated, class of competitive interactions. We are far from understanding the full extent of the effects of invasive species on native ones. Further investigation of the contribution of noise interference to native species' decline in the presence of invasive species will significantly increase our understanding of an important class of interactions between invasive and native species.

Keywords Acoustic communication · Bioacoustics · Invasive species · Masking · Soundscape

Introduction

The sound profiles of many landscapes are changing (Barber et al. 2009; Shannon et al. 2016b). The soundscape, i.e., the composition of sound in a landscape, typically consists of biotic sounds, such as animal vocalisations, and abiotic sounds, such as wind and rain, but worldwide, soundscapes are becoming dominated by novel noises (Pijanowski et al. 2011). In particular, anthropogenic noises have changed environmental sound profiles significantly, because of an increase in both the volume, and spatial and temporal variation, of noise (Warren et al. 2006). The calls (i.e., vocalisations) of invasive species are an

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overlooked and, potentially, underappreciated source of novel noise that could also significantly alter soundscapes.

For wildlife, these changes present new challenges. Novel noises can mask acoustic signals energetically, when the noise and the signal occur at the same time, so signals must be louder for the receiver to hear them amidst the noise (Klump 1996; Brumm and Slabbekoorn 2005; Gelfand 2009). Loud, long, or similar-frequency noises are those most likely to energetically mask acoustic signals of native species (Barber et al. 2009; Shannon et al. 2016b). Even noises that are not especially similar to native species calls can cause masking. Energetic masking occurs peripherally in the cochlea, whereas another type of masking, information masking, occurs in the auditory system's central processor (Gelfand, 2009). Signals that should be audible in the cochlea, and are not energetically masked (e.g., signals that are spectrally separated from noise) can still be informationally masked by noise, because it is difficult to identify signals amidst noise (for more detail, see Chapter 10 of Gelfand, 2009). Vital information encoded in acoustic signals can be masked, effecting individual survival and reproductive success, leading to population declines and changes in community composition (Stone 2000; Habib et al. 2007; Slabbekoorn and Ripmeester 2008; Halfwerk et al. 2011b).

The vocalisations of invasive species are potential sources of novel noise detrimental to native wildlife (Both and Grant 2012; Bleach et al. 2015; Tennesen et al. 2016; Medeiros et al. 2017). Compared to anthropogenic noise, the calls of invasive species have received little research attention, limiting our knowledge of the responses of native species to invasive species' calls. The effect of invasive species calls warrants further investigation for two main reasons. First, studies of anthropogenic noise show that the reproductive success and population sizes of species that rely on detecting auditory signals can decline in response to novel noises (Stone 2000; Habib et al. 2007; Slabbekoorn and Ripmeester 2008; Halfwerk et al. 2011b). Just like anthropogenic noise, the calls of invasive species are novel to native species, but their biological origin means they have sound properties different from it. Thus, responses of native species to invasive species' calls may differ from their responses to anthropogenic noise. Second, biological invasions are increasing globally (Secretariat of the

Convention on Biological Diversity 2014). Invasive species often outcompete native species for essential resources, which may lead to population decline in native species (Davis 2003). Studies have focused on competitive interactions between invasive and native species, over shelters (Downes and Bauwens 2002), or food (McGee et al. 2015). Although largely overlooked as a negative effect, invasive species' calls represent a significant potential additional avenue for competition among species, especially given the importance of call competition within and among native species (Gerhardt and Huber 2002; Burt and Vehrencamp 2005; Otter and Ratcliffe 2005). Thus, given the possible severity of impact, the effect of invasive species' vocalisations on native species needs to be assessed.

In this review, we examine the threat to native species of vocalisations from invasive species, and identify areas in need of further research. Although the calls of invasive species could affect native species in many ways, for example by sounding threatening or attractive, this review will focus on masking of acoustic signals by invasive species' calls, the effects most likely to be important to a range of species. First, we briefly review the function and evolution of hearing and acoustic signalling in animals. Then, using the research on anthropogenic noise as a foundation, we review the effect of noisy habitats on the ability of animals to receive and process sound, and translate signals into appropriate behavioural responses. Then, to assess the potential impact of invasive species' calls on native species, we identify similarities and differences between anthropogenic noise and invasive species' calls, and describe their likely impacts on native species. To support our conclusions, we review the small number of studies that have examined the effects of invasive species' vocalisations. Finally, we recommend areas of future research required to quantify the nature and magnitude of the effects of invasive species' calls on native species.

Function and evolution of hearing and acoustic signalling

Many vertebrates can receive, recognise and respond to sounds in their native soundscapes. The evolution of hearing predates vocalisation in vertebrates, and thus, animals can often hear a wider frequency range of sounds than they can produce (Fay and Popper

2000; Barber et al. 2009). Many species recognise vocalisations and movement-related sounds produced by heterospecifics (Bradbury and Vehrencamp 1998; Goerlitz et al. 2008). For example, individuals can avoid the sound of a predator's footsteps (Magrath et al. 2007; Haff and Magrath 2010) or calls (ter Hofstede and Ratcliffe 2016), or heed the warning calls of other species (Magrath et al. 2015).

Although individuals react to many sounds, vocalisations have evolved mainly for intraspecific communication. Conspecifics can be differentiated from heterospecifics and other noises using vocalisations (Wilkins et al. 2013). For example, banded wood frogs (*Batrachyla taeniata*) respond more strongly to the calls conspecifics than those of sympatric congeners, using differences in pulse rate (Penna 1997; Penna and Velásquez 2011). Individuals are typically more sensitive to signals produced by conspecifics, because there are often tight correlations between a species' sound production and its reception capabilities (Ryan and Wilczynski 1988; Manley and Kraus 2010). Acoustic signals may also contain individual-level information that inform conspecifics about, for example, a caller's size, sex, reproductive status, or lineage (Wilkins et al. 2013). Female frogs, for example, generally prefer low frequency conspecific calls, a call trait that often indicates larger body size (McLean et al. 2012; Gingras et al. 2013).

Habitat plays a key role in the evolution of acoustic signals. Selection should favour sounds that propagate effectively in specific habitats (Morton 1975). Attenuation, or the loss of signal intensity, and sound degradation, or the loss of signal form, increase with structural complexity of habitats, and with atmospheric turbulence, caused by wind and thermal effects (Morton 1975; Bradbury and Vehrencamp 1998; Wilkins et al. 2013). For example, densely vegetated, closed forests have many reflective surfaces, reducing signal transmission distance. Longer, and lower frequency sounds travel further than higher frequency sounds, and are favoured in closed forests, as they have a greater chance of reaching the intended receiver (Ey and Fischer 2009). Convergence of signal properties in acoustic communities occupying the same habitat may occur (Morton 1975). For example, multiple *Nanorana* frog species in the Himalayas produce short duration calls within a narrow frequency band that propagate well in their noisy, stream habitat

(Dubois and Martens 1984). In contrast to signal convergence within habitats, signals may diverge in populations of the same species occupying different habitats. For example, Satin Bower Birds (*Ptilonorhynchus violaceus*) living in rainforest produce lower frequency calls than conspecifics in open forests (Nicholls and Goldizen 2006). These examples demonstrate that acoustic adaptation to habitat can drive acoustic signal evolution (Wilkins et al. 2013).

Convergence in signal design may create problems. Producing a vocalisation adapted to propagate achieves efficient signal transmission, but if multiple species produce similar signals, receivers may have difficulty identifying conspecifics. Species within a community should, therefore, evolve vocalisations that partition the acoustic space. For example, following the colonisation of the Large Ground Finch (*Geospiza magnirostris*) on Daphne Major Island in the Galapagos, sons sang faster-trilled songs than their fathers in resident Medium Ground Finches (*G. fortis*) and Cactus Finches (*G. scandens*), and by doing so, reduced call similarity with the Large Ground Finch (Grant and Grant 2010). Overlap in call traits should be avoided because the production of species-specific vocalisations allows receivers to identify conspecifics amidst the noise of the acoustic community, avoiding masking and costly errors, for example mistaking heterospecifics for conspecifics (Krause 1987, 1993). Acoustic niche partitioning, like acoustic adaptation to the habitat, is an important process thought to shape species' calls (Wilkins et al. 2013).

Acoustic signal evolution is also constrained by traits of the signalling species. Phylogenetic history may influence the sounds made by individuals (Wilkins et al. 2013) determined, for example, by morphological constraints on the signaller, such as body and beak size (Podos 2001) or neurophysiological constraints on the receiver, such as the sensitivity of hearing structures (Römer 1993). Multiple pressures and constraints, including all those outlined, influence the evolution of species-specific acoustic signals, producing signals that increase fitness in specific physical and biotic environments (Boncoraglio and Saino 2007; Wilkins et al. 2013). Thus, we expect that changes in the physical or biotic environment, such as the introduction of a novel invasive species'

call, could alter the effective transmission of acoustic cues in that environment.

The problem of acoustic masking by novel noise

Anthropogenic noise is a severe form of habitat disturbance, and has been the focus of many studies (Shannon et al. 2016b), providing an understanding of animal responses to novel noises in general. Typically, anthropogenic noise masks movement-related or vocal sounds produced by other wildlife (Francis and Barber 2013; Shannon et al. 2016b). Anthropogenic noise masks signals used by mammals (Siemers and Schaub 2010), birds (Huet des Aunay et al. 2014), amphibians (Bee and Swanson 2007), fish (Codarin et al. 2009), and insects (Bent et al. 2018). When masking happens, communication, movement, vigilance, mating and foraging can be negatively affected (Shannon et al. 2016b) (Fig. 1).

Regardless if the source is anthropogenic, if a noise is loud enough, any acoustic signal can be masked. However, short sounds are particularly easily masked, as are low frequency sounds, because ambient noise typically has higher energy in lower frequencies (Okanoya and Dooling 1990; Lohr and Dooling 1998; Brumm and Slabbekoorn 2005; Gelfand 2009). Additionally, noise occurring at the same frequency as an acoustic signal will have a significant masking effect (Klump 1996; Lohr et al. 2003; Brumm and Slabbekoorn 2005; Gelfand 2009). Anthropogenic noise is typically loud, low-frequency (Warren et al. 2006), and may be constant and long-term or chronic, making it a potent masker of (particularly low frequency) acoustic signals, potentially leading to a lack of, or atypical, responses to important cues (Francis and Barber 2013). Although long-term or chronic exposure can lead to habituation or accommodation in some cases (e.g., Smith et al. 2004; Ditmer et al. 2018),

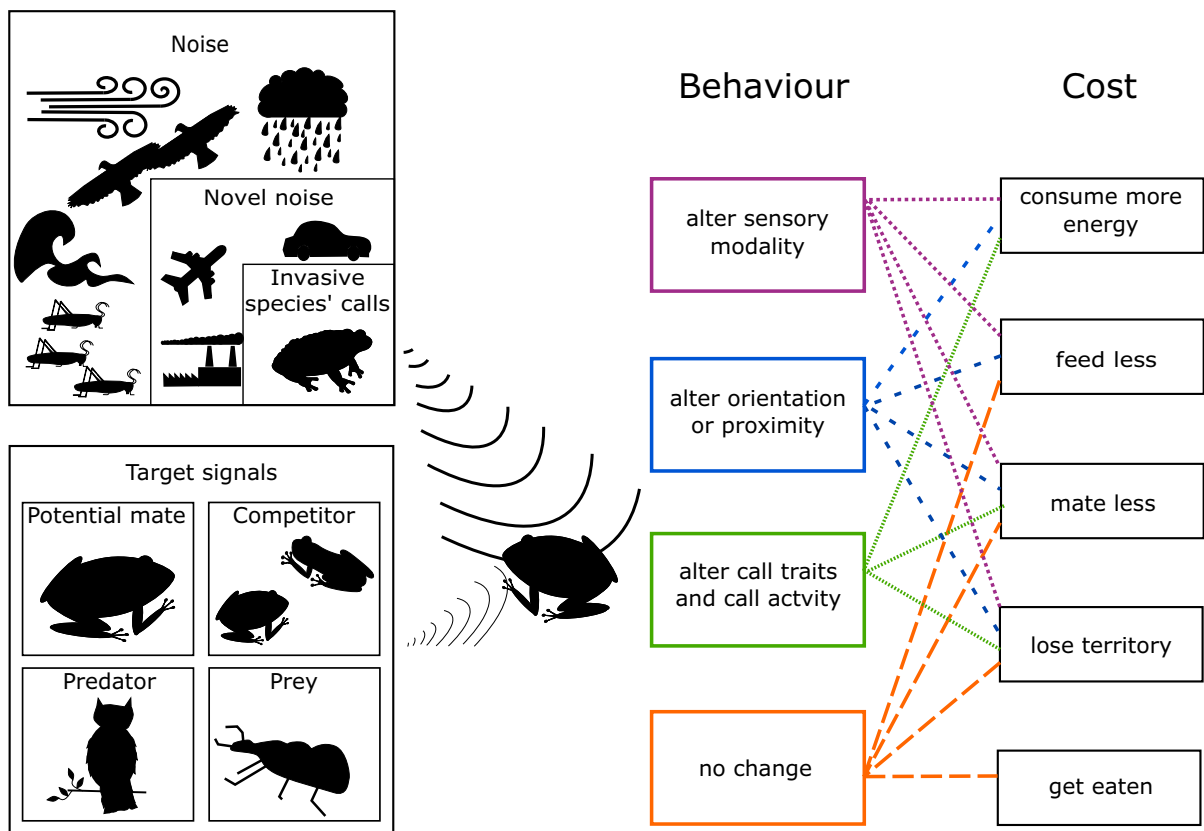


Fig. 1 Behaviours and costs associated with masking of native species calls by the calls of invasive species

there is evidence that it can have negative effects in nature. For example, foraging success of greater mouse-eared bats (*Myotis myotis*) is reduced near noisy roads, because it masks the rustling of prey that they use to forage (Siemers and Schaub 2010).

Much of the research examining the effects of masking by anthropogenic noise has focused on masking of intraspecific communication (Shannon et al. 2016b). Males of many species, especially birds and anurans, call to attract females (Bradbury and Vehrencamp 1998) and calls may be broadcast to fewer potential mates amidst anthropogenic noise (Barber et al. 2009). For example, female Canaries (*Serinus canaria*) presented with urban noise have reduced responsiveness to lower-frequency male calls (Huet des Aunay et al. 2014). Vocal plasticity in the sender, however, allows some species to avoid masking. Vocal plasticity occurs when it is possible for a sender to alter spectral or temporal properties of their calls, or produce louder calls (Fuller et al. 2007; Slabbekoorn 2013; Templeton et al. 2016). For example, high frequency bird calls typically elicit greater responses from conspecific receivers amongst anthropogenic (which is typically low frequency) noise than do unmodified calls (Halfwerk et al. 2011a; Pohl et al. 2012; Huet des Aunay et al. 2014; LaZerte et al. 2017). However, these adjustments can come at a cost. When species' vocalisations have evolved to function as signals of fitness (notably male quality), altering vocalisations may reduce signal quality (Slabbekoorn and Ripmeester 2008). Typically, females prefer low-frequency songs, so males with higher-frequency songs have lower reproductive success than those with lower-frequency songs (e.g., in Great Tits, *Parus major*, Halfwerk et al., 2011a, b). Because of female preferences, singing at higher frequencies may not necessarily improve reproductive success, despite improving signal transmission (Slabbekoorn and Ripmeester 2008; Halfwerk et al. 2011a).

Elevated stress levels have been observed in several animals exposed to novel anthropogenic noise (Shannon et al. 2016b). One reason that animals might experience stress is because they feel threatened by the noise. For example, Harlequin Ducks (*Histrionicus histrionicus*) increased alertness (e.g., raising head, flushing) and ceased courtship behaviours in response to military jet flyover (Goudie and Jones 2004). Similarly, beaked whales (*Ziphius*

cavirostris) and blue whales (*Balaenoptera musculus*) have been observed terminating foraging behaviour and swimming away from naval sonar, behaviours typically initiated in response to a threat (Tyack et al. 2011; Goldbogen et al. 2013). Another reason that animals may experience increased stress is because they are unable to hear important acoustic signals amidst novel noise, and some individuals do appear to adjust their behaviour to counter the masking effect of anthropogenic noise. They may, for example, increase vigilance for predators, initiating predator avoidance behaviours, such as flight, earlier in the presence of anthropogenic noise (Meillère et al. 2015; Shannon et al. 2016a). Although this tactic allows individuals to react appropriately to cues, taking flight and sacrificing foraging opportunities is energetically costly (Preisser et al. 2005; Shannon et al. 2016a). Therefore, the masking effects of novel noise can impact an individual's physical fitness through behavioural adjustment costs and elevated stress levels.

Invasive species vocalisations versus anthropogenic noise

Studies of anthropogenic noise have examined the masking effects of novel noise on wildlife extensively. They have identified the noise properties most likely to mask wildlife sounds, and the effects of masking. Their findings can be generalised to predict the response of native species to the calls of invasive species. Like anthropogenic noise, the calls of invasive species are often loud, sometimes louder than those of native species. For example, cane toads (*Rhinella marina*) can call at a volume of 85 dB at 1 m, which is as loud as a standard household vacuum cleaner, and louder than many native frogs in invaded regions of Australia (Bleach et al. 2015). Similarly, invasive Cuban treefrogs (*Osteopilus septentrionalis*) (Olson et al. 2012) and American bullfrogs (*Lithobates catesbianus*) (personal observation) can dominate the soundscape where they occur. Also like anthropogenic noise, invasive species' calls can also be frequent, or of very long duration, or both. For example, over the course of one year, invasive Pekin Robins' (*Leiothrix lutea*) calls made up 37% of all bird songs in a forest in their invaded range in Europe (Farina et al. 2013). Likewise, the calls of invasive birds such as Common Mynas (*Acridotheres tristis*), Rock Doves (*Columba livia*) and European Starlings (*Sturnus*

vulgaris) seem to dominate the urban environments they have invaded (personal observation). So, loudness and high rate of occurrence are characteristics of the calls of many invasive species, that, like some anthropogenic noises, can have negative effects on native species. In response to loud, persistent noise, individuals are likely to experience similar negative impacts to those described previously.

Although invasive species' calls and anthropogenic noises share some features, these noises are also different in important ways. Thus, we expect the effect of invasive species calls to have other effects not observed in response to anthropogenic noise. The distribution of sound energy constitutes a major difference between invasive species' calls and anthropogenic noise is (Fig. 2). Typically, sound energies in animal vocalisations are concentrated in particular frequencies, i.e., they have harmonics, (Bradbury and Vehrencamp 1998), whereas anthropogenic noise is typically broad-spectrum energy, concentrated in lower frequencies (Slabbekoorn and Peet 2003; Slabbekoorn and Ripmeester 2008). Animals also call or sing in notes (Bradbury and Vehrencamp 1998), whereas anthropogenic noises may sound constantly for long or unpredictable periods of time, for example traffic or machinery (Habib et al. 2007; Francis et al. 2009). Also, frequency modulation, the distribution of energy across frequencies over time, is more variable in the calls of animals than in anthropogenic noise. Finally, animal call components are typically of different lengths and frequencies, whereas anthropogenic noises are often monotonous and unmodulated (Fig. 2).

Because of differences between invasive species' calls and anthropogenic noises, we expect the effects of invasive species' calls on native species to be different. Animals may habituate to anthropogenic noise, and cease to react to it (Smith et al. 2004; Ditmer et al. 2018), but if native species can better detect, or pay more attention to the sounds of other animals than to anthropogenic noise, then invasive species' calls may have a greater effects on their ecology than anthropogenic noise. For example, if an invader is related to, or has a similar ecology to species in the recipient ecosystem, its call may sound like those of native species, at least in general. Species may share call properties if they have shared ancestry, or there may have been convergence of call properties caused by similar ecological or morphological constraints (Morton 1975; McCracken and Sheldon 1997). Correlations exist between a species' vocal properties and its hearing range in many taxa (Moiseff et al. 1978; Ryan and Wilczynski 1988; Manley and Kraus 2010; Zuk et al. 2017). Native species may, therefore, be attuned to vocalisations that sound similar to conspecific calls, and if an invader's call fits into this category for the reasons outlined above, the calls of invasive species may have more of an effect on native species than does anthropogenic noise.

The timing, diurnal or seasonal, of invasive species' calls and anthropogenic noise may differ. Anthropogenic noise is often aseasonal (e.g., traffic, urban noise), whereas seasonal activities critical to fitness, such as breeding, may overlap in native and invasive species, especially when the invasive species is in the same broad taxonomic group. In the case of

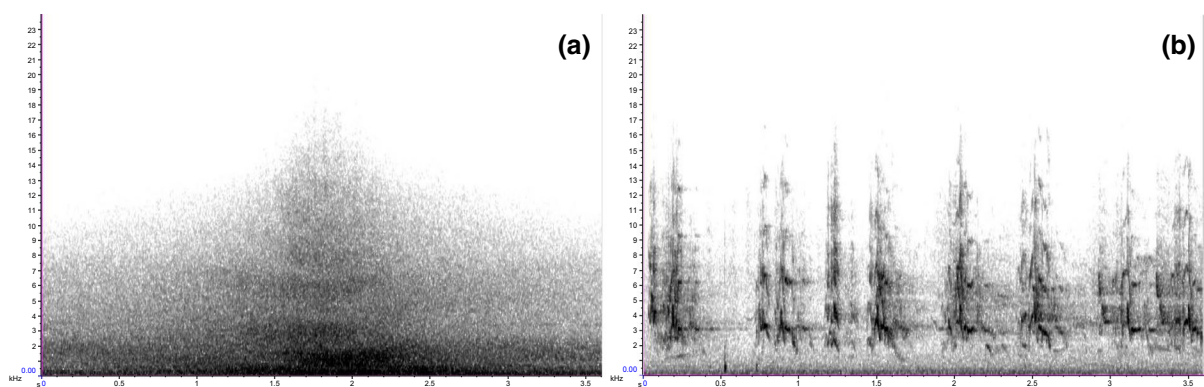


Fig. 2 Spectrogram view from Raven Pro 1.5 (Bioacoustics Research Program 2014) of: **a** a passing car; **b** a Common Myna (*Acridotheres tristis*) song segment

breeding season overlap, the likelihood of masking increases. For example, native birds and anurans chorusing may face acoustic competition with breeding invaders that chorus at the same times of day and year (Farina et al. 2013; Bleach et al. 2015).

Compared to invasive species' calls, many types of anthropogenic noise may peak at times that do not really influence native species' activities. There is, for example, more traffic noise in daylight when people are most active (Barber et al. 2009). Native animals may avoid the negative effects of anthropogenic noise at these times if they are not important activity periods, whereas noisy, ecologically similar invaders are more likely to interfere at the same activity times. An overlap in activity periods between native and noisy invasive species may elicit changes in native species' behaviour. For example, if native individuals cannot hear conspecific calls amongst the calls of invasive species, they may have fewer mating opportunities.

The effects of invasive species' calls on native vocal communication

Very few studies examining the effects of novel noise on animals have focused on the calls of invasive species. Those that have done so have measured the vocal responses of native species to masking by the calls of invasive species. The responses from native species, even in these few studies, have been variable. For example, some native anurans altered call frequency, note duration, call rate or amplitude when exposed to invasive species vocalisations (Both and Grant 2012; Bleach et al. 2015; Tennessen et al. 2016; Medeiros et al. 2017, Hopkins et al. in press), while others showed no response (Bleach et al. 2015; Tennessen et al. 2016).

One study suggested that native species whose calls overlap in frequency with the invader's call were most likely to alter call traits. Tennessen et al. (2016) presented two native treefrog species with calls of invasive Cuban treefrogs (*Osteopilus septentrionalis*) and white noise with the same or higher frequency than the invader's call, and recorded native treefrogs' calls. The native treefrog (*Dryophytes cinereus*) that called at a similar frequency to the invader produced louder, shorter calls when presented with the invader's call, or white noise of the same frequency, but not white noise of higher frequency. The other native treefrog (*D. femoralis*), which called at a different

frequency to the invader, did not alter its call during any of the noise treatments. These results indicate that the degree of spectral overlap between an interfering noise and an individual's call can influence whether it will alter its call when signalling amidst the noise (Tennessen et al. 2016). Frequency overlap is also a predictor of signal change in birds exposed to anthropogenic noise (Hu and Cardoso 2010; Francis et al. 2011), indicating signal adjustment may be a general response to novel noise overlapping in frequency with an individual's call, and is employed to avoid masking (Slabbekoorn and Peet 2003).

Another study suggested that native species with fast call rates are those most likely to alter calls, regardless of the degree of frequency overlap. Bleach et al. (2015) found that a fast-calling native frog (*Limnodynastes convexiusculus*) reduced call rate during playback of invasive toad (*Rhinella marina*) calls, lawn mower noise, and the calls of sympatric native frogs. It also increased call rate during silent periods. The authors suggested the fast-calling frog saved energy by reducing calling rate at times when calling was likely to be masked. Another native frog, with a slower call rate (*Litoria rothii*), did not adjust call behaviour in response to any of the noise treatments, perhaps because energy savings would have been negligible (Bleach et al. 2015).

A third study suggested that both biotic and abiotic properties of noises influence vocal responses of native species. Medeiros et al. (2017) tested whether the calls of invasive species had a greater impact than sympatric native species' calls or synthetic noise on the vocal properties of native anurans' calls. Frogs changed calls in response to each noise, however, the types of changes differed among noises. In general, frogs produced similar calls when presented with the invasive bullfrog (*Lithobates castesbianus*) and a native toad call (*Rhinella icterica*), however, they produced different calls when hearing synthetic noise. Additionally, the types of vocal adjustments differed among the native species examined. The authors suggested anurans may be more attuned to anuran calls than to other sounds (Medeiros et al. 2017). Acoustic signals have specific traits, such as harmonics and frequency modulations, (Marler and Slabbekoorn 2004), which receivers can identify (Cynx et al. 1990; Vignal et al. 2008). Likely, receivers that identify such traits can distinguish between biotic and abiotic noises. In these cases, receivers should be more attuned to and,

therefore, more affected by a masking biotic noise (e.g., heterospecific calls) than a masking abiotic noise (e.g., synthetic noise) (Medeiros et al. 2017).

The theory that invasive species are more attuned to and, therefore, affected by biotic than abiotic noise has been further examined. Hopkins et al. (MS in prep) found that native Australian floodplain toadlets (*Uperoleia inundata*), Black-throated Fiches (*Poephila cincta cincta*) and Peaceful Doves (*Geopelia striata*) modified at least one call property when exposed to the calls of invasive species. These species also modified call properties when exposed to synthetic noise controls, so that calls or call rates resembled those produced when the species were exposed to invasive species' calls. These results indicate that these species respond similarly to invasive species' calls and biologically irrelevant synthetic noise controls, in contrast to conclusions drawn by Medeiros et al. (2017). It is likely that, rather than a biotic origin per se, specific properties of noise influence native species' call responses in the presence of the noise.

Overall, the vocal plasticity observed in these studies indicates that native species try to counter masking by temporarily occupying a different acoustic niche. These studies demonstrate that invasive species' calls are important sources of novel noise which can cause changes in native individuals' behaviour, however, whether these changes incur fitness costs remains unexplored. This field of study is new, and more work is needed to understand the range of ways in which native animal behaviour can be affected by masking from invasive species calls, and importantly, how populations and communities may be impacted.

New approaches to studying the effects of invasive species' calls

In this section, we propose avenues of future research examining the impacts of invasive species' calls on native species. The goal of any future research on this topic should be to understand: (1) the effect of the calls of invasive species on native species; (2) what characteristics of invasive species and their calls affect the behaviours and fitness of native individuals; and (3) what characteristics of native species influence their susceptibility to the effects of invasive species' calls.

As outlined in the above section, the only studies that we are aware of to date that have examined the effects of invasive species' calls on native species have observed that vocal adjustments reduce the masking effects of the invasive species' calls (Both and Grant 2012; Bleach et al. 2015; Tennessen et al. 2016; Medeiros et al. 2017), and concluded that vocal plasticity is the native species' response. While reduction of masking may be the outcome, the change in behaviour may not occur for that reason. For example, several anuran species are thought to use high noise levels in general as a proxy for high competition (Schwartz and Bee 2013), so call adjustments may occur in response to perceived higher competition, rather than masking. The only way to truly determine the importance of masking is to examine the responses of the intended receiver. For example, if a receptive female frog orients or moves towards a male conspecific call in the presence of an invasive species' call, it is likely that the male's call is not masked by the invasive species' call. Similarly, if territorial birds continue to approach conspecific intruder calls in the presence of an invasive species' call, it is also likely that the intruder's call is not masked by the invasive species. Studies examining receiver responses to conspecific calls amidst invasive species' calls will complement the existing studies examining anuran vocal plasticity, and resolve the relative role of masking versus other factors in eliciting vocal plasticity in anurans exposed in invasive species' calls.

To better predict and manage the impacts of invasive species' calls on native species, we need to understand which characteristics of an invader's call, and which ecological traits influence the severity of masking. We consider several traits as potentially important predictors of masking, and suggest that future research should be aimed at examining questions related to these traits.

Timing of sound production is an important trait of invasive species which probably differs from most anthropogenic noise, and that likely has strong effects on native individuals. Vocalising invaders often have daily or seasonal peaks in calling activity that coincide with the same peaks in activity (both vocalising and other activities) in native species. If, for example, an invasive bird and a native bird call most intensely during the dawn chorus, the invader's call will occur with (and potentially mask) the native vocalisations. Native callers that are unable to effectively send their

acoustic signals to conspecifics in such situations will likely suffer reduced mating success and higher energy consumption, for example if they try to counter masking effects by calling more frequently, for longer periods or at louder amplitudes. We suggest that temporal overlap in key activity periods between invasive and native species is probably an important predictor of fitness consequences in native species, and future studies should aim to examine this hypothesis. For example, a long-term acoustic monitoring study would be useful in examining the degree and consequences of temporal overlap between invasive and native species' sexual advertisement calls. If invasive and one or more native species initially call most intensely, for example, at the same time of day, and over time one or more of these native species begins to call most intensely at a slightly different time of day, it would suggest that these native species are avoiding signalling at the same time as the invader. Additionally, by concurrently monitoring reproductive output of native species, conclusions can be drawn on the influence of such changes on call timing and, therefore, reproductive success.

Sound properties of invasive species' calls will also likely influence their degree of impact on native species. When species invade a new soundscape, they may introduce noises that are loud (Farina et al. 2013; Llusia et al. 2013) or overlap in sound properties with native species' calls or other important sounds (Azar and Bell 2016). Masking could be particularly severe for native species that call alongside an invader in a similar niche, and that share call properties with the invader. We suggest examining the relative masking effect of properties of invasive species' calls on the sounds used by native species. It is well-established that masking is primarily a function of signal-to-noise ratio, but it is also influenced by target signal duration, and spectral overlap between the target signal and noise (Okanoya and Dooling 1990; Klump 1996; Dooling et al. 2000; Dooling 2004). However, invasive species' calls are markedly different from noises that have been used to examine masking in previous studies, such as anthropogenic noise or synthetic broadband noise, or pure tones. Invasive species' calls are diverse, and may consist of, for example, single tonal chirps, trilled notes, or complex songs with varying duration, amplitude, and frequency modulation. Identifying the sound properties of invasive species' calls responsible for masking could be achieved

by manipulating the amplitude, frequency or temporal parameters of an invader's call and documenting a native's responses. Understanding which invasive species call traits (e.g., long, loud, tonal or broadband calls) are most likely to have the greatest impact on native species will help in prioritising prevention or management of invasions.

To complement our understanding of the ecological and vocal traits of invasive species that cause the greatest impact, we need to identify the characteristics of native species that make them most susceptible to these impacts. We suggest that behavioural plasticity in native species likely influences the level of impact of invasive species' calls. One could argue that masking by invasive species' calls is most likely to affect individuals that are unable to modify their behaviours, although it depends on the cost of modifications made by species with vocal or behavioural plasticity. Behavioural adjustment in response to hearing impairment in noisy environments occurs in animals exposed to anthropogenic, biotic, and synthetic noise (McClure et al. 2013; Huet des Aunay et al. 2014; Meillère et al. 2015; Medeiros et al. 2017), but is not universal. It is important to understand whether behavioural adjustments by signallers or receivers improve signal reception and discrimination, and the cost of such adjustments to fitness.

The studies outlined earlier that examined native species exposed to invasive species' calls, demonstrated that vocal plasticity is one type of behavioural adjustment used by individuals (Both and Grant 2012; Bleach et al. 2015; Tennessen et al. 2016; Medeiros et al. 2017), but that not all species appear to use it. Although not clear, the outcome of vocal adjustments is probably improved signal transmission. To complement the studies we reviewed on invasive anurans, the responses of native species to adjusted and unadjusted conspecific calls, expressed amidst the calls of invasive species, should be examined. We suggest that in cases where native species do not adjust call properties in response to invasive species' calls, native species' calls could be digitally altered to contain improved signal transmission properties (e.g., higher call rate, longer calls, calls with lower spectral overlap with invasive species' calls). Such studies would help to determine whether this behavioural adjustment in the signaller improves signal reception in the receiver and whether failing to adjust signals translates to lower signal reception rates. Again, using,

for example, the responses of receptive female anurans or territorial birds to altered calls could reveal if adjusted calls reduce masking effects by invasive species' calls.

Receivers may also apply behavioural adjustments to improve signal reception and discrimination rates amidst the calls of invaders. For example, orienting or moving towards a target signal or away from an invasive species call may reduce the masking effect of the invader's call, as has been similarly demonstrated in female grey treefrogs (*Dryophytes chrysoscelis*) exposed to male conspecific calls played alongside chorus-shaped synthetic noise in an experimental, circular arena (Bee 2008). Alternatively, receivers may abandon attempts to hear a target signal, and instead rely on a different sensory modality, such as vision. A study of birds exposed to experimental traffic noise found that they spent more time with their heads upright in noisier treatments. This increased vigilance indicated that the birds were compensating for the masking effect of the traffic noise by using vision to obtain information (McClure et al. 2013). We suggest that examining behavioural modifications in receivers, such as those described here, would be useful to determine whether these adjustments can compensate for the effects of the calls of invasive species. Additionally, the physiological costs associated with these behavioural modifications, such as increased stress levels and energy consumption, should be quantified, to assess fitness costs associated with behavioural modification.

Conclusion

There is extensive research documenting the effect of anthropogenic noise on animals, but few studies have examined the impact of the calls of invasive species on native species. Invasive species' calls differ from anthropogenic noise, and, thus, may affect native species in different ways. The vocalisations of invasive species have potential to impact native species, particularly calls with acoustic properties that dominate the soundscape. Studies of the impact of invasive species' calls have found that these novel noises can affect the behaviour of native species that communicate vocally, expressed via changes in native species' calling. Little is understood about the impact of masking by invasive species on native species, and a greater degree of understanding of these interactions

is urgently needed. Invasive species with loud, long calls, and with similar ecology and phylogenetic background to native species seem the most likely to negatively impact natives, and determining the native species most likely to be impacted, and what these impacts are likely to be should constitute the goal of future research. Answering these questions will help us to determine the degree to which soundscape intrusion by invasive species should be considered in future conservation initiatives.

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