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# Raising a racket: invasive species compete acoustically with native treefrogs

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Environmental noise is increasing worldwide, limiting the space available for species to send and receive important acoustic information. Many invasive species produce acoustic signals that alter the spectrotemporal characteristics of available signalling space. This provides an opportunity to test ideas about competitive exclusion by quantifying whether species with shared requirements for acoustic resources will become excluded or partition resource use to permit coexistence. We conducted a field playback experiment to test whether native treefrogs (green treefrogs, *Hyla cinerea*; pine woods treefrogs, *Hyla femoralis*) modify their acoustic behaviour to minimize acoustic competition from chorus noise of the invasive Cuban treefrog, *Osteopilus septentrionalis*. We demonstrate that noise from an invasive species differentially affects the vocal behaviour of native species. Those with similar calls (*H. cinerea*) shortened calls, called louder and persisted calling in response to masking stimuli while those with different calls (*H. femoralis*) did not modify behaviour. This evidence suggests that acoustic competition by invasive *O. septentrionalis* has altered the acoustic community structure, identifying acoustic competition as a mechanism by which invasive species can impact communities. Furthermore, these results broaden the concept of noise pollution, demonstrating fitness-relevant consequences of noise produced by invasive species.


Many species depend on acoustic advertisement displays to communicate in mixed species breeding aggregations, including chorusing species of insects, birds and frogs (Amézquita, Flechas, Lima, Gasser, & Hödl, 2011; Brumm & Slabbekoorn, 2005; Gerhardt & Huber, 2002; Sueur, Windmill, & Robert, 2010). Ambient noise has increased in recent decades (Barber, Crooks, & Fristrup, 2010), creating a variety of new pressures for species that rely on acoustic cues for important life functions (see reviews in: Barber et al., 2010; Francis & Barber, 2013; Kight & Swaddle, 2011). Invasive species can be a source of noise, since many produce acoustic signals to attract mates and defend territories (e.g. Vargas-Salinas, 2006), and these sounds may dominate particular frequency or temporal patterns, thereby altering available signalling space (Bleach, Beckmann, Both, Brown, & Shine, 2015; Both & Grant, 2012). It is well established that invaders can modify native species' survival, development, distribution and behaviour (e.g. Case & Bolger, 1991; Langkilde, 2009; Suarez & Case, 2002; Wauters, Tosi, & Gurnell, 2002). The effects of the novel noise produced by invasive species on acoustic communication of native species have rarely been explored (but see Bleach et al., 2015; Both & Grant, 2012), yet are fundamental to understanding the novel pressures that invasive species exert on native communities.

The dynamic nature of the sounds within ecological communities can lead to intense competition for acoustic space, the multidimensional channel through which species send and receive acoustic signals (Brumm, 2006; Foote, Fitzsimmons, Mennill, & Ratcliffe, 2011; Luther, 2009; Marler, 1960). Sounds that overlap calling species in time, frequency and space can interfere with their signalling networks by reducing the signal's active space, thereby compromising communication ranges (Barber et al., 2010; Patricelli & Blickley, 2006). Acoustic space is, therefore, a limited resource

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(Bradbury & Vehrencamp, 2012). Competitive exclusion theory predicts that, when faced with such limited resources, species with shared requirements for resources will either (1) become competitively excluded, or (2) partition their resource use to permit coexistence (Gause, 1934). Therefore, given limited acoustic space, species whose acoustic signals are similar to competitors' signals may either become excluded from successfully signalling at a particular time or frequency, or may employ vocal compensation to partition their acoustic space to minimize competition (Brumm, 2006; Foote et al., 2011; Luther, 2009). Evidence of acoustic resource partitioning is provided by the fact that vocalizations in South American frog communities are more widely and regularly spaced in use of acoustic frequency and call timing than expected by chance (Chek, Bogart, & Lougheed, 2003), and birds singing in dawn choruses in the Amazonian rainforest partition their signalling space through spatiotemporal changes in singing behaviour or evolved differences in songs (Luther, 2009). Furthermore, when acoustic space is limited by ambient anthropogenic noise, such as by mechanized transportation (e.g. Barber et al., 2010; Tennessen, Parks, & Langkilde, 2014), species across many taxa including birds, mammals, anurans and fish partition their signalling space by using vocal compensation through short-term vocal behavioural modifications such as altering the duration, amplitude, frequency or rate of their calls (for reviews, see: Brumm & Slabbekoorn, 2005; Hotchkin & Parks, 2013; Warren, Katti, Ermann, & Brazel, 2006). Frogs in particular have demonstrated vocal plasticity to increased anthropogenic noise (e.g. Cunnington & Fahrig, 2010; Lengagne, 2008; Parris, Velik-Lord, & North, 2009; Penna & Hamilton-West, 2007; Schwartz, Brown, Turner, Dushaj, & Castano, 2008). Thus, while few studies have explored the role of competition for acoustic space in structuring acoustic communities, the documented behavioural responses of species to changes in their acoustic environments suggest that acoustic competition may be an underlying mechanism.

The invasion of the Cuban treefrog, *Osteopilus septentrionalis*, in Florida provides an excellent opportunity to study how novel sound produced by an invasive species affects native acoustic communities. *Osteopilus septentrionalis* is an anuran hylid native to Cuba, the Cayman Islands and the Bahamas, and has been introduced to many tropical and subtropical locations, including Florida (Lindsay & Cooper, 2008; Meshaka, 2001; Owen, Perry, Lazell, Petrovic, & Egelhoff, 2005). *Osteopilus septentrionalis* was observed in southern Florida by 1931 (Barbour, 1931), having probably arrived through materials shipped for the garden nursery industry (Meshaka, 2001), and subsequently spread rapidly northward, facilitated by the ornamental plants trade and by hitchhiking on vehicles and in cargo (Meshaka, 2001). Presently, *O. septentrionalis* is established throughout most of the Florida peninsula, with isolated observations from the Florida panhandle (S. Johnson, personal communication, 15 January 2015). In addition to depredating native species (Wyatt & Forys, 2004), *O. septentrionalis* produces a nocturnal breeding call that has been described as a 'grating squawk' (Meshaka, 2001). These calls represent pressure on acoustic space within native anuran communities throughout Florida.

We predicted that novel sounds created by invasive *O. septentrionalis* would cause native treefrogs whose calls overlap in frequency and timing with those of *O. septentrionalis*, to partition acoustic space through vocal modification in order to minimize acoustic competition, but have no effect on native treefrogs with acoustically different calls. To test this hypothesis, we conducted a field playback experiment with two native species, one whose breeding calls are similar in frequency, structure and timing to *O. septentrionalis* (green treefrogs, *Hyla cinerea*) and one whose breeding calls are not (pine woods treefrogs, *Hyla femoralis*). Our findings reveal a poorly understood pathway through which invasive species may alter the behaviour of native species, and suggest that acoustic competition for limited acoustic space is driving native species responses.

## METHODS

### *Study Sites and Species*

*Hyla cinerea* and *H. femoralis* are native hylid species found throughout the southeastern United States. *Hyla cinerea* inhabits wetlands between central Texas and Florida, extending north to eastern Maryland and Delaware. *Hyla femoralis* is found between Louisiana and Florida, extending north to Virginia (Dorcas & Gibbons, 2008). Breeding occurs in permanent (*H. cinerea*) and temporary (*H. femoralis*) bodies of water at approximately the same time of year, between March and October, overlapping *O. septentrionalis* breeding activities in space and time (Dorcas & Gibbons, 2008; Meshaka, 2001). All species call from perches or within clumps of emergent vegetation (Dorcas & Gibbons, 2008). While closely related, the breeding calls produced by male *H. cinerea* and *H. femoralis* differ substantially in dominant frequency, duration, rate, intercall interval and structure (Fig. 1, Table 1). *Hyla cinerea* calls are composed of a series of harmonics, with two emphasized at approximately 1000 and 3200 Hz. *Hyla femoralis* calls are pulsed with peak energy at approximately 2100 and 4500 Hz. *Osteopilus septentrionalis* calls are harmonic in structure, like *H. cinerea*, and emphasized at approximately 1100 and 2500 Hz.

We conducted night field playback experiments with *H. cinerea* and *H. femoralis* in the southeastern United States over two seasons. Playback trials with *H. cinerea* were conducted at artificial ponds at the Harrison Lake Fish Hatchery (HLFH) in Charles City, VA (coordinates: 37°20′24″N, 77°11′24″W) during 16–18 July 2013. These ponds were located within an area of mixed hardwood and southern pine forest, and contained emergent vegetation (primarily *Juncus* sp., *Polygonum* sp., and grasses). Trials with *H. femoralis* were conducted at an ephemeral pond at the Archbold Biological Station (ABS) in Venus, FL (coordinates: 27°10′53″N, 81°21′26″W) during 16–17 July 2012. These ponds were located within scrubby flatwoods and contained emergent vegetation (primarily *Panicum* sp.). HLFH is located north of the northernmost part of the *O. septentrionalis* invasion front. While *O. septentrionalis* has been present at ABS for at least 20 years (since the early 1990s), the population remains restricted to the immediate vicinity of buildings at the station headquarters (Rothermel, Forsburg, & Phillips, 2013). Therefore, both pond sites represent areas that have not experienced the invasion, and thus playback subjects were naïve to *O. septentrionalis* breeding calls. Temperatures during the playback experiments ranged from 21.4 °C to 28.8 °C, and playback's occurred between 2050 and 0115 hours.

### *Playback Experiment*

To conduct the acoustic playback trials, we searched for calling male treefrogs located on vegetation within or adjacent to ponds. Once a focal male was located, we placed an AN Mini speaker (Anchor Audio Portable Sound Systems, Carlsbad, CA, U.S.A.) on a stand, approximately 1 m away from the caller and at approximately the same height. This speaker was connected to an iPod Nano (Apple, Inc., Cupertino, CA, U.S.A.) (system frequency response: 100–15 000 Hz flat) that played the acoustic stimulus, either an *O. septentrionalis* chorus, masking white noise, or upshifted white noise (Fig. 2; see Playback Stimuli Design), which we selected using a stratified-random procedure. The playback trial