

Evolutionary divergence in acoustic signals: causes and consequences

Matthew R. Wilkins¹, Nathalie Seddon², and Rebecca J. Safran¹

¹ Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309-0334, USA

² Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, UK

Acoustic signals mediate mate choice, resource defense, and species recognition in a broad range of taxa. It has been proposed, therefore, that divergence in acoustic signals plays a key role in speciation. Nonetheless, the processes driving divergence of acoustic traits and their consequences in terms of speciation are poorly understood. A review of empirical and comparative studies reveals strong support for a role of sexual selection in acoustic divergence, but the possible concomitant influences of ecological context are rarely examined. We summarize a conceptual framework for testing the relative significance of both adaptive and neutral mechanisms leading to acoustic divergence, predictions for cases where these processes lead to speciation, and how their relative importance plays out over evolutionary time.

The widespread importance of acoustic divergence in speciation

In taxa as diverse as frogs, insects, mammals, birds, and to an underappreciated extent, spiders and fish, acoustic signals function in mate choice, resource defense, and species recognition [1]. Unlike signals that require close proximity of receivers, acoustic signals can be detected at a distance. Moreover, these signals often concurrently encode information about signalers' identity, location, and condition, thereby reducing the costs associated with direct encounters. Acoustic signals are therefore especially suited to mediate discrimination within and between species. Additionally, the simple genetic architecture of some acoustic signals [2] or cultural mutations gained in the acquisition of learned acoustic traits [3], allow for rapid changes in signal structure which can facilitate divergence (Box 1). Thus, it is not surprising that rapidly speciating lineages are often only identified by differences in acoustic signals (e.g., cicadas [4], swordtail crickets [5], and green lacewings [6]), and playback experiments in many systems demonstrate that signal divergence effects species recognition (see Glossary and [7] for discussion) and mate choice [8–13]. Moreover, phylogenetic comparative studies reveal lineage-specific acoustic differences [4,5] and show that divergence in acoustic traits predicts patterns of diversification across genera [14]. Together these findings indicate a key role for acoustic signals in diversification – either early or late in the process – in a broad range of organisms.

Corresponding author: Wilkins, M.R. (wilkinm@colorado.edu).

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Despite accumulating evidence for a major role of acoustic signals in speciation, several fundamental questions remain. In particular, the importance of adaptive versus neutral processes in acoustic divergence is unknown in most studies, and there is currently no clear hypothesis-testing framework to differentiate the relative significance of drivers of acoustic divergence. Additionally, it is currently unclear whether acoustic divergence is more important in facilitating speciation by providing a pre-mating barrier early (where there is little genetic and no morphological divergence between taxa) [5,6] or later in the speciation

Glossary

Acoustic Adaptation Hypothesis: nested within the Sensory Drive Framework, predicts that habitat structural differences influence signal evolution through effects on signal transmission.

Acoustic window: the acoustic parameter space which is available for signal evolution in a given taxon in a given habitat; multidimensional axes of this window, including amplitude, pitch, and temporal signal characteristics, might show different patterns of constraint on the transmission or audibility of different acoustic features within a particular environment.

Cultural drift: changes in the composition of culturally acquired and transmitted signals in a population which are due to random differences in which variants are learned and reproduced.

Dobzhansky–Muller incompatibilities: deleterious interactions resulting when alleles which have diverged in independent lines are brought together in a hybrid genome.

Ecological selection: differential survival and reproduction as a result of genetic adaptation to a particular environment.

Ecologically-based assortative mating: individuals mate by ecotypes; acoustic signals used in mating are associated with ecological benefits; this contrasts with preference-based mating, which does not require correlations between mating signals and traits related to ecological adaptations.

Genetic drift: changes in gene frequencies in a population due to random differences in survival and reproduction of individuals or sampling error of alleles in small population sizes.

Magic trait: a trait involved in divergent ecological adaptation which has a pleiotropic effect on reproductive isolation via assortative mating.

Mutation-order speciation: process by which different, incompatible alleles fix among populations adapting to similar environments, resulting in reproductive isolation.

Preference-based mating: mate selection is based on sexually-selected acoustic traits which are not necessarily linked to ecological adaptation.

Reinforcement: the strengthening of pre-mating barriers between incipient species in response to reduced fitness of interspecific matings.

Reproductive character displacement: pronounced differences in mating signals found in sympatry with another species, compared to the signal found in allopatry; differences can arise from increased divergence or convergence.

Sensory drive: predicts that signals, sensory systems, and microhabitat choice coevolve as a function of habitat structure, ambient noise profiles, presence of predators and parasitoids, and other sensory and physiological considerations.

Sexual selection: differential reproductive success resulting from competition for mates and fertilizations.

Species recognition: process through which individuals modulate behavior based on cues that differ between populations.

process (i.e., during secondary sympatry, where genetic divergence has led to Dobzhansky–Muller incompatibilities between taxa) [15].

Here we begin by discussing factors which limit standing variation in acoustic traits and potential evolutionary outcomes of acoustic divergence (Table 1, Box 2). We then: (i) review support for processes leading to acoustic divergence, proposing guidelines for testing the relative contributions of neutral and adaptive drivers of divergence (Table 2); (ii) provide a summary of current knowledge related to the causes and consequences of acoustic divergence (Table 3); and (iii) offer predictions for testing the timeframe over which acoustic divergence initiates or finalizes speciation (Figure 1). We conclude by suggesting methods and lines of inquiry most likely to provide key insights into outstanding questions at the interface of acoustic signaling and speciation.

Limits on acoustic divergence

Table 1 summarizes the major factors determining the parameter space, or ‘acoustic window’, within which acoustic signals can evolve. Much work attempting to understand these factors has focused on testing the Acoustic Adaptation Hypothesis [16] or the broader Sensory Drive Framework, devised by Endler [17] to describe the coevolution of signals, sensory systems, and microhabitat choice. While much evidence for sensory drive comes from visually communicating systems [18], its role in shaping acoustic communication is less well supported. Previous acoustic work has shown a match between signal variation and measures of optimal signal transmission as a function of habitat structure [9,19–24], community composition [19,25–29], ambient noise profiles [21,26,30], and sender/receiver physiology [31–36]. For example, divergence between Amazonian bamboo-specialist bird species and their nearest relatives in *terra firme* forest correlates with habitat sound transmission properties, rather than genetic distance, ambient noise, or mass [19]. However, we stress that the Sensory Drive Framework itself is not a mechanistic explanation of evolutionary change responsible for signal divergence (see Box 2). Rather, we suggest that this

Box 1. Learning and acoustic divergence

In contrast to genetic mutations, copying errors or novel variants in culturally acquired signals can be transmitted both within and among generations between unrelated individuals [80], and often have higher heritabilities than genetic traits [80]. Accordingly, vocal learning has been suggested to accelerate the process of acoustic divergence [3]. The fact that oscine songbirds, in which vocal learning occurs, are a very speciose clade has been indicated as evidence that the learning process can facilitate divergence [3] (but see [81]). However, recent work in diverse subsocial radiations that lack learning suggest that this argument is weak [14,19,39,82], and evidence for a role of learning in accelerating speciation is scarce. Perhaps the only evidence comes from the *Vidua* indigobirds, which are brood parasites of several African estrildid bird species. Within *Vidua*, male song and female preferences are learned through sexual imprinting on host song, resulting in host-specific races of these brood parasites which are reproductively isolated unless host specificity is imperfect [83].

The development of dialects can lead to assortative mating within dialect boundaries, as local song can indicate overall condition or degree of local adaptation [84,85]. However, learning could impede speciation [82,86,87] if post-dispersal learning occurs [82,84,86], as this would remove the link between acoustic signal and local adaptation and facilitate hybridization between incipient species on secondary contact [86,87].

Our understanding of the role of learning in speciation is partially limited by an incomplete knowledge of which taxa have culturally acquired acoustic signals. Vocal learning occurs in humans and other mammalian lineages, in addition to three orders of birds [88]. Within these taxa, learning provides a rapid means for the accumulation and transfer of mutations within populations; however, we know little about the timing of learning in relation to dispersal, or variation in the strength of preference for local signals. These factors will both affect the likelihood of forming stable dialects necessary to initiate reproductive isolation. Moreover, for those species which do form dialects, strong selection for improved learning programs should result in genetic assimilation of species-specific signals [89]. However, there are no clear examples of this in the literature [90] and the role of genetic assimilation in population divergence remains untested. Future work should also aim to assess how novel constraints on ‘acoustic windows’ [30], as well as neutral and adaptive processes [91], shape learned signals over time, and how each of these processes contributes to population divergence.

approach defines the amount of standing acoustic variation available for ecological selection, sexual selection, and drift in a given habitat.

Table 1. Major constraints affecting acoustic signal evolution

Factor	Effect	Examples	Refs
Physical features of habitat	Limits standing variation	Emphasized frequencies (i.e., pitch) of vocalizations have been shown to match those expected for optimization of signal transmission (i.e., minimize attenuation and reverberation) in a given habitat for some passerine birds, insects, spiders, frogs, and mammals.	[9,19–24]
Community composition		The presence of community members that produce acoustic signals may lead to strong divergent selection on signal structure to avoid masking interference, as shown in frogs and birds. Presence of predators or parasitoids may also select for reduced signal elaboration, or signal loss.	[19,25–29]
Ambient noise		Certain taxa may be excluded from a habitat, or will adapt signal structure to avoid masking interference by biotic and abiotic sources of ambient noise.	[21,26,30,61]
Phylogenetic history		Shared derived or ancestral traits (e.g., body size or beak morphology) evolved in other social or ecological contexts may limit the variation available for signal evolution.	[21,31,33]
Sender morphology and neurophysiology	Limits potential evolutionary outcomes	Acoustic signals are often constrained by morphological (e.g., beak shape or body size) and neurological limits.	[31–34]
Receiver morphology and neurophysiology		Receiver morphology (e.g., hearing structures) and neurophysiology (i.e., the neurological structures affecting perceptual and cognitive abilities) may restrict elaboration by signalers.	[33,35,36]

Box 2. The acoustic window

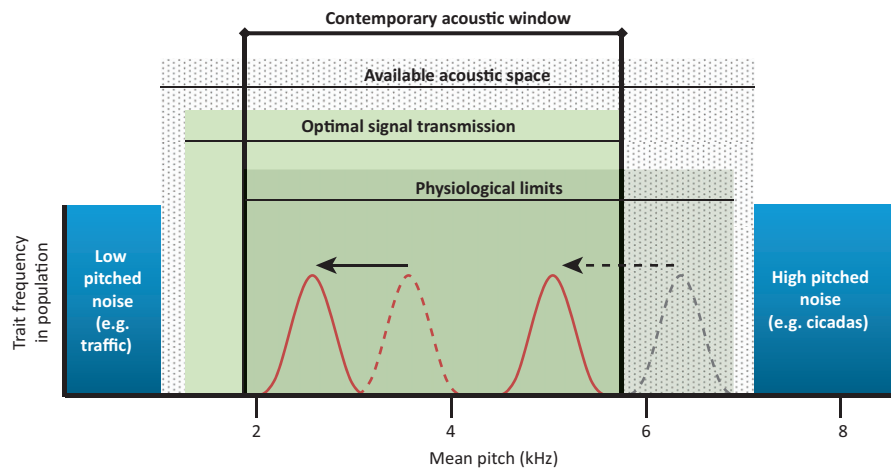
For a given population, aspects of habitat structure, ambient noise, presence of parasitoids and predators, and the neurophysiology of senders and receivers will determine the effective ‘acoustic window’ available for evolutionary change in signals (see Figure 1). Changes in any of these factors (e.g., movement into a new habitat) will affect the acoustic window, truncating variation available for adaptive or neutral evolution.

A recent meta-analysis in birds showed that habitat structure (coarsely defined as open versus closed) had a significant effect on peak frequency, but much weaker or nonsignificant effects on other spectral traits and interval duration [62]. Thus, for birds, limits on audible signal variation imposed by habitat structure lead to predictable effects on song pitch via sensory drive, while much of the differentiation among populations must be due to other adaptive and neutral processes.

As illustrated by the broken arrow in Figure 1, sensory drive only has explanatory value where the ancestral and novel acoustic windows do not overlap. Sensory drive will explain little of the acoustic signal variation among taxa which are capable of a wide variety of sounds, adopt behavioral mechanisms to avoid heterospecific interference, inhabit environments with high signal propagation, or have reduced selection by acoustically orienting predators.

Examples supporting sensory drive highlight taxa with narrow and non-overlapping acoustic windows among populations and could over-represent the general importance of constraints on acoustic divergence. The relatively low effect of sensory drive shown in birds [62] suggests that signal divergence within an acoustic window (unbroken arrow, below) might be the more common scenario. Other factors not generally considered in sensory drive, such as phylogenetic history, could also limit signal evolution. Previous adaptations (e.g., body size or beak morphology) [21,31,33] evolved in other social or ecological contexts can impose limits on how signals can respond to selection. Moreover, physiological tradeoffs might result in holes in the multidimensional parameter space of the acoustic window (e.g., trill rate only increases at the expense of frequency bandwidth) [31,32].

Thus, identifying factors which define the acoustic window and determine the possible directions for signal evolution within it allows for a clear understanding of how constraint affects signal distributions available to selection and drift. However, in order to better understand the mechanism by which signal distributions move into and within an acoustic window, the contributions of neutral and adaptive processes should be considered directly (see Table 2 in main text).



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Figure 1. Example of one axis (pitch) of the acoustic window for a given taxon in a given habitat. The contemporary acoustic window is defined by the intersection of available acoustic space, physiological limits, and optimal signal transmission characteristics. Arrows indicate signal evolution occurring between an ancestral population (broken curves) and a contemporary population (unbroken curves). The broken arrow at right represents movement into a novel acoustic window from a different habitat through sensory drive (i.e., ecological selection for efficient signal transmission). The ancestral curve for this example is in gray to emphasize that the ancestral trait distribution resulted from a different acoustic window defined by a different set of selection pressures. The unbroken arrow represents signal evolution within a temporally stable acoustic window through other processes (ecological selection, sexual selection, and drift).

Adaptive and neutral mechanisms of divergence

In this review we consider ecological and sexual selection separately and outline testable predictions for determining the relative contribution of each of these processes to adaptive acoustic signal divergence (Table 2).

Ecological selection

Sources of acoustic divergence

If acoustic differences between populations result primarily from divergent ecological selection, ecological trait divergence is predicted to covary with the degree of acoustic differentiation between sister taxa, while strength of preference for local variants or strength of sexual selection does not (Table 2). Here, we discuss cases where ecological selection was likely the dominant driver of signal divergence.

In bats, disruptive ecological selection commonly acts on echolocation frequency, in association with specialization on different prey size classes [37]. In this way direct ecological selection on signal function leads to acoustic divergence. Another example is derived from correlated ecological selection on morphological traits involved in sound production. For example, differentiation of beak size for efficient seed extraction has had a pleiotropic effect on song trill rate in Galápagos finches: birds with larger bills produce slower-paced trills [31].

Ecological selection for body size represents another potential driver of acoustic divergence. There is a general tendency for larger animals to have lower pitched (frequency) acoustic signals [21,38,39] due to a positive correlation between body size and the mass of sound-producing structures: larger structures produce lower-pitched sounds [21].

Table 2. Testable predictions for signal divergence under four different selection regimes: ecological selection, sexual selection, a combination, or drift (absence of selection)

Selection regime (i.e., primary contributor to acoustic divergence)	General expected patterns under each selection regime				Testable predictions for empirical studies		
	Acoustic signal variation <i>within</i> populations covaries with:	Acoustic signal divergence <i>among</i> populations covaries with:	Mate selection pattern (assortative or preference-based*)	Population-level acoustic trait variation	Field-based comparative study: what is the relative contribution of ecological and sexual selection in the evolution of acoustic divergence?	Phylogenetically controlled correlated trait evolution: is acoustic signal evolution correlated with ecological selection, sexual selection, or both?	Experimental evolution study: what causes acoustic divergence between replicated lines?
Ecological selection	Survivorship or ecological performance, as a result of direct (e.g., on bat echolocation call) or correlated selection (e.g., finch beak size).	Ecological divergence (e.g., differences in beak depth, body size), features of the environment (e.g., climatic variables, signal transmission properties), or ecological performance (e.g., capture of certain prey sizes by echolocation).	Assortative	Low; signals do not function as quality indicators, but may instead serve as recognition cues, with greater trait variation between than within populations	Within separate populations, acoustic signals covary with ecological traits including morphological features related to signal production. Acoustic divergence occurs primarily as a function of environmental divergence (e.g., diet, predators, parasites, and acoustic environment) and corresponds with assortative mating.	Divergence in ecological traits (e.g., beak size or wing length in birds) predicts acoustic divergence.	Population signals converge in a common garden setting within replicated lines.
Sexual selection	Reproductive success, strength of mate preference or level of intrasexual competition.	Divergence in the intensity of sexual selection or strength of preference for local signal.	Preference-based	Relatively high; acoustic signals serve as quality indicators	Within separate populations, acoustic signals covary with intensity of sexual selection, controlling for ecological differences. Signal divergence is driven by divergent preferences such that individuals show greatest response to the most exaggerated form of the local signal.	Divergence in sexual signaling traits (e.g., degree of sexual dimorphism) or intensity of sexual selection (e.g., degree of polygyny) predicts acoustic divergence.	Population signals diverge or remain constant in a common garden setting within replicated lines.
Ecological and sexual selection	Divergence in both ecological and sexual traits/intensity of sexual selection.	Divergence in both ecological variables and intensity of sexual selection between closely related populations.	Preference-based	Relatively high; acoustic signals are indicator traits and vary among individuals	Within separate populations, acoustic signals covary with both ecological and sexual traits/intensity of sexual selection. Individuals show greatest response to the most exaggerated form of the local signal.	Divergence in both ecological traits and sexual traits predicts acoustic divergence.	Population signals converge to maximize signal efficacy, while stochastic targets of sexual selection may lead to increased divergence in some signal features among replicated lines.
Drift	Divergence in neither ecological nor sexual traits/intensity of sexual selection.	Divergence in neither ecological variables nor intensity of sexual selection between closely related populations.	Random mating with regard to acoustic signals	No specific predictions	Acoustic signals do not covary with ecological or sexual traits/intensity of sexual selection and individuals do not show greatest response to any particular variant of the local signal. Acoustic distance accrues linearly with neutral genetic distance.	Acoustic divergence is not associated with ecological or sexual trait divergence.	Population signals vary stochastically across replicates.

*See Glossary for definitions.

Table 3. Summary of the best-studied taxa for acoustics and speciation

Common name	Taxon	Level of comparison	Constraints	Processes				Summary	Refs
			Sensory drive tested?	Ecological Selection tested?	Sexual Selection tested?	Role of Drift tested?	Proposed driver of AD ^a		
Peters' dwarf frog <i>Engystomops petersi</i>	Amphibian	Population	No	In part, tested correlation between signal and landscape features	Yes	Yes	SS	Sexual selection for call complexity has driven divergence in calls and associated structures; ecological selection (as tested) not important; sensory drive untested.	[40,92]
Cricket frog <i>Acris crepitans</i> (now <i>Acris blanchardi</i>)	Amphibian	Population	Yes	Body size only	Yes	No	SS	Females select for lower pitched signals, regardless of population identity; sensory drive explains salient differences between populations in different habitats.	[24,93,94]
Swordtail crickets <i>Laupala</i> spp.	Insect	Species	No	No ecological distinctions found	Yes	No	SS	Sexual selection for pulse rate has driven rapid divergence, without obvious ecological adaptation; role of drift unknown; sensory drive untested.	[5,50,85]
Treehoppers <i>Enchenopa binotata</i>	Insect	Host races	Yes	Habitat categories (host plant)	Yes	No	ES + SS	Sexual selection following host shift strongly supported; ecological selection and drift not directly tested; sensory drive important.	[55]
Green lacewings <i>Chrysoperla</i> spp.	Insect	Songtype species	Yes	No	Yes	No	SS	Sexual selection proposed, but a relationship between signal variation and fitness not demonstrated. Mutation order speciation may be more likely; sensory drive not very important.	[13,66]
Amazonian birds	Suboscines and nonpasserines (i.e., no song learning)	Closest relatives in bamboo and <i>terra firme</i> habitat (congeners, but not sisters)	Yes	Yes	No, thought unlikely to be important	Yes	Unk	Sexual selection thought to be unlikely, and ecological traits not found to predict signal variation; sensory drive important in signal divergence.	[19]
Song sparrow <i>Melospiza melodia</i>	Oscine passerine	Subspecies	Yes	Yes, through parasite loads	Yes	Yes	Unk	Sexual selection for locally common song elements supported; local song element sharing inversely correlated with parasite load; drift supported; sensory drive explains significant amount of signal variation.	[20,95]
Greenish warblers <i>Phylloscopus trochiloides</i>	Oscine passerine	Subspecies	Considered, not tested	No	Indirectly, through playbacks to males	Yes	Drift and SS	Sexual selection for complexity along northern gradient and drift proposed to explain song divergence; ecological selection untested; sensory drive untested.	[10,56]
Medium ground finch <i>Geospiza fortis</i>	Oscine passerine	Populations	Yes	Yes	Indirectly, through playbacks to males	No	ES	Ecological selection for beak size results in population divergence through assortative mating; unknown whether song characteristics relate to mating success; sensory drive not well-supported; drift untested.	[8,96,97]

^aAbbreviations: AD, acoustic divergence; ES, ecological selection; SS, sexual selection; Unk, unknown.

Even more generally, body mass explains much of the variation in signal pitch and duration across the major acoustically signaling animal lineages [38]. As a result, selection on signal pitch can lead to inversely correlated effects on body size and vice versa, as shown in frogs [40,41]. Evolution of acoustic traits resulting from ecological adaptation might be widespread, due to the generality of the size-pitch relationship across taxa.

Consequences of acoustic divergence

To demonstrate that speciation results primarily from ecologically-selected acoustic divergence, studies should show that divergence in signals (i) corresponds with ecologically adaptive trait variation (directly or through trait correlation) in each population and (ii) is associated with assortative mating by ecotype. Following the above examples, ecologically-selected changes in echolocation call frequency among Wallacea's bats is hypothesized to cause pre-mating isolation through effects on mating signals and perception [42]. Similarly, a population of the medium ground finch at El Garrapatero, Galápagos has experienced disruptive selection for beak size. Because of correlated bioacoustic effects of these adaptations, small-beaked morphs have broader frequency bandwidth songs, and both morphs respond more strongly to homotypic (i.e., same morph) song [8]. Although acoustic divergence in bats results from direct selection on signal function, and divergence in finches results from correlated selection on beak size, both traits are considered 'magic traits', because ecologically adaptive changes in these traits results in assortative mating; reviewed in [43].

Sexual selection

Sources of acoustic divergence

If sexual selection has been the dominant driver of acoustic divergence, strength of preference for, or intrasexual aggression elicited by [44], local acoustic signals should be a stronger predictor of acoustic divergence than differentiation in ecological traits. A key prediction of this model is that ecological differences play little or no role in shaping patterns of acoustic signal divergence. Sexual selection has been proposed as the primary driver of acoustic divergence between populations in a diversity of taxa, including frogs [40], green lacewings [45], crickets [46,47], and birds [10,48]. For example, female preference for greater signal complexity is thought to have driven acoustic divergence between two species of winter wren [48], subspecies of greenish warbler [10], and populations of Peters' dwarf frog [40]. However, the mechanisms by which preferences diverge in these systems are not well understood.

Consequences of acoustic divergence

To clearly demonstrate speciation via sexually-selected acoustic divergence, studies should show that divergence in signals (i) corresponds with sexual selection in each population and (ii) is associated with divergent preferences. Usually, data are available for criterion (i) or (ii), but not both (but see [49]). Additionally, phylogenetic techniques have been employed to test whether patterns such as increased signal complexity, an expected product of sexual selection, could explain patterns of species diversity

[5,14,40]. The best example which combines all of these levels of inquiry is the radiation of the Hawaiian swordtail crickets (*Laupala* spp.). In *Laupala*, phylogenetic methods have shown that genetic differences between species are associated with differences in call pulse rate [5]. Moreover, experimental work within divergent populations of *Laupala cerasina* has shown that (i) females prefer mean values of local male pulse rates, and (ii) these differences correspond with preferences for local mates [50]. Thus, acoustic divergence, initiated by divergent sexual selection, has occurred without apparent ecological adaptation [5].

Ecological and sexual selection

Theory suggests that ecological adaptation and mechanisms of mate choice are closely entwined, and can be mutually reinforcing [51–53]. In particular, sexual traits and preferences will always be expressed within an ecological context and might therefore be subject to ecological selection [53,54]. Further, sexual selection might accelerate population divergence initiated by disruptive ecological selection [51] and potentially facilitate ecological adaptation by displacing populations from optimal viability peaks [52].

Sources of acoustic divergence

If ecological and sexual selection acting in combination are largely responsible for signal divergence, acoustic differences among populations should covary with divergence in both ecological variables and sexual traits. One of very few systems where data are available on both of these sources of selection is the *Enchenopa binotata* treehopper complex. In this complex, host plant shifts are associated with ecologically-selected changes in signal pitch, corresponding with optimal signal transmission through plant substrates [22]. Thus, the acoustic window for each host plant habitat is limited to a narrow frequency band. Further signal evolution within these bounds results from sexual selection by female choice [55]. Additional examples from cricket frogs and song sparrows show correlations between sexually-selected acoustic traits and body size and parasite load, respectively (Table 2).

Consequences of acoustic divergence

For speciation to result from divergent ecological and sexual selection on acoustic signals, studies should show that divergence in signals (i) covaries with ecologically adaptive trait variation and (ii) sexual selection pressures in each population, and (iii) is associated with divergent preferences. Treehoppers are the only study system we are aware of which satisfy these criteria. Here, signal variation corresponds with ecologically adaptive transmission properties based on signaling substrate [22], signals across populations correspond to strength of female preference [49], and local signals are preferred, resulting in reproductive isolation [55].

Neutral and mutation-order processes

Sources of acoustic divergence

To demonstrate that neutral evolution is most important in driving acoustic divergence, studies should invalidate criteria for each potential selection regime (Table 2), and

show that acoustic trait divergence increases linearly with genetic or geographic distance (Figure 1, blue broken line). The latter pattern was shown for greenish warblers [56], frogs [57], and singing mice [58], where it was attributed to drift. [For animals with vocal learning (Box 1), cultural and genetic drift will be difficult to separate.] However, a linear accumulation of acoustic differences over time might also result from a mutation-order (M-O) process [54,59]. If populations adapting to similar environments randomly gain beneficial (but incompatible) mutations in a clocklike fashion, and there are minor fitness differences between alleles, this can lead to M-O speciation. Although drift should be more important in smaller population sizes, the interaction between drift and M-O processes merits further investigation [60]. Thus, demonstrating the first criterion, that selection has had a minor effect on acoustic divergence, is not trivial. In many cases, such as in greenish warblers, acoustic divergence may occur through a combination of selection and drift [10,56].

Consequences of acoustic divergence

To demonstrate speciation resulting from acoustic divergence by drift, studies should show that (i) acoustic signals have evolved through drift, with little effect of selection, and (ii) there is assortative mating by population. Drift will most likely lead to speciation where population demographics or time in allopatry allow for greatest divergence in signal, preference, or both.

Framework for identifying mechanisms driving acoustic divergence and speciation

To accelerate progress in understanding acoustic divergence and speciation, Table 2 outlines a conceptual framework for determining the relative contributions of ecological, sexual selection, and drift to acoustic divergence. The patterns and study methodologies provided in Table 2 allow one to determine which process(es) are largely responsible for acoustic divergence. Because one single methodology is not applicable to all study taxa, we also provide specific testable predictions for distinguishing between these primary sources of selection through a variety of approaches. Accordingly, this framework can be applied to empirical studies examining two or more closely related populations, or to larger-scale phylogenetic comparative studies. Complementary studies utilizing preference tests or phylogenetic studies of diversification patterns should aim to verify that acoustic differences are related to reproductive isolation. Ideal systems for testing the role of sexual and ecological selection in acoustic signal divergence (i.e., birds, crickets, spiders, and frogs) have a wealth of acoustic, ecological, and phylogenetic data available, as well as information on sexual selection pressures among populations.

Current knowledge on the causes and consequences of acoustic divergence

Table 3 summarizes our current understanding of the role of different drivers of acoustic divergence in speciation for the best-studied taxa (see also supplementary table). Most studies have not attempted to test the relative contributions of evolutionary constraints, adaptive processes, and neutral

mechanisms in acoustic divergence. Evidence that sensory drive plays a role in acoustic divergence comes from birds [19–21,26,27,30–32,34,61], insects [22,28,29,33,35], spiders [23], frogs [24,35,36], and mammals [9], suggesting the importance of selective shifts between acoustic windows. For example, host plant characteristics result in narrow frequency bands (of the order of 100 Hz) for optimal transmission of vibrational signals in treehoppers [22]. Thus, transmission properties severely limit acoustic windows in substrate-signaling treehoppers, while ambient noise may impose greater limitations on the acoustic windows of aerially signaling birds [21,26,30], whose songs commonly encompass more than 1000 Hz. Moreover, habitat transmission properties might be important in affecting emphasized frequencies or frequency bandwidth, but not the fine-scale spectral characteristics or temporal patterning of birdsong [62]. Habitat is also generally less important in explaining variation in frog [63] and insect [64] signals, perhaps due to larger effects of evolutionary constraint, available acoustic space, or the direction of sexual selection. A focus on sensory drive is important, but further resolution on signal divergence can be gained from testing the adaptive or neutral processes underlying transitions between and shaping variation within acoustic windows.

A role of sexual selection in acoustic divergence features prominently in the best-studied taxa. Of the nine taxa included in Table 3, chosen to represent a broad range of animal groups for which many factors influencing acoustic divergence have been considered, eight indicate an important role for sexual selection. A broader dataset of 18 taxa (supplementary table), including less well-studied groups, illustrates a similar pattern. We argue that these results represent a real trend, stemming from the general importance of acoustic signals in sexual communication, and the propensity for changes in these signals among populations to lead to speciation. This is consistent with a recent meta-analysis of comparative studies indicating a significant positive effect of sexual selection on speciation rates, although much depended on the depth of phylogenetic sampling [65]. However, for studies showing a role of sexual selection in acoustic divergence, we know very little about the contribution of ecological selection to signal variation.

The timing of acoustic divergence

We suggest that certain characteristics, discussed below, will make acoustic divergence more important early (initiating) versus later (in finalizing) the speciation process. Figure 1 shows predicted relationships between acoustic and neutral genetic distance resulting from different processes over different timescales.

Early acoustic divergence

For acoustic signal divergence to provide the primary isolating barrier early in speciation, there should be changes in signals and/or perception which are tightly coupled with assortative mating. This process should be facilitated by reduced constraints on signal or perceptual evolution, controlled by simple genetic architecture or subject to rapid cultural evolution, especially where there is tight linkage between signal and preference [2]. The key

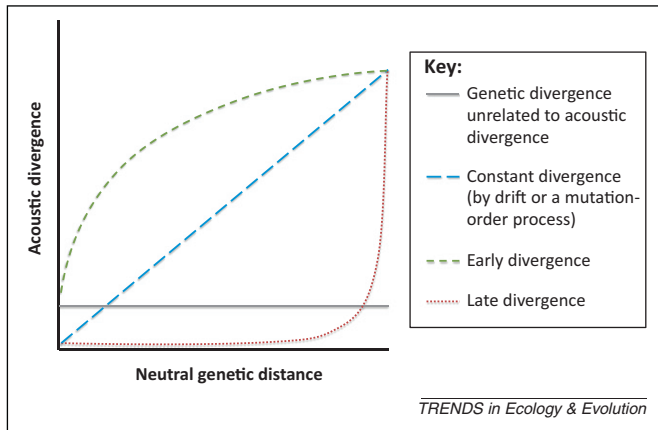


Figure 1. Predictions for comparisons of acoustic and genetic divergence across populations, which are expected to result from different processes. Predicted patterns are as follows: there is no relationship between acoustic and genetic divergence, perhaps due to context-specific environmental or demographic factors (gray, unbroken line); acoustic and neutral genetic distances accrue in a clocklike fashion, as expected through drift or a mutation-order process (blue, long-broken line); acoustic signals diverge faster than neutral genetic loci, as a result of ecological, sexual selection, or a combination (green, short-broken line); or acoustic signals diverge slowly until neutral genetic differences have accrued, and then rapidly increase, as expected by reinforcement (red, broken line). The green, short-broken line is consistent with a role for acoustic divergence in initiating speciation in the lineage under study, while the red, broken line is consistent with the importance of acoustic divergence in finalizing speciation. This predictive framework is amenable to comparative studies.

expectation for the importance of acoustic divergence early in speciation is that signal differences will accumulate much faster than genetic differences. Thus, the best-fit function between genetic and acoustic divergence will have a non-zero intercept (Figure 1, green broken line).

This pattern is likely to be especially important in organisms such as vibratory-signaling insects (e.g., lacewings and treehoppers), which are able to adapt spectral and/or temporal characteristics of signals through a simple mechanism that does not require large-scale changes in signaling organs [66,67]. Additionally, organisms with tight linkage of signal and preference (e.g., swordtail crickets) [47] might be predisposed to speciation via early acoustic divergence.

Such rapid speciation should primarily occur through two processes. The first involves magic traits, whereby ecological differentiation is associated with reproductive isolation. For example, in a Neotropical bird radiation, [32] selection on beak size has had correlated effects on song production, leading to reproductive isolation. In the second process, M-O speciation, a mutation affects acoustic signal production and species recognition, but is selectively equivalent among populations from an ecological standpoint. Perhaps the best example of this process is the green lacewing radiation. These duetting insects appear to speciate readily through simple mutations which directly cause assortative mating through effects on the signals of males and females [6]. Although sexual selection might affect later signal evolution, the fact that species recognition is based on a simple mutation, which does not appear to have adaptive transmission properties [66], makes this system a good candidate for M-O speciation.

Acoustic divergence later in speciation: a role of reproductive character displacement

Great effort has been spent investigating the effects of secondary contact between divergent taxa on acoustic divergence. Once post-zygotic genetic incompatibilities have arisen, selection should favor increased divergence in signals and their discrimination. Such a pattern of reproductive character displacement (RCD) has been demonstrated in a wide range of taxa, including insects [68], frogs [41], bats [69], and birds [27,39,70]. Because signal displacement in zones of contact can lead to isolation from closely related, yet geographically isolated populations [41], RCD has been proposed as a powerful means for diversification [71].

Because reinforcement implies a cost of hybridization, this mechanism of RCD will generally occur later in the speciation continuum (Figure 1, broken red line). By contrast, many other proposed mechanisms of RCD, involving competition or predator-prey interactions do not require genetic incompatibilities between acoustically displaced populations. Thus, these mechanisms of RCD might show early or inconsistent patterns of divergence among population pairs (Figure 1, broken green and unbroken gray lines, respectively). Identifying conditions favoring divergence versus convergence, assessing the prevalence of these conditions, and collecting acoustic data for populations differing in genetic relatedness will help clarify the mechanisms and timescale over which acoustic divergence facilitates speciation.

Suggestions for future research

Consider multiple processes and study environments

We advocate that the role of sexual selection in signal divergence be explored within systems where research has generally focused on ecological selection, and vice versa. Additionally, the heritability of acoustic traits, and therefore their availability to selection, is not known for most systems in the wild (but see [27]). Thus, future work should aim to bridge the gap from lab to field in order to benefit from existing knowledge on the genetic architecture of signal evolution and mate preferences. Such approaches (recently applied to zebra finches [72] and crickets [73]) provide an unprecedented opportunity to ground-truth assumptions and connect experimental and genetic data to biological reality in the wild.

Incorporate receiver perception

Most speciation studies have focused on signal divergence. However, it is becoming increasingly apparent that receivers can modify behavior based on subtle variation in signal structure [11,36,50,74–76]. Meanwhile, overt signal divergence might not be meaningful to receivers [77]. Future studies should strive to quantify behavioral responses to observed signal variation in order to determine its relevance to population divergence.

Broaden consideration of sender–receiver dynamics

Very few studies consider the evolutionary significance of female traits or heterospecific sender–receiver dynamics. However, new studies increasingly show the importance of female signals in reproductive isolation, whether as signals used by males in mate choice or by females in resource

defense [44,78]. Moreover, recent evidence suggests that heterospecific competition can occasionally drive signal convergence in both sexes through social selection [79] for defense of resources [74]. As such, we suggest a broader scope for defining sender-receiver acoustic communication to include intrasexual communication, female signalers, and the influence of heterospecifics, in both reproductive and non-reproductive contexts.

Concluding remarks

Here we synthesize research on the role of adaptive and neutral processes in driving acoustic divergence and speciation. Because research has typically not considered each of these processes within the same study system, we summarize a set of testable predictions to determine the relative importance of each to acoustic divergence. Additionally, sensory drive has been a focus of many studies on acoustic divergence, yet we argue that this framework does not itself provide an explanation for the underlying mechanisms of acoustic divergence. The acoustic window concept offers a way to incorporate sensory drive considerations of habitat- and sensory-based constraints on standing variation and evolutionary opportunity into investigations of the mechanisms shaping acoustic variation within and between populations. Moreover, assessing patterns by which acoustic divergence accrues with genetic distance can help identify the processes involved in divergence and the timescale over which they are important for speciation. We suggest that applying this conceptual framework broadly to the study of acoustic divergence will help to better understand the processes governing speciation in the wide range of acoustically signaling taxa. Further, this framework is easily adaptable to other behavioral and morphological features which mediate mate selection and conspecific recognition within and among closely related populations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2012.10.002>.

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