



ECOLOGICAL SPECIATION

Ecological speciation in Darwin's finches: Ghosts of finches future

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The theory of ecological speciation posits that adaptive divergence among incipient species raises incidental barriers to reproduction, thus catalyzing the emergence of new species. In this study, we conducted an experimental test of this theory in Galápagos finches, a clade in which beaks and mating songs are mechanistically linked. We forecasted the acoustic structure of songs for a set of possible evolutionary futures (successive droughts spurring increasingly large beaks) and, in a field assay, presented resulting song simulations to territorial males. We found that responses to songs dropped off after six simulated drought events, to degrees roughly comparable to drops in response to songs that diverged through cultural drift and acoustic adaptation. Our results support, in Darwin's finches, the feasibility and mechanistic bases of an ecological speciation hypothesis.

Speciation, the process by which new species emerge, often has an ecological component (1–3). In one widely recognized mechanism of “ecological speciation,” divergent trajectories of morphological adaptation among incipient species enhance probabilities of subsequent reproductive isolation by driving incidental changes to cues or signals that animals use for mate recognition (4–9) (Fig. 1A). Cases of ecological speciation are often recognized retrospectively, in correlations among adaptive and signaling traits, after speciation is already complete (5, 6). By contrast, we lack predictive data regarding how and when, as speciation proceeds, ecological divergence and its impacts on mating traits actually elevate species recognition barriers.

One group of animals for which ecological factors have been long recognized as foundational to speciation are Darwin's finches of the Galápagos Islands, Ecuador. Divergence in this adaptive radiation has centered largely on beak form and function, which we now know adapt through natural selection to local food resources and interspecific competitors (10–16). In theory, divergence in Darwin's finch beaks could enhance, as a secondary impact, species discrimination and reproductive isolation among diverging incipient species (16, 17). One reason for this is that beaks are not only the primary loci of finch adaptive evolution, they also shape the production of these birds' vocal mating signals. While singing, Darwin's finches (like many songbirds) modulate their beak gapes in synchrony with vocal source (syrinx) activity, presumably to maintain effective resonance filtering and tonality across varying source frequencies (18–20). Accordingly, evolutionary changes in finch beaks and seed-crushing capacities should influence, as a secondary con-

sequence, the structure of some song traits, especially those requiring rapid or pronounced beak gape modulations [(21–23); see (24–27) for parallel examples in other Neotropical bird clades]. Given beak-song linkages and the central role of mating songs in Darwin's finch species recognition (16), ecological divergence among incipient species could, in principle, enhance finches' ability to distinguish diverging lineages by song and could consequently foster speciation (Fig. 1B). This proposed mechanism, however, has not yet been subject to direct empirical tests (28, 29). We do not yet know how much ecological change and matched evolution of beaks and songs would be required to elevate barriers to reproductive isolation. We also have been unable to assess the impacts on species recognition of beak-related song divergence, as per the ecological speciation hypothesis, relative to other factors, especially cultural drift and acoustic adaptation, that can also drive song divergence and reproductive isolation.

In this work, we start to fill these gaps for a population of Darwin's medium ground finches (*Geospiza fortis*) at El Garrapatero, Santa Cruz Island, Galápagos. This population features discrete small and large morphs that have diverged markedly in body and beak dimensions (30). These morphs are favored over intermediate-sized birds through disruptive selection (31, 32), specialize on partially distinct sets of food resources (33), sing songs that match their divergent beak morphologies (22), and mate assortatively by morph (34). In a prior study (35) with this population, territorial males responded more strongly to playback of songs of their own morph, consistent with a hypothesis of ecological speciation (21, 23, 34). However, that study did not isolate the functional (communicative) relevance of song variation linked specifically to beak divergence, as the playback songs in that study (same or different morph) differed acoustically not just because of beak divergence but also because of cultural drift, i.e.,

the accumulation of song-copying inaccuracies or innovations across generations (36), which, with sufficient time and isolation, can also cause songs to diverge and thus enhance species discrimination. Songs of songbirds in isolated lineages can also diverge through independent trajectories of acoustic adaptation, which is selection for efficient transmission through distinct acoustic environments that the incipient species occupy, for example, through the evolution of low-frequency, slowly repeated notes in woodland habitats (37–39). Beak divergence, cultural drift, and acoustic adaptation can thus be regarded as alternative drivers of vocal reproductive isolation (40–42), and sorting among them is necessary for assessing the relative weight in the Darwin's finch radiation of the proposed ecological speciation mechanism.

Projecting beak-related impacts on song structure

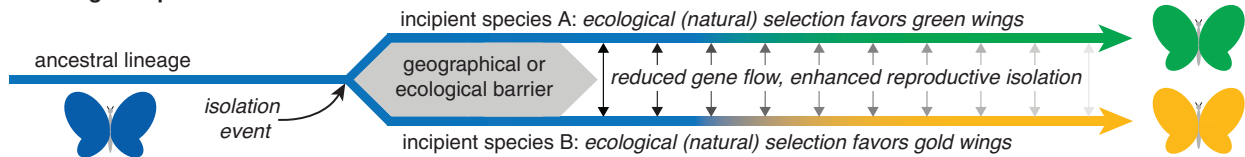
As a first step in our study, we constructed song stimuli to be used for playback trials that incorporated acoustic changes that we anticipated would occur along one possible course of future evolution in beak morphology. Toward this end, we selected a sample of songs in our study population recorded previously (22) from birds of known beak sizes, and then for each, we generated three digitally modified songs, “ghosts of finches future,” that projected expected impacts on song structure that would in principle be caused by one, three, or six cumulative future drought events (Fig. 2). Our process was guided by three observations: (i) A classic long-term study of *G. fortis* from Daphne Major showed that droughts tend to spur natural selection for larger beaks (12, 14); (ii) the evolution of larger beaks and associated increases in bite force capacity (23) should diminish birds' vocal performance and, in particular, birds' abilities to match source frequency changes with vocal tract modulations required for rapid trills with broad frequency bandwidths [vocal parameters that can be captured in a single performance metric, “vocal deviation” (21, 22)]; and (iii) as morphological impacts of droughts accumulate, songs should evolve toward increasingly diminished trill rates and frequency bandwidths, diverging incrementally from present-day songs. The average change in beak depth after six simulated drought events, following values reported by Grant and Grant (43), approximates actual degrees of separation in beak depth at our study site between both (a) the small and large *G. fortis* morphs and (b) the large *G. fortis* morph and *Geospiza magnirostris* (30).

Field test of the ecological speciation hypothesis

We presented song stimuli to 12 *G. fortis* males using a simulated territorial intrusion assay.

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A Ecological Speciation



B Ecological Speciation in Darwin's Finches

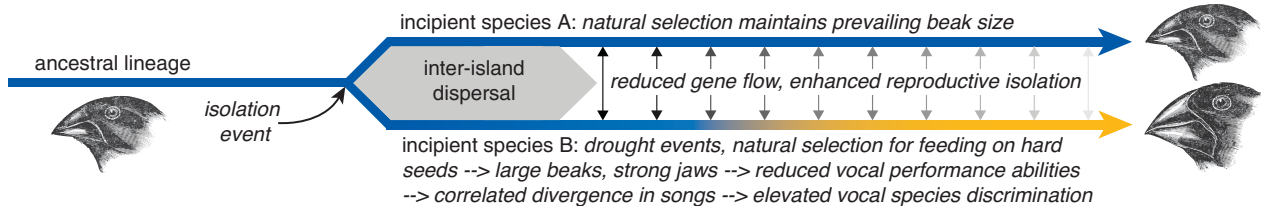


Fig. 1. The process of ecological speciation. (A) Ecological speciation begins when an ancestral lineage (blue line, evolving from left to right, illustrated for a hypothetical lineage of butterflies) experiences an isolation event, such as when encountering a new geographic or ecological barrier (gray shading) that splits the ancestral lineage into multiple descendant lineages. These lineages, now incipient species, may experience distinct ecological environments and thus divergent trajectories of natural selection and phenotypic evolution. In the example shown, natural selection favors wing colors that enhance survival in the butterflies' new habitats, for example, by minimizing detection by predators. Ecological speciation ensues if diverging adaptive traits or genetically correlated (pleiotropic) traits also mediate mate choice, for example, if female butterflies prefer to mate with like-colored males (green with green or gold with gold). In such cases, diverging lineages should experience increasingly reduced gene flow on secondary contact, thus enhancing interlineage reproductive isolation and

fostering speciation. **(B)** Ecological speciation in Darwin's finches is expected because a primary locus of natural selection, beak form and function, can invoke knock-on divergence in acoustic mating signals, given that beak movements mediate not just feeding but also song production. In one of numerous possible routes for ecological speciation in the finches, an ancestral line splits owing to interisland dispersal. The original population, now incipient species A, experiences stabilizing natural selection and maintains its prevailing beak size, whereas the dispersed population, now incipient species B, encounters drought conditions and evolves corresponding adaptations, larger beaks and stronger jaws, for husking larger, tougher seeds. Accordingly, birds in incipient species B are predicted to experience linked evolutionary reductions in performance-related vocal traits (such as trill rate and frequency bandwidth), which could, on secondary contact, reduce interlineage acoustic species recognition and thus enhance reproductive isolation. Finch sketches were reproduced from Darwin (54).

Each male was presented with playback of a natural song from another male of its own size morph plus that song's three simulated versions (Fig. 2, right). The four song treatments (control, one-drought event, three-drought events, and six-drought events) were presented to each bird over the course of a week; birds heard one treatment per test day in 3-min blocks, with each test day separated by a nontest day to limit carry-over effects. Treatment order was counterbalanced across the experiment, and all birds were tested with a unique stimulus set. As in three prior studies with this species on this island (35, 44, 45), stronger aggressive responses to playback are interpreted as reflecting greater stimulus salience. Guided by those studies, we measured response strength primarily with respect to birds' flight behavior (latency to fly off the starting perch, flight rate, and proximity to the playback speaker), as birds appeared to search for the simulated intruder. We also measured latencies and rates of vocal responses (songs), even though the three prior studies noted above generally did not detect effects of playback treatment on finches' vocal activity. Our main prediction was that beak-related changes in song structure, as a stand-alone factor, would cause de-

tectable and increasingly severe decrements in birds' responses to playback because such songs should be less likely to be recognized and categorized by subjects as belonging to their own species. A major alternative potential outcome was that the acoustic changes implemented would not impact vocal species recognition. Such an outcome would imply that finches base their assessment of species identity on acoustic features not linked to beak evolution.

Our first main finding was that birds responded less strongly to the most extreme stimulus manipulation (six-drought songs) relative to control (zero-drought) songs (Fig. 3 and table S1). In terms of flight latencies (Fig. 3A and table S1), birds hearing control songs left their starting perches much earlier than when they heard six-drought songs (estimated marginal means, 16.2 versus 63.4 s; z -score = 2.383, $P = 0.02$). In flight rates, birds flew 31% less often in response to six-drought songs than to control songs (Fig. 3B) (z -score = -2.094, $P = 0.04$). In approach distances, birds challenged with control songs approached the speaker more closely, by an average of 1.4 m for perched distances (Fig. 3C) (z -score = 1.864, $P = 0.06$) and 2.2 m when also accounting for over-

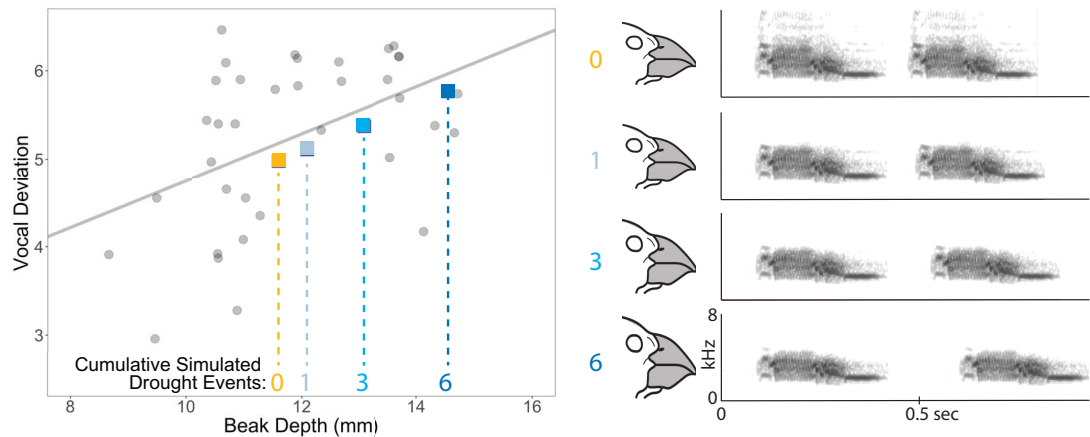
flights of the playback speaker (Fig. 3D) (z -score = 2.066, $P = 0.04$). The flight and approach results support our prediction that beak-related changes to song would lead to diminished responses. By contrast and consistent with prior studies with this species on this island (35, 44, 45), no strong effects of treatment were found for singing latencies or rates (fig. S1). The overall stronger response to control songs versus six-drought songs was corroborated in a principal components analysis that included all response variables (table S2) (principal component (PC) 1, z -score = -2.068, $P = 0.04$). These results together support the feasibility of an ecological mechanism in driving species recognition among diverging finch species, at least when beak divergence is substantial, here approaching natural levels of divergence among related ground finch species or morphs. It is also clear that our study subjects did recognize the six-drought simulated songs as salient, even though their responses were diminished. This implies that the acoustic modifications we introduced to songs did not completely obstruct cross-lineage recognition.

Next, we considered the intensity of finches' responses to one- and three-drought playback

Fig. 2. Logic and method for constructing song playback stimuli to test the ecological speciation hypothesis, illustrated here for 1 of our 12 stimulus sets.

(Left) The gray dots and gray line represent vocal deviation (a measure of vocal performance) as a function of beak depth for *G. fortis* at our study site. The plot was constructed from data collected and analyzed during a prior study (22). Higher vocal deviation values correspond to lower vocal performance

(21). The orange square marks one male finch's beak depth (11.61 mm) and the corresponding vocal deviation value for his song; digital recordings of his song provided the basis for constructing this stimulus set. Blue squares, increasingly dark in hue, mark projected beak depths and corresponding vocal deviations for this male and his song, following one, three, and six cumulative simulated drought events [magnitudes of beak evolution follow (43)]. Larger beaks, under positive selection in drought years to crack tough seeds, are associated with reduced vocal



performance and manifest here in larger vocal deviations. (Right) Sketches of beaks (scaled to indicate simulated changes in relative beak depth) plus spectrograms of playback songs for control (top row) and simulated songs (remaining rows) for birds with increasingly large beaks and corresponding projected reductions in vocal performance. Eleven other stimulus sets were constructed from the songs of 11 other finches with different beak sizes. Beak sketches were adapted from drawings by Bowman (11).

songs relative to control and six-drought songs. It was possible that decrements in response would accumulate in roughly linear fashion, in concordance with the graded nature of the acoustic changes that we introduced across drought treatments. Another possible outcome was that birds' responses would drop off immediately for one- and three-drought songs, relative to their responses to control songs. Such an outcome would suggest a particularly strong (and evolutionarily early) impact of beak-related vocal evolution on species recognition. Yet another potential outcome, that birds would respond to one- and three-drought songs with degrees of vigor similar to that for control songs, would imply that song retains lineage-specific signatures even during mild to moderate changes in beaks and associated song attributes. Such an outcome would imply that functional impacts of beak-song linkages on species recognition emerge only toward later stages of incipient species divergence. Our results support the third interpretation. Virtually all response levels did not differ between playback of control songs and their one- or three-drought song counterparts (Fig. 3 and table S1). One weak exception to this pattern concerned flight rates (Fig. 3B), for which birds flew 26% less often in response to one-drought songs than to control songs (z -score = -1.784 , $P = 0.07$). This exception was also captured by the analysis of PC3 (z -score = -2.250 , $P = 0.02$), which loaded heavily for numbers of flights (table S2); by contrast, no differences across zero-, one-, and three-drought treatments were detected in analyses of the remaining PCs (1, 2,

4, and 5). Our results together suggest that beak-driven changes to song on their own would require a substantial degree of divergence, corresponding to between three and six drought events, to enable vocal discrimination among diverging finch species, at least as indicated here in the responses of territorial males.

Contribution of beak-related song divergence to vocal species recognition

Our next goal was to weigh the impact on species recognition of song evolution related to beak divergence relative to impacts related to cultural drift and acoustic adaptation. Toward this end, we evaluated outcomes from the current study (control versus six-drought songs; Fig. 4) relative to outcomes generated in a prior playback study (35) conducted with the same population, playback protocol, and repeated measures design. In that study, birds' responses to control songs were compared to their responses to probe songs from the same location but of the other morph (same location/different morph; Fig. 4) or from a different location (Borrero Bay, Santa Cruz Island) but of the same morph (35) (different location/same morph; Fig. 4).

For the same location/different morph comparison, we can presume that control and probe playback songs differed from each other acoustically not just owing to beak-related song divergence but also owing to distinct morph-specific trajectories of cultural drift, given that (i) young birds likely only learn and introduce copy errors to songs from adults of their own morphs and that (ii) females tend to prefer

mates of their own type, thus favoring true-to-morph song learning (34). By contrast, for this comparison, we can negate any impact of differential acoustic adaptation, as the two morphs at El Garrapatero overlap in habitat, sometimes singing from the same perches. In this comparison, we observed elevated contrasts of responses to probe versus control song categories for all parameters relative to the contrasts reported in the current study. These elevated contrasts, also revealed in a comparison of effect sizes (table S4, compare columns 1 and 2), delineate an extra gain in vocal discrimination capacities enabled by the interaction of beak divergence and cultural drift in driving song divergence.

For the different location/same morph comparison, we can presume that control and probe songs differed from each other owing to both cultural drift and acoustic adaptation to distinct habitats, yet without any impact of beak-related song divergence. We can make this latter presumption for two reasons: all birds recorded at Borrero Bay were small-morphed, and we restricted our consideration of response data to only small-morphed subjects. Figure 4 and table S4 (compare columns 1 and 3) illustrate that the interaction of cultural drift and acoustic adaptation bears strongly on species recognition, markedly more so than beak-related song divergence alone yet marginally less so than the interaction of beak-related song divergence and cultural drift. We also evaluated response data for a fourth control versus probe song comparison from a study in which territorial males at El Garrapatero were presented with control songs and probe songs

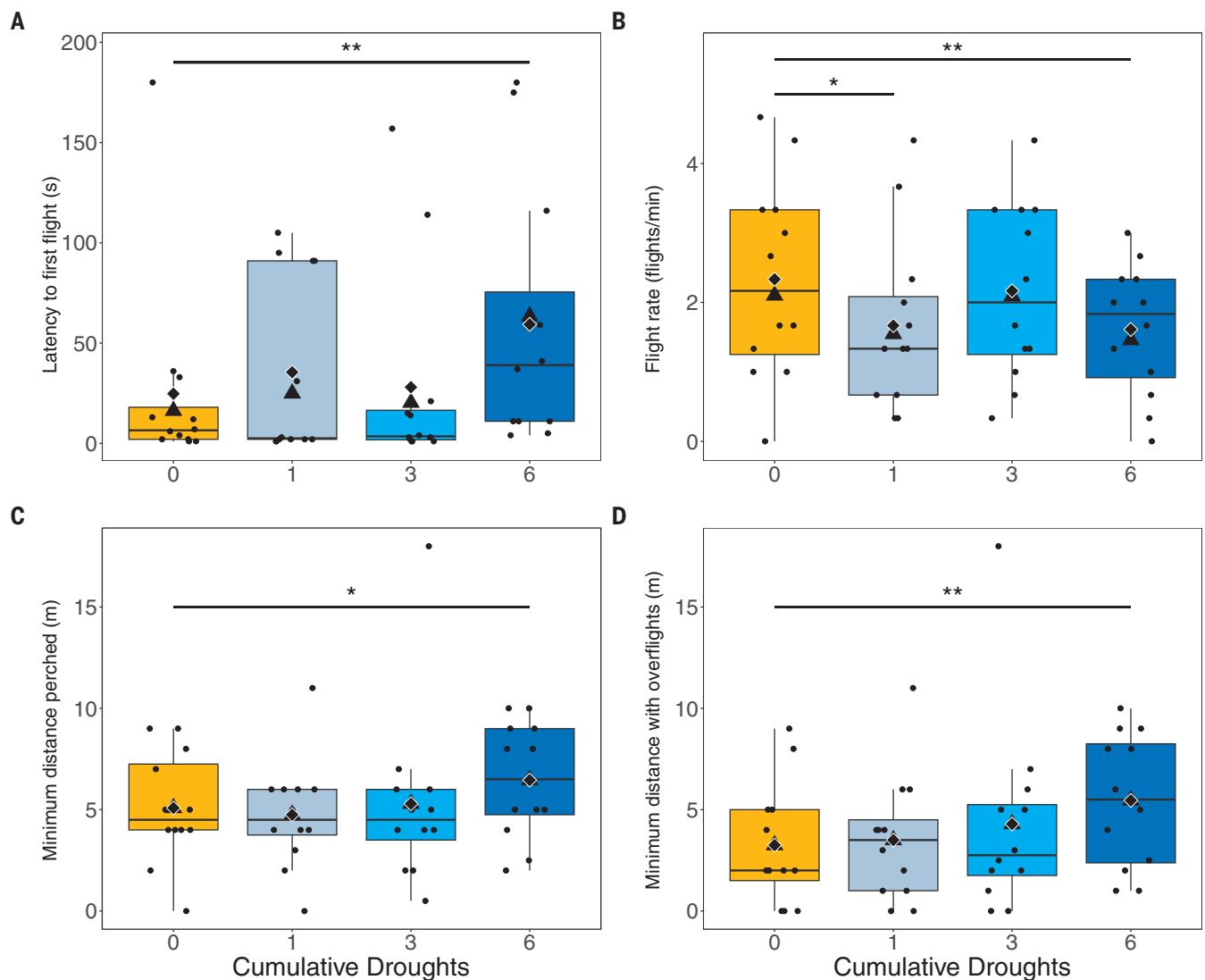


Fig. 3. Flight responses of territorial male *G. fortis* to playback of control songs (zero-drought treatment) and simulated songs (one-, three-, or six-drought treatment). Flight responses include latency to first flight (A), flight rate (B), minimum distance perched (C), and minimum distance with overflights (D). Treatment colors correspond to those in Fig. 2. Dots refer to individual data

points; hinges of the box and whisker plots refer to 25th and 75th percentiles; middle lines, triangles, and diamonds, respectively, describe medians, estimated marginal means, and arithmetic means; and whiskers denote data ranges, excluding outliers $>1.5\times$ the interquartile range from the hinge. $N = 12$ *G. fortis* males. $*P < 0.1$; $**P < 0.05$.

from yet another locality, Academy Bay (44). In that study, however, beak size morphs were not accounted for in either the stimuli presented or the study subject tested, which limits the value of cross-study comparisons. Nevertheless, a notable pattern emerged (fig. S2): the contrast in responses to control versus probe songs was more pronounced than in each of the other three comparisons, consistent with the fact that probe songs differed from control songs not just because of cultural drift and acoustic adaptation but also, to some extent, their interactions with beak divergence. As more factors contribute to song divergence, more acoustic cues for song-mediated species recognition presumably emerge, which should further enhance cross-species vocal recognition.

Ecological speciation in Darwin's finches

Speciation in many animal clades, including Darwin's finches, is catalyzed by the evolutionary divergence of communication cues or signals that, on secondary contact, can facilitate species recognition, assortative mating, and reproductive isolation (1–9, 40–42). Understanding probabilities and dynamics of speciation thus requires attention to factors that drive cue or signal divergence and to when and how animals discriminate among diverging cue or signal variants. For Darwin's finches, we can narrow our focus down to vocal signals given a series of observational and experimental studies that have demonstrated a central role for song and its divergence in species recognition and assortative mating (16, 46–49).

Thus, the central pending question for testing an ecological speciation hypothesis in Darwin's finches is this: As incipient finch species diverge, what types and magnitudes of divergence in song will enable species discrimination and, accordingly, assortative mating and reproductive isolation?

Most broadly, our results support the feasibility of an ecological speciation hypothesis for *G. fortis*. Cumulative effects on song of three to six 1977-level drought events, predicted to drive increases in beak depth of about 1.5 to 3.0 mm and corresponding changes in vocal trill rate and frequency bandwidth, appear sufficient to disrupt vocal recognition among diverging lineages. We are not aware of prior studies that have linked anticipated evolutionary

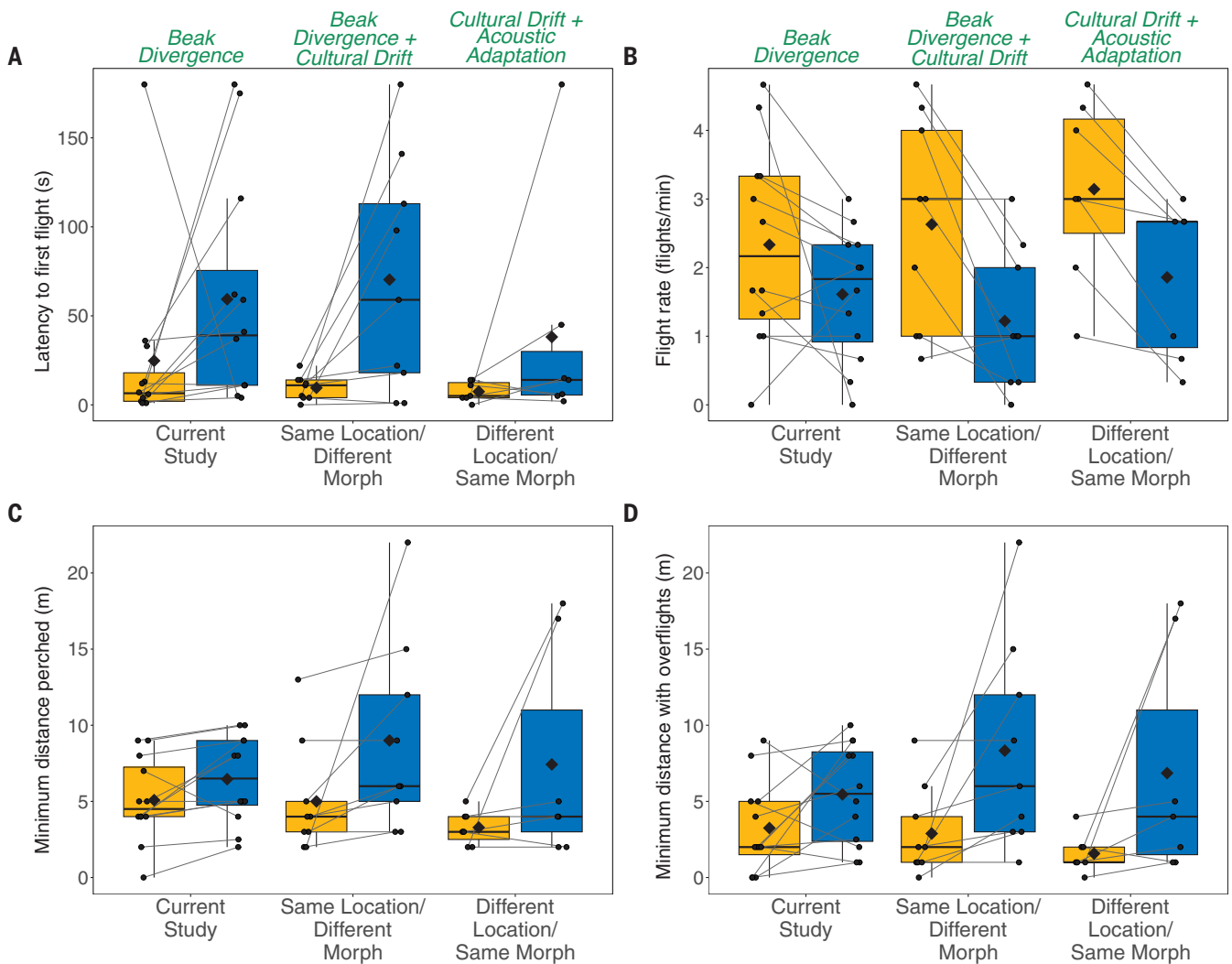


Fig. 4. Flight responses of territorial male *G. fortis* at El Garrapatero to playback of control songs and to three sets of probe songs, compiled across studies. The control song treatments (same location/same morph) are shown in orange, and the probe song treatments are shown in blue. For the current study, control and probe songs differed owing to simulated beak divergence only (data also shown in Fig. 3; zero versus six); for the same location/different morph comparison [data from (35)], control and probe songs differed owing to beak divergence plus cultural drift; and for the different location/same morph comparison [data from (35)], control and probe songs

differed owing to cultural drift plus acoustic adaptation. Weaker responses to probe songs versus control songs are evident across the board in lower values for flight rate (B) but in higher values for the remaining response parameters (A, C, and D). Greater contrasts in responses to control versus probe songs imply more severe loss of recognition of the probe songs. Dots refer to individual data points with gray lines connecting trials on the same individual; hinges of the box and whisker plots refer to the 25th and 75th percentiles; middle lines and diamonds describe, respectively, medians and arithmetic means; and whiskers describe the range of data, excluding outliers $>1.5\times$ the interquartile range from the hinge.

adaptive responses to dynamic environmental conditions, corresponding expected changes in the structure of cues or signals used for mate recognition, and the potential for species recognition and behavioral isolation among lineages inhabiting those environments. Moreover, our comparisons of response patterns and effect sizes across studies (Fig. 4 and table S4) indicate how beak-related vocal divergence works alongside cultural drift and acoustic adaptation as drivers of species recognition.

These inferences might be regarded as conservative for at least three reasons. First, our study focused solely on responses to playback of males, whereas the most important decisions

about breeding and mate choice in Darwin's finches are made by females. One might assume that patterns of vocal discrimination in males should apply directly to females, which is a case that has already been made for Darwin's finches (49). Yet, in general, females might evolve to be more discriminating in their assessment of vocal signals, as the main fitness costs of errors made in species recognition are generally more severe for females (cross-species breeding) than for males (momentarily defending their territories against heterospecific males) (50–52). If so, we might predict that female Darwin's finches' responses to song will be dampened earlier in the course of beak and

song structure divergence. A second reason that our inferences might be conservative is that, as beaks diverge, songs will likely diverge not just in trill rate and frequency bandwidth, as manipulated here, but also in more fine-scale performance-related phonological dimensions (53) that we did not attempt to represent in our simulated songs. A third reason is that finches might also assess beak divergence and thus species identities visually. Available evidence suggests that in the absence of vocal signals, finches indeed modulate their responses to simulated territorial intruders in accordance with intruders' beak sizes (17). Redundancy of visual and vocal signals should

further enhance accurate species recognition and thus foster speciation earlier in divergence than implied by our song-only data (29). Ultimately, quantifying how ecological divergence elevates reproductive barriers requires experiments such as ours that test how the animals themselves respond to ecologically selected cue and signal variants.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adj4478
Materials and Methods
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