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Widespread cultural change in declining populations of Amazon parrots

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Species worldwide are experiencing anthropogenic environmental change, and the long-term impacts on animal cultural traditions such as vocal dialects are often unknown. Our prior studies of the yellow-naped amazon (*Amazona auropalliata*) revealed stable vocal dialects over an 11-year period (1994–2005), with modest shifts in geographic boundaries and acoustic structure of contact calls. Here, we examined whether yellow-naped amazons maintained stable dialects over the subsequent 11-year time span from 2005 to 2016, culminating in 22 years of study. Over this same period, this species suffered a dramatic decrease in population size that prompted two successive uplists in IUCN status, from vulnerable to critically endangered. In this most recent 11-year time span, we found evidence of geographic shifts in call types, manifesting in more bilingual sites and introgression across the formerly distinct North–South acoustic boundary. We also found greater evidence of acoustic drift, in the form of new emerging call types and greater acoustic variation overall. These results suggest cultural traditions such as dialects may change in response to demographic and environmental conditions, with broad implications for threatened species.

1. Introduction

In animals, vocal dialects are one of the most prevalent examples of animal culture [1]. Vocal dialects are defined as mosaic patterns of acoustic similarity over geographic areas [2] and have been documented in parrots [2–4], bats [5], cetaceans [6], songbirds [7–9], hummingbirds [10,11] and humans [8]. The temporal stability and spatial distribution of these mosaic patterns suggest that vocal dialects play an integral role in the maintenance of social systems [12–14], perhaps by promoting social cohesion and bonding [4,15–17]. When group sizes are large, converging on shared calls may facilitate group recognition and allow animals to avoid the cognitive burden of memorizing many individual signatures [18].

Given the key roles that vocal dialects may play in animal social systems, research into cultural evolution in the face of anthropogenic change is warranted [1,19]. Earth is currently undergoing a sixth mass extinction with species being lost at a rate that has not been seen for 65 million years [20,21]. Species worldwide are suffering from habitat loss, population fragmentation, overexploitation and climate-related disasters [21,22]. While changes to population size or reproduction (e.g. demographics) can generally be detected [20], impacts on more subtle behaviours, such as culturally transmitted behaviours, may be more difficult to discern. Since cultural traditions

are transmitted via social learning [4,9,23,24], such nongenetic transmission may be disrupted when populations are diminished or their age structure is altered [25]. Data from a limited number of studies indicate that learned behaviours have been lost or changed when populations have declined in such varied taxa as birds, elephants, seals and humans [25–28], sometimes with grave impacts on individual fitness and population health [25,29,30]. Thus, an improved understanding of how animal cultural traditions are impacted by changes in population demography will be essential for effective planning of wildlife conservation efforts [31,32].

Cultural traditions in learned vocalizations are expected to be especially susceptible to rapid evolutionary change, because their transmission via social learning can occur vertically, horizontally or obliquely, and thus learned traits may change faster than those inherited genetically [33–35]. Cultural mutations may arise more often than genetic mutations [33], and population fragmentation or decline resulting from anthropogenic impacts may promote rapid cultural drift and fixation of these mutations [36]. If so, then species that have experienced population decline should exhibit a greater change in the structure of learned vocalizations over time, as well as altered patterns of acoustic variation over geographic areas [34]. Such patterns have been observed in several species of birds, with impacts ranging from greater song divergence between distant populations, loss of song diversity and heterospecific imitation due to lack of species-specific tutors [25,34,37,38].

Long-term studies of animal culture are particularly important for understanding whether and how cultural traditions persist over time in the face of intensifying human habitat modification. One example is our ongoing study of vocal dialects in the yellow-naped amazon (*Amazona auropalliata*), a large parrot that inhabits dry forests from southern Mexico to southern Costa Rica [39]. Yellow-naped amazons exhibit a fission–fusion lifestyle in which parrots aggregate in evening roosts and disperse to forage in smaller groups during the day [40]. During the breeding season, mated pairs also maintain small, defended nesting territories [39]. Three distinct vocal dialects (North, South and Nicaragua) were first documented in this species's contact calls in Costa Rica in 1994 [40]. A subsequent survey in 2005 revealed that the integrity of both dialect call structure and geographic boundaries was maintained over an 11-year period [14]. In addition, dialects have recently been found to span the entirety of the parrot's range [41]. Population genetic surveys, playback studies and translocation experiments indicate that dialects in yellow-naped amazons are maintained through vocal convergence by social learning of vocalizations, rather than through genetic isolation and subsequent cultural drift [42–45]. Moreover, these findings also suggest that the signalling of group membership may help promote dialect maintenance, such that calls may serve to mediate social interactions and help individuals gain access to groups or resources [4,46,47].

Between the period of 2005 to 2016, the population of yellow-naped amazons in Costa Rica underwent a sharp decline, with surveys demonstrating a 54% decrease in population [48]. This population decline is thought to be particularly severe in the 11-year period following our 2005 survey of vocal dialects [4] and is probably caused by nest poaching for the pet trade, habitat loss and fragmentation [39]. Based on these findings and evidence of broad population declines across the entire range [49], the International Union for Conservation of Nature (IUCN) uplisted this species's status, first to endangered in 2017 and to critically endangered in 2021 [50].

Here, we report the results of a third dialect survey conducted in 2016 and evaluate the temporal stability of learned contact calls of yellow-naped amazons over a 22-year period. We assessed whether the acoustic structure of each historical dialect call type remained stable among our sampling years (1994, 2005 and 2016), whether geographic boundaries of historical dialects in Costa Rica shifted, whether the 2005–2016 population decline was associated with changes in acoustic variability and whether patterns of variation in the contact calls are related to geographic isolation of roosts or roost size. Overall, we predicted that we would see an increase in acoustic variation across Costa Rica, with greater separation between call variants, as predicted by metapopulation theory and the theory of island biogeography [35,51]. As populations decline and tutors decrease in number, or as isolation increases, cultural drift is predicted to increase [34,35,37,38,51]. We also hypothesized that more acoustic change would occur within the South dialect than the North, due to greater distance (e.g. isolation) among the South dialect roosts. Alternatively, some cultural traditions might be resistant to the considerable demographic changes observed over this time period.

2. Methods

(a) Contact call recording, classification and pre-processing

In June 2016, we sampled calls from yellow-naped amazons across their range within Costa Rica following methods used for the original surveys performed in 1994 and 2005 [2,14]. We recorded calls at communal night roosts from 17.00 until dusk (approx. 18.30), and in the morning from dawn (approx. 05.00) until 06.30, while birds were entering or leaving roosts. To sample variation within individuals, we aimed for 6–10 birds per site, and 10 high-quality calls per bird, although this was not always possible given low numbers of birds and environmental conditions.

We classified contact calls into the three discrete historic dialect types (North, South and Nicaragua) that were previously documented in 1994 and 2005, based on visible patterns of acoustic similarity on spectrograms [52,53] (figure 1). For each site, we also identified bilingual sites (sites in which more than one historical call type was used), and the dominant call type (the call type used by the majority of birds). Unlike our previous two surveys, for which it was straightforward to classify calls into three distinct dialects, we found that call-type classification to these historical dialects was difficult in 2016, especially in the traditional geographic region of the South dialect. We observed more variation in acoustic structure than in prior years, and although we were still able to reliably identify the original three dialectal call types, we identified four new call types that, based on their acoustic structure, appeared distinct from the classic North or South call types. To simplify our labelling process in the

text, all calls that appeared structurally and acoustically distinct from historic call types were labelled as variants of the call type that they most closely resembled (e.g. variants of the South call types were called South A, South B, etc.; figure 1; electronic supplementary material, S1.1). This visual classification approach allowed us to assess the acoustic and geographic stability of historical dialects over time.

We used call classification labels from the larger dataset of calls prior to quality-control processing to assess the locations of all call types relative to the geographical boundaries of the three historical call types (electronic supplementary material, table S1). Following call classification, we standardized audio files across years and performed quality-control processing to yield another dataset of calls that we used for quantitative analyses. Details on the steps that we used for standardization and quality-control processing can be found in electronic supplementary material, S1-1.2 and table S2 [17,27].

(b) Measuring acoustic similarity

We performed spectrographic cross-correlation (SPCC) with Pearson correlation for all calls across our three surveys using a Hanning window, window length of 450 samples, window overlap of 90 samples and bandpass filter of 0.5–8 kHz with the warbleR package [54,55]. Multidimensional scaling (MDS) was used to reduce the dimensionality of the SPCC matrix, which yielded coordinates for calls in a low-dimensional trait space, or 'acoustic space'. Following optimization to reduce MDS stress (electronic supplementary material, S1.4), we used the first two dimensions of an MDS solution with 18 total dimensions for quantitative assessments of temporal changes in call structure. We also used unsupervised random forests on a combination of 27 standard spectral acoustic measurements, 179 descriptive statistics of Mel-frequency cepstrum coefficients and the 18 SPCC MDS dimensions as a complementary acoustic similarity measurement throughout all analyses [56]. Results from our parallel series of analyses were largely consistent between the two similarity methods. Below we focus on results from SPCC; results from random forests can be found in electronic supplementary material, S1.3 [56].

(c) Assessing acoustic stability of historical dialects over time

Next, we addressed whether the acoustic structure of the three historical call types originally identified in 1994 remained stable. We designed a novel 'acoustic drift index' to quantify the relative magnitude of changes in acoustic structure over time. This symmetric index yields the relative separation between two categories of calls (e.g. the same call type recorded in 2 years) in low-dimensional acoustic space. The index is calculated by measuring the degree of overlap in acoustic space between 95% kernel density polygons for each pair of categories in a given comparison, using approaches similar to those outlined in [56]. We used spatial analysis tools to generate 95% kernel density polygons from MDS coordinates obtained from reducing the dimensionality of a given similarity matrix. The acoustic drift index ranges from 0 to 1, in which a value of 0 represents complete overlap in acoustic space between two polygons (e.g. no acoustic drift), and a value of 1 indicates complete separation between polygons (e.g. complete acoustic drift) (electronic supplementary material, S1.4). In this analysis, we calculated acoustic drift between polygons representing two different sampling years for the same historical call type. We excluded new variants identified in 2016 to focus on changes in the historical call types between each span of years and used either SPCC or random forest (RF) analyses in separate calculations. Initially, we used the full set of 1881 calls classified as historical call types in each sampling year. Then, we repeated these calculations across additional datasets that controlled for call quality in the full set of calls for the North, Nicaragua and South call types, as well as randomly subsampled datasets that controlled for variation in sample size as well as call quality for the North and South call types only (electronic supplementary material, S1.5).

For each historical call type, we used Mantel tests to determine whether calls recorded in the same year were significantly more similar compared with calls recorded in different years. As with acoustic drift calculations above, we excluded new variants identified in 2016 to focus on the three historical call types [14,40]. Since sample sizes within call types varied across years, we set up the Mantel tests to control for variation in sample sizes over time. We identified the minimum number of calls recorded for each call type across years and randomly sampled this minimum number of calls for each call type in each year. For the North and South call types, we randomly sampled calls without replacement over three sampling years (1994, 2005 and 2016). For the Nicaragua call type, we performed random sampling without replacement over the two sampling years in which this call type was identified through call classification (1994 and 2005). We performed Mantel tests using the package vegan v. 2.6-2 [57]. The datasets included 242 calls in each of the 3 years for the North call type, 167 calls in each of the 3 years for the South call type, and 40 calls in each of the 2 sampling years for the Nicaragua call type. We carried out a separate series of Mantel tests with SPCC and with RF similarity matrices, tested against binary matrices of year identity, and conducted each test over 9999 permutations. In all, we performed six Mantel tests in total over the three historical call types and two similarity methods. We adjusted alpha of 0.05 using a Bonferroni correction to account for this multiple testing. We used statistically significant p-values under the corrected alpha as indicators that there were significant differences in call structure over time within each historical call type.

(d) Determining acoustic and geographic stability of historical dialects over time

Next, we assessed temporal stability in acoustic structure within and between the historical geographic regions of the North and South dialects. For this analysis, we included all calls recorded within the traditional geographic North and South dialect boundaries, including new variants. We delineated the traditional geographic regions of the North and South dialects using the historical boundaries of the call types from 1994 [2]. Calls used in this analysis were restricted to those recorded at the ten sites
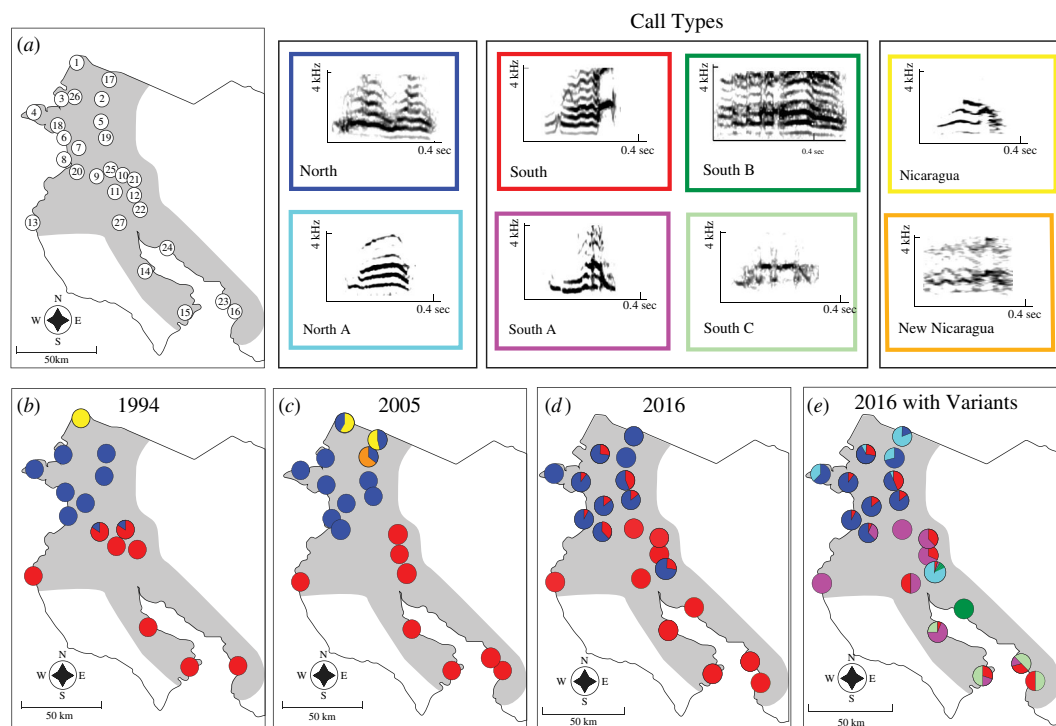
Figure 1. Maps of northwestern Costa Rica showing the distribution of roosts and vocal dialects surveyed. (*a*) Site names, (*b*) 1994, (*c*) 2005, (*d*) 2016 and (*e*) 2016 with call variants. Each call type and variant is represented by a unique colour corresponding to the call-type legend. Original dialect call types are North = blue, South = red and Nicaragua = yellow. New call variants were identified in 2005 (New Nicaragua = orange) and 2016 (North A = light blue, South A = pink, South B = dark green, South C = light green). Representative spectrograms of all major call types sampled are also shown. Each roost site is represented with a pie chart, and the composition of calls for each site is depicted on the chart. Raw data for the pie charts can be found in electronic supplementary material, table S2. Sixteen roosts were recorded in 1994: (1) Peñas Blancas, (2) Hacienda Inocentes, (3) Playa Junquillal, (4) Murcíelago, (5) Pelon Altura, (6) Playa Naranjo, (7) Horizontes, (8) Playa Cabuyal, (9) Finca Gisa, (10) Hacienda, San Jeronimo, (11) Finca Zapolita, (12) Pelon Bajura, (13) Playa Grande, (14) Puerto San Pablo, (15) Curu, (16) Tarcoles. Seven additional roosts were sampled in 2005: (17); Parceles Santa Elena, (18) Parque Santa Rosa (19) Finca Ahogados, (20) Las Trancas, (21) Finca Palenque, (22) Taboga/Finca El Cortijo and (23) Tivives. Four new roosts were added in 2016: (24) La Enseñada, (25) San Fidel, (26) Cuajiniquil and (27) Palo Verde.

that were sampled in each of the three sampling years. The number of calls we recorded at each site varied depending on the sampling year, so we randomly sampled calls per site and sampling year to maintain consistency for each site over time (651 calls total across sites were used per sampling year; see sample sizes per site in electronic supplementary material, S1.6). In this analysis, all calls randomly sampled per site were included regardless of the call type or variant category to which they had been assigned. We assigned each of the ten sites to one of the two geographic regions (five sites per region). Then, we calculated the acoustic drift index between acoustic space polygons representing calls recorded in the historical North or South region in each year. We repeated this analysis using another randomly subsampled dataset that controlled for variation in sample size and call quality per site (electronic supplementary material, S1.6). As above, we performed these calculations using both SPCC and RF similarity.

As the analysis of temporal stability in call structure by historical geographic region did not depend on call classification performed after 1994, we leveraged our call classification data to assess how the geographic boundaries of the historical call types changed over sampling years for the 10 sites above. We summarized the number of calls classified into each of the historical call types across these 10 sites in each sampling year. Call variants in each year were assigned to their main historical call-type categories (e.g. North A was counted as a North call in 2016).

(e) Quantifying acoustic differentiation of 2016 variants

We determined whether call variants identified in the most recent sampling year (2016) were structurally similar or distinct to the historical call types identified in earlier sampling years (1994, 2005) by calculating an acoustic drift index between each 2016 variant (North A, South A, South B, South C) and each historical call type recorded in each sampling year (North and South in 1994, 2005 and 2016, and Nicaragua in 1994 and 2005 only). For this analysis, we merged the two Nicaragua variants identified in 2005 into a single Nicaragua call type. To establish a baseline threshold for high distinctiveness, we calculated the mean acoustic drift between the North and South call types recorded in 1994 and 2005. We calculated this threshold separately for SPCC and RF similarity. For this analysis, we controlled for variation in sample sizes across all call types and temporal comparisons, and we repeated the calculations with a randomly subsampled dataset that controlled for variation in sample size and call quality (electronic supplementary material, S1.7).

(f) Testing the impact of roost isolation and size on acoustic variation

For these analyses, we determined whether site-level patterns of acoustic variation were associated with estimates of geographic isolation among roosts and roost size. First, we used increasing mean distance among a given site and its three nearest neighbours in a given sampling year as an indicator of greater geographic isolation. Second, we used previously published roost size estimates for a subsample of sites [48]. In each of these analyses, we performed Pearson's correlation tests to obtain the observed correlation between a site-level acoustic distinctiveness measurement and the given site-level characteristic (mean nearest neighbour distance or roost size estimates). To obtain the site-level acoustic distinctiveness calculation, we calculated the mean difference in acoustic similarity within a site compared with similarities among the same site and its three nearest neighbours in the given sampling year (this acoustic distinctiveness measurement was derived directly from the SPCC or RF similarity matrix). After obtaining each observed correlation, we permuted both variables used in each test 1000 times. We used the permuted correlation statistics to calculate a *p*-value that reflected the number of times that the observed correlation was greater than or less than or equal to the permuted statistics (depending on our expectations for the given test), divided by the total number of permutations. For our analysis addressing geographic isolation, we performed the observed and permuted correlations in all three sampling years to assess whether increasing nearest neighbour distances were associated with greater site-level acoustic distinctiveness. For our analyses with roost size, we performed this permuted correlation routine for 2005 and 2016 only since we did not have sufficient sites with both call recordings and roost counts in 1994 (see roost size data in electronic supplementary material, table S1). We calculated whether site-level acoustic distinctiveness decreased with increasing roost size, such that larger roosts were more acoustically similar to their nearest neighbours. We conducted geographic isolation and roost size analyses with both SPCC and RF similarity and with a Bonferroni correction to account for multiple tests across sampling years and similarity methods (six total tests for the geographic isolation analyses, and four tests total for the roost size analyses; electronic supplementary material, S1.8).

3. Results

(a) Sampling and new variants identified

The original dataset included 4019 total calls (electronic supplementary material, table S1). The final dataset post-quality control that we used for quantitative analyses had a total of 2461 calls (electronic supplementary material, table S1). For the quantitative analysis dataset, we retained 499 calls from 53 birds and 16 roosts in 1994. For 2005, we used 882 calls from 118 birds and 19 roosts. For 2016, we retained 1080 calls from 122 birds and 21 roosts. In 2016, we did not observe the Nicaragua dialect or its 2005 variant within Costa Rica. We observed the classic North and South calls, as well as their four variants: North A, South A, South B and South C (figure 1).

(b) Structural changes in historical dialect call types over time

Auditory and visual sorting of calls indicated that both the North and South call types observed in 1994 were still present in 2016 within Costa Rica (figure 1). We did not locate the Nicaragua call type in 2016, although it was observed within neighbouring Nicaragua during concurrent surveys there [41]. We found evidence of temporal change in acoustic structure for all three historical call types across the years they were detected (Nicaragua data was re-analysed for 1994 and 2005), in that the acoustic space for all dialect calls increased over time (figure 2).

Our analyses of acoustic drift showed that the historical call types changed in acoustic structure over time. The time period of greatest acoustic drift for the North and South dialects was between 1995 and 2005 (figure 2). We found some evidence that the North call type was more structurally stable than either the South or Nicaragua call types, with lower measures of acoustic drift as compared with the South dialect for all time intervals (figure 2). We recapitulated findings of relatively high temporal change in the Nicaragua historical call type between 1994 and 2005, which was previously described as two variants in 2005 (figure 2) [14]. Since the Nicaragua dialect was not located within Costa Rica in 2016, no comparisons could be made with that time period. These results were robust to controlling for variation in sample size over time as well as call quality and were concordant between our two similarity measures (electronic supplementary material, figure S1).

Overall, Mantel tests supported the finding above; calls were significantly more similar within years than among years, with all tests being significant (table 1). Mantel tests also supported the finding of greater variation between sampling years in the South than in the North call type (table 1; electronic supplementary material, table S3). The Mantel test statistic representing the correlation between acoustic distance and year was smaller for the North call type (0.05) compared with the South call type (0.15). In other words, there was a stronger effect of year on the South call acoustic structure than the North. Nicaragua calls had the largest test statistic (0.19), which reflects the two clear variants that arose in 2005.

(c) Geographic shifts in historical call type

We found evidence that calls recorded in the historical geographic regions of the North and South dialects became increasingly structurally similar over time. In 1994, calls recorded in these regions were structurally distinct, as indicated by the low degree
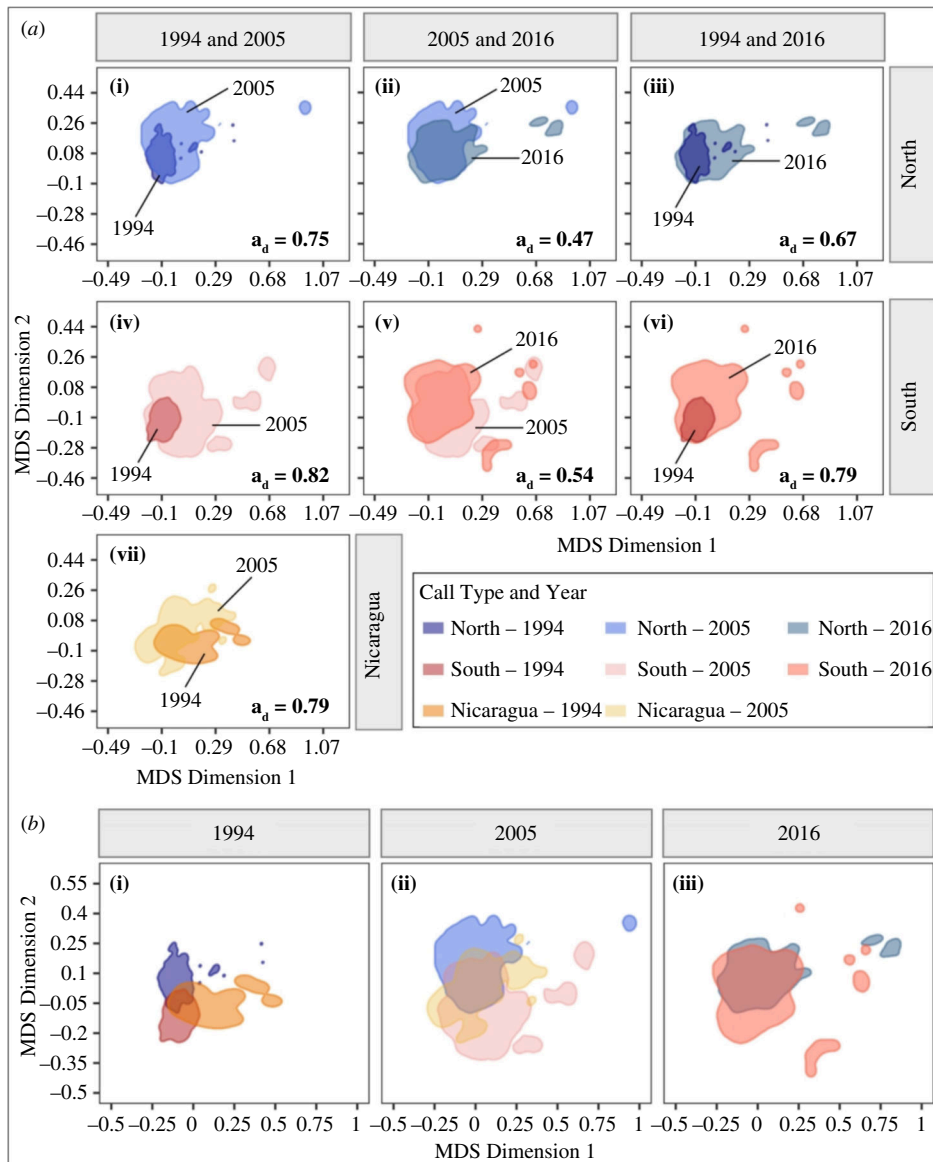
Figure 2. The historical call types are shown in the following colours; blue for North, gold for Nicaragua and red for South. We identified structural stability and change in the three historical call types recorded over time, with the exclusion of call variants. Here we show patterns of relative overlap of 95% kernel density polygons in low-dimensional acoustic space for each historical call type. Acoustic space was generated using multidimensional scaling on a spectrographic cross-correlation similarity matrix. (a) The overlap in acoustic space between two sampling years for the given call type is demonstrated. Acoustic drift measurements (a_d) are shown in the lower right of each panel, in which larger values indicate greater acoustic drift between sampling years. The North dialect call type remained the most stable over time (panels (i)–(iii)), with lower acoustic drift scores, while the South call type (panels (iv)–(vi)) and Nicaragua (Nica) call type (panel vii) showed more structural change between sampling years. (b) The patterns of overlap and differentiation among the main historical call types in each sampling year, with call-type colours following the legend in (a).

Table 1. Calls of each call type were more similar within years compared with among years using spectrographic cross-correlation (SPCC) similarity and the Mantel test.

call type	years	calls per year	total calls	Mantel r	Mantel p[a]
North	1994, 2005, 2016	242	726	0.05	0.0001
South	1994, 2005, 2016	167	501	0.15	0.0001
Nicaragua	1994, 2005	40	80	0.19	0.0001

[a]Mantel test results were statistically significant using a Bonferroni-adjusted alpha of 0.008 to account for conducting six total tests with SPCC and RF similarity matrices (shown in electronic supplementary material, table S4).

of overlap between acoustic space polygons for the North and South regions, as well as the high acoustic drift index calculated between the two dialects for that sampling year (figure 3a). However, in 2005 and 2016, these regional polygons overlapped more and displayed lower acoustic drift indices, showing that calls in the two historical dialect regions became increasingly similar in acoustic structure over time (figure 3a). Indeed, by 2016, the acoustic space of the traditional geographic region of the North dialect was nearly completely encompassed by the acoustic space of the historical South dialect region (figure 3a).

In addition, our call classification data pointed to a shift in the geographic boundaries of the South dialect in 2016 compared with 1994 and 2005. By 2016, the South dialect call type had shifted northwards and was identified at three of our subsampled sites that had only displayed the North dialect call type in 1994 and 2005. All three of those sites were bilingual; the sites still used the North call type originally recorded in 1994, as well as the South call type (figure 3b(iii)). This geographic shift of the South call type coincided with the increase in acoustic similarity between the subsampled North and South regions (figure 3a(iii)). These results were sustained after controlling for variation in sample size over time, controlling for call quality and comparing similarity methods (electronic supplementary material, figure S2).

When we expanded our analyses to include all sites recorded in 2016, the larger dataset also demonstrated an increase in bilingual sites and birds. We found eight bilingual sites in 2016, as opposed to just three in 2005 and two in 1995, as well as a greater proportion of bilingual birds in 2016 (proportion of bilingual sites: 1994, 12.5%; 2005, 15.8%; 2016, 47.6%; electronic supplementary material, table S2).

The bilingual region also shifted north in 2016 into what was previously the traditional geographic North dialect. The predominant call types at bilingual sites in the historical North region remained the North call type, however, with 60% of birds using this call type (electronic supplementary material, table S2). At the single site where the Nicaragua dialect was recorded in 1994, we identified the North and North A variant call types in 2005 and 2016, but we did not identify the traditional Nicaragua dialect call type.

(d) A trend of structural differentiation of 2016 call variants

When we quantified the acoustic drift between 2016 call variants compared to each historical call type recorded in each sampling year, we found that all 2016 call variants were structurally similar to at least one dialect call type (electronic supplementary material S1.7 and figure S3). For example, using our conservative threshold for identifying structural differentiation, the North A variant identified in 2016 did not emerge as acoustically distinct from the classic North call type recorded in all three sampling years (electronic supplementary material, figure S3). However, each of the South variants from 2016 were identified as structurally different from the South call type recorded in 1994 for one or both similarity measurements. For instance, the South A 2016 variant was identified as structurally distinctive from the South call type recorded in 1994 by both SPCC and RF similarity (electronic supplementary material, figure S3). We found consistent results when this analysis was repeated while controlling for variation in sample size and call quality (electronic supplementary material, figure S2).

(e) Impact of roost isolation and size on acoustic variation

Neither nearest neighbour distance nor roost size, which we used as proxy variables for isolation, were good predictors of acoustic distinctiveness. In addition, neither variable had a statistically significant association with site-level acoustic distinctiveness (All p > Bonferroni-corrected values of 0.008–0.012, figure 4; electronic supplementary material, S2.2 and S4). Modest support for our hypothesis came only from 2016, in which we observed a non-significant trend in which sites with more distant nearest neighbours were more acoustically distinct (figure 4).

4. Discussion

Our long-term monitoring of variation in the learned contact calls of the yellow-naped amazon across Costa Rica reveals a complex picture of both stability and change in cultural patterns. Our third survey, conducted 22 years after our initial mapping, demonstrated the long-term persistence of the North and South dialects described in 1994. It also revealed changes in the acoustic structure of these call types, and in their geographic distribution. In §§4a,b, we discuss these changes in detail and their possible relation to the severe demographic declines experienced by this species over the same time period.

(a) Structural and geographic shifts in dialects

Our findings of clearly recognizable historical call types 22 years after their initial description suggest that vocal dialects are persistent cultural phenomena and that the use of these regionally specific call types provides a fitness benefit to individuals. One hypothesis for the long-term persistence of these vocal dialects for over two decades is that they serve a group recognition function [1,4,18,19,40]. Yellow-naped amazons are highly social, fission–fusion species that move between groups of conspecifics that vary in number throughout the day to forage, roost or nest. According to the group recognition hypothesis, individuals that converge on the local dialect may receive more benefits from other group members, such as information sharing, access to foraging areas and roosting privileges [4,18]. This hypothesis would imply that birds who share dialects act as cohesive populations with an interchange of individuals common within dialects and rare across dialects.

These historical dialects are, however, in the process of changing both acoustically and geographically. Specifically, we documented an increase in the acoustic space of both the North and South dialect types, the addition of four new call variants in 2016, a large increase in bilingual sites and birds in 2016, and a shift in the geographic range of the three traditional dialects. Both time periods of 1994–2005 and 2005–2016 experienced increases in the acoustic space occupied by the dialects, with 1994–2005 exhibiting more change (figure 3a). The 2005–2016 time period experienced the greatest change in the geographic boundaries of dialects and the rise of new acoustic variants, especially in the South.
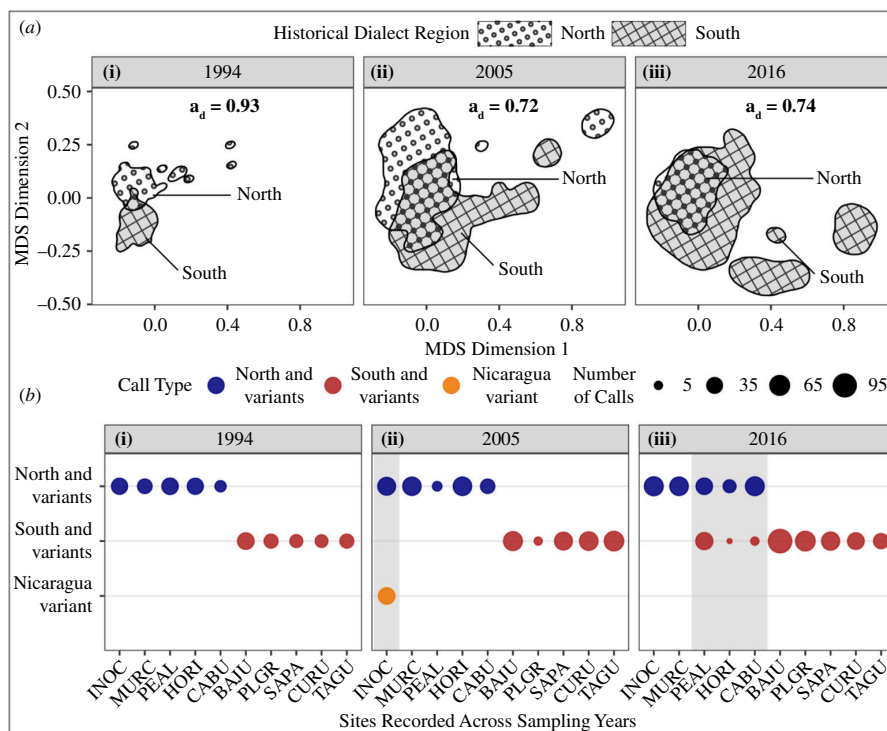
Figure 3. (a) The relative overlap between the 95% kernel density polygons of calls recorded in 1994, 2005 and 2016 within the historic geographic boundaries of the North and South call types, including all call variants. The acoustic space polygons were built using multidimensional scaling of spectrographic cross-correlation similarity values. Polygons for the historic geographic regions of the North and South call types are shown with patterns (open circles or grey hatching, respectively), and the acoustic drift values are shown at the top of each panel, in which lower values indicate increasing structural similarity of calls between geographic regions. (b) The number of calls classified into a historical call-type category across sites ordered from left to right by decreasing latitude. The historic call-type categories are encoded in colours (North in blue, South in red and Nicaragua in gold), and the number of calls sampled per size is encoded using dots of different sizes, in which sample sizes were obtained from the pre-processed dataset used for quantitative analyses. The grey shading in the panels for 2005 and 2016 represents sites with calls classified as two historical call types. The same ten sites recorded in each sampling year were used for rows A and B.
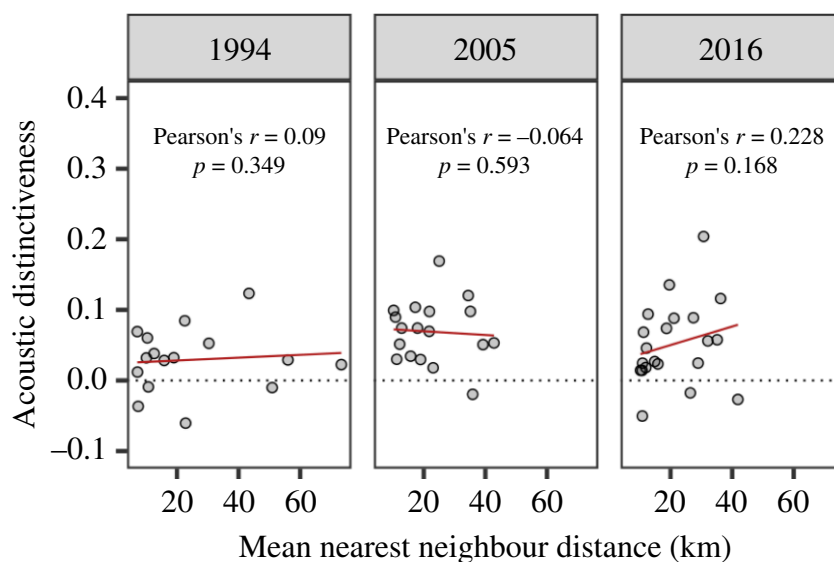

Figure 4. The observed Pearson's correlation was conducted between the mean difference in spectrographic cross-correlation similarity and mean geographic distance for a given site compared with its three nearest neighbours in each sampling year. The red line and text per panel represent the observed correlation statistic, and the p-value shown in each panel was obtained from a permutation analysis. The number of sites used in this analysis was not the same across sampling years, and we did not identify statistically significant correlations using a Bonferroni-corrected alpha of 0.017. We identified a weak trend of increasing acoustic distinctiveness of sites in 2016 that were more geographically distant from their three nearest neighbours.

Our *a priori* predictions, based on current theories of cultural evolution and the well-documented population decline experienced by this species over the same time, correctly anticipated some, but not all, of these changes [35,48,51]. Specifically, we predicted that with declining populations we would observe an overall increase in acoustic variation, greater acoustic separation between call variants, and greater acoustic change within the South dialect than the North. We also predicted an association between local population size, geographic isolation and acoustic distinctiveness. Our prediction that smaller or more geographically isolated roosts would be more acoustically divergent was not supported. Our prediction of increasing variation

in the dialects over time was supported, but our prediction of greater acoustic separation between dialects was not. Instead, as variation increased within the North and South dialects, their acoustic space became more similar, rather than more distinct, over time (figures 2 and 3). In 1994 and 2005, the dialect regions had a clear boundary, and there were very few bilingual sites between these borders [40]. However, in 2016, we found evidence of a northward shift of the traditional South dialect, with an increase in the number of bilingual sites (e.g. using both North and South dialects). Finally, although we did not identify calls belonging to the Nicaragua dialect within Costa Rica in 2016, some were recorded just over the international border in Nicaragua, which suggests a longer range geographic shift in dialect boundaries rather than a true extinction of a dialect call type [41].

Although we did not find the separation between the dialects as originally predicted, we did observe the formation of more call variants in the South dialect region. These South variants were also more distinct in acoustic form than the new North variant (electronic supplementary material, figure S3). Greater distance between roosts in the South may thus be inhibiting movement and promoting cultural drift, while the denser concentration of roosts in the North may have facilitated inter-roost movement and subsequent surge in bilingualism (mean nearest neighbour distance as calculated from each site and their three nearest neighbours and summed across sampling years = 85.86 ± 44.4 km (s.d.) for South versus 60.92 ± 47.1 km (s.d.) for North). In sum, our data do not present a simple picture, either over time or across Costa Rica.

Many factors can lead to cultural change including degree of isolation, population size, habitat quality, habitat heterogeneity, ranging distance and population turnover [35,58]. We have evidence for some of these factors but can only indirectly associate them with our data. We documented a large population decline of 50% between 2005 and 2016 at the same survey sites recorded for this study [48]. This decline led to successive IUCN status changes, first to endangered and then critically endangered by 2021 [50]. We also observed a switch from ranching to agriculture in some surveyed areas, resulting in a substantial decline in habitat quality (C Dahlin, personal observation, 2016). For example, Ahogados, a North roost site that had historically consisted of many acres of cattle ranch that provided habitat for parrots, was converted to a monoculture sugar cane plantation. Although we were able to record a few birds on site in the morning hours, perched in remnant roadside trees, the evening roost count was zero [48]. While it is possible these birds were extirpated, we think it is more likely that they moved to neighbouring roosts that were surrounded by better habitats for foraging and nesting. Thus, both changes in habitat and in demographics may have contributed to the complex patterns of change that we observed.

The movement of birds probably led to one of the more striking geographic shifts we observed, namely the increase in bilingual sites in the North. Bilingual birds have long been reported in Costa Rica, albeit at lower levels, and were also recorded at other sites across their range in a recent expanded survey [2,14,41]. In the past, bilingual birds were typically recorded at sites that bordered two distinct dialects, but in 2016, we found more bilingual birds distributed further from the historic dialectal border (figure 1, figure 3b). We propose two hypotheses to explain the increased presence of these bilingual birds: code-switching and dispersal facilitation. In code-switching, adult birds would benefit from learning a second dialect to facilitate regular interactions with other individuals that use a foreign dialect. Bilingual humans will readily code-switch to accommodate their conversational partners, the social group or the setting they are in [59]. Although similar functionality has not been documented in birds, songbirds have been observed changing their songs to escalate or de-escalate territorial disputes [60]. Yellow-naped amazons are fission–fusion species, and birds that reside along borders that code-switch would have a greater ability to join birds from neighbouring dialects during foraging, roosting or other activities [2,41]. The habitat conversion we have observed provides one potential explanation for why parrots may have changed foraging and roosting behaviour, generating a need for birds to roam farther in search of food or nest sites [61]. In this scenario, adult birds should benefit from learning new dialects to facilitate interactions with conspecifics over a wider geographic range. Prior research on yellow-naped amazons found that ranging movements were 10 times higher in areas with dispersed as opposed to dense vegetation [61].

Our alternative hypothesis, dispersal facilitation, proposes that bilingualism results when juveniles occasionally disperse from one dialect and subsequently acquire both a new dialect but also retain their old one [41,42]. The typical patterning of bilingualism along borders would be supported if birds generally disperse within their natal dialect, and do not normally disperse far from their birthplace. In dispersal facilitation, the retention of natal dialects may not necessarily serve a functional purpose in a new dialect region but may also not be disadvantageous. One of the key differences between the two hypotheses is the timing of learning. Previous research in the form of a translocation experiment offered limited support for this hypothesis in that a single translocated juvenile yellow-naped amazon learned a new dialect, while none of the translocated adults did [42]. The absence of observed dialect learning by adults in this single study combined with a small sample size does not rule out the possibility that adults can continue to learn new dialects, particularly as many parrots, including this species, are known to be adept lifelong learners in captivity [62]. The dispersal facilitation hypothesis also fails to explain the surge in bilingual sites between 2005 and 2016. Thus, we believe the code-switching hypothesis offers the best explanation for the expansion of bilingualism in 2016. Critically, our long-term observations of vocal culture have allowed us to detect probable changes in population dynamics that otherwise would have gone unnoticed.

(b) Vocal culture is a key component of biodiversity

Conservation biologists are generally aware of genetic threats posed by fragmented populations, including genetic drift, Allee effects and inbreeding depression [63]. Threats to cultural diversity may be less familiar but no less important [16,31,64]. Both fragmentation and population loss can disrupt culturally transmitted behaviours [38,63]. Population loss in other species, including Dupont's larks (*Chersophilus duponti*) Hawaiian honeycreepers (Drepanididae sp.), elephant seals (*Mirounga angustirostris*) and humans, has exhibited effects ranging from copying from other species to complete loss of dialects and/or language

[25,26,28,34,65]. One question that arises is, do these acoustic changes have a functional significance? In many songbirds, acoustic variation may be necessary to acquire territories and mates. In Dupont's larks and North Island kokakos (*Callaeus wilsoni*), smaller populations with less complex songs experienced lower population growth [65,66]. In the case of the Hawaiian honeycreepers, inter-species song convergence may lead to hybridization [25]. Populations of regent honeyeaters (*Anthochaera phrygia*) have declined so dramatically that a lack of male tutors has resulted in more simplified songs [37]. Growing evidence thus implies that cultural changes caused by population declines and fragmentation can negatively impact the persistence and integrity of endangered species. Regardless of the impact, dramatic changes to dialects can serve as indicators of fragmentation and isolation.

In many parrots, dialects serve to signal group membership and familiarity [4,67]. For the yellow-naped amazon, translocation experiments and playback experiments indicate that using dialects appropriately is important to social integration [42,43]. Yellow-naped amazons were less responsive to playbacks of a foreign dialect than a local dialect, indicating that communication may be impeded when dialects aren't shared [43]. However, individuals of both the yellow-naped amazon and the Puerto Rican parrot (*Amazona vittata*) have shown the ability to acquire new dialects [42,68]. Whether acoustic change and boundary shifts in formerly stable vocal dialects of this parrot will have substantial impacts on key social or life history behaviours, (such as mate acquisition, reproduction and roosting) remain open and are important questions for future research. Some of this change could be disruptive, with the potential to further exacerbate population declines. However, an increase in bilingual sites could also be a sign of adaptability, as suggested by the code-switching hypothesis. Ultimately, monitoring cultural behaviours, such as the rate of change in dialects, can help wildlife managers understand anthropogenic impacts, population dynamics and conserve species [31].

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