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ARTICLE

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Acoustic richness and composition changes of humpback whale (*Megaptera novaeangliae*) songs on breeding grounds off the coast of Ecuador

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Abstract

Song evolution and revolution events recorded through time are typical cultural features for humpback whale (*Megaptera novaeangliae*) populations worldwide. However, it is unknown if song dynamics are equivalent among subpopulations or breeding stocks of the South Pacific Ocean. To contribute to the understanding of the temporal song dynamics of humpback whale song off the coast of Ecuador, we analyzed acoustic richness and repertoire composition based on unit, phrase, and song composition over consecutive breeding seasons from 2012 to 2019. We observed incomplete song revolutions (all themes were replaced except one) and a nonsignificant variation in the acoustic richness during the study period. Our results show that over the years, humpback whale singers incorporate acoustic material from different subpopulations such as Central South Pacific (French Polynesia) and western South Atlantic (Brazil) into their song repertoire. The temporal acoustic contact of different subpopulations migrating through the eastern South Pacific may be reflected in their particular acoustic richness and temporal evolution. Off the coast of Ecuador, humpback whale song patterns point towards an alternative scenario of song evolution, indicating how cultural transmission among subpopulations can alter the song patterns in specific breeding grounds due lack of geographical barriers surrounding the southeastern Pacific region.

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KEYWORDS
cultural transmission, Ecuadorian coast, humpback whale, song patterns, southeastern Pacific region

1 | INTRODUCTION

Baleen whales produce a variety of sounds, including vocalizations within structured sequences termed songs. For example, blue whales (*Balaenoptera musculus*) combine simple tonal vocalizations into low-frequency songs (Malige et al., 2020; McDonald et al., 2006), while humpback whales (*Megaptera novaeangliae*) produce long and complex songs covering a wide frequency range of tonal and broadband sounds (Payne & McVay, 1971). Humpback whales utilize a large acoustic repertoire composed of different units and phrases (a specific combination of units), which are then repeated in themes, and a specific combination of themes is called a song (Payne & McVay, 1971). In the marine realm, the humpback whale is a great composer due to the acoustic diversity of their songs with complex and repetitive acoustic sequences, which can be exchanged among different breeding populations (Cholewiak & Cerchio, 2022).

Theoretical systems applied in animal communication, including sequential acoustic complexity among conspecifics, suggests that acoustic behavior can transmit different types of information (McCowan et al., 2002). For example, the large and complex acoustic repertoires in some oscine bird species, such as the House Wren (e.g., *Troglodytes aedon*), are composed of different types of song and are associated with mate attraction traits (Kaluthota et al., 2020). As a reproductive strategy, humpback whale song repertoire may provide information about the singer's learning ability (e.g., Allen et al., 2018). Specifically, interindiviual variability in singers based on sequence of units and phrases could be used as a signal to attract females (Lamoni et al., 2023; Winn & Winn, 1978), potentially when males constantly sing while escorting females (Cholewiak et al., 2018; Darling et al., 2006; Frankel et al., 1995; Murray et al., 2018; Smith et al., 2008; Tyack, 2011; Winn & Winn, 1978). However, clear evidence that individual song characteristics influence a female's choice or preferences is lacking and more research on multiple individually identified singers is needed (Garland & McGregor, 2020; Mercado III, 2021). Song repertoires may also transmit hierarchical information among males possibly to repel rival males, observed when singers stop vocalizing after joining groups formed by other males and when singers maintain a considerable distance from each other (Frankel et al., 1995; Tyack, 2011) or function as biological sonar to detect, localize, and track conspecifics (Mercado III, 2018). The song repertoire can also contain messages with antagonistic intentions to initiate competition or social coalitions (Cholewiak et al., 2018; Darling et al., 2006; Tyack, 2011). Therefore, it is most likely that humpback whale song has a "multimessage function" in the humpback whale's mating system similar to bird songs (Herman, 2017; Murray et al., 2018).

Within a breeding season, all humpback whale singers usually adopt similar theme types and order within a current version of song termed song type (Arraut & Vielliard, 2004; Payne & Payne, 1985). Within a song, the complexity of song composition may be driven by the presence of transitional phrases (unusual repetitive units at the transition from one theme to the next) or even irregular themes such as "shifting" and "unpatterned" themes (Allen et al., 2018; Cholewiak & Cerchio, 2022). Humpback whale songs evolve through time or across breeding seasons with gradual changes or new subunit, unit, phrase, or theme level variations (e.g., Allen et al., 2018). Song evolution has been described for all known populations (e.g., North and South Atlantic, North and South Pacific) and may be a learned or innate feature of the species. For example, the song from one season to the next season evolves progressively, but in some cases, a cultural diffusion termed "revolution" occurs through a drastic or abrupt change in complexity and/or structure of the song within a population (Allen et al., 2018, 2022; Garland et al., 2021; Gonçalves et al., 2023; Kershenbaum et al., 2016; Noad et al., 2000). Such revolution events are characterized by the adoption of a new song type, mostly compiled of simpler acoustic sequences, throughout the entire breeding population,

which can be transmitted at a regional scale (Gonçalves et al., 2023; Noad et al., 2000) or even at the ocean basin level (Garland et al., 2011). Most spatio-temporal comparisons of song have been made between populations of Oceania and the western South Pacific (Garland et al., 2011; Noad et al., 2000). In the South Pacific, these comparisons have evidenced a west-to-east horizontal cultural transmission, for example, between multiple breeding areas from western, to eastern Australia, to the central Pacific Island populations such as New Caledonia, Tonga, the Cook Islands, and French Polynesia, and to Ecuador in the southeastern Pacific region (Garland et al., 2011; Noad et al., 2000; Owen et al., 2019; Schulze et al., 2022).

Humpback whales of the southeastern Pacific region migrate from their feeding areas in the Southern Ocean and Chilean Patagonia to their tropical breeding areas off the coast of northern Peru, Ecuador, Colombia, Panama, Costa Rica (Acevedo et al., 2007, 2017), and even as far north as Nicaragua (De Weerdt et al., 2020). The Ecuadorian coast is characterized by the Humboldt Current bringing a mixture of cold saline waters from the south and warm, low salinity waters from the north through the Panama Current (Cruz et al., 2003). Coastal surface waters off Ecuador oscillate between 25 and 28°C (Fiedler & Lavin, 2017), providing habitat conditions for reproduction and nursing humpback whale calves around the continental slope or in shallow waters <50 m depth (e.g., Denkinger et al., 2023; Oña et al., 2017). In their social aggregations off the coast of Ecuador, from July to September, humpback whales show diverse surface behaviors and social groups such as pairs, competitive groups, singers, and mother-calf groups with the highest concentrations of whales off the coast of Esmeraldas and Manabí (Denkinger et al., 2023; Félix, 2004; Félix & Botero-Acosta, 2011, 2012; Félix & Haase, 2001; Oña et al., 2017; Scheidat et al., 2000).

Here, we evaluate humpback whale song dynamics on the Ecuadorian breeding ground and analyzed acoustic richness and song composition of three to four humpback whale singers per season over multiple years (i.e., from 2012 to 2019). Our results provide the first formal description of temporal dynamics of eastern South Pacific humpback whales belonging to the subpopulation or breeding stock G (BSG) (IWC, 2016).

2 | METHODS

2.1 | Study area

From 2012 to 2019, humpback whale songs were recorded off the Ecuadorian coast from Santa Elena in the South to Esmeraldas in the North. Most recordings ($N = 22$) were obtained from Esmeraldas, at the Galera San Francisco Marine Reserve (GSFMR N 0°49′10.15″, W 80°02′55.67″) to the Bajos de Atacames breeding ground extending to the mouth of the Esmeraldas River (N 0°59′54.1″; W 79°38′37.7″; Figure 1), where singers are widely distributed in shallow waters over muddy and hard substrates consisting of rocky platforms with rocky reef formations and coral patches (see Oña et al., 2017). Four song recordings were obtained in offshore waters off the coast of Santa Elena, Manabí, and Esmeraldas (Figure 1).

2.2 | Data collection

From 2012 to 2015, songs were recorded with an omnidirectional hydrophone (H2a-XLR; linear frequency response from 20 Hz to 100 kHz), and a Delphinus Pro Hydrophone (linear frequency response from 1 to 24,000 Hz) was used for sound recordings from 2016 to 2019. Both hydrophones, with a rope wrapped in a long spiral around the cable to reduce vibration noise, were submerged to 7–10 m, while the research platform (e.g., artisanal boat or sailboat) was floating with the engine turned off. Acoustic samples were recorded on Tascam DR-40 and/or ZOOM H4nPro digital tape recorders, set for recording WAV files at a sampling rate of 44.1 kHz and 16 bits.

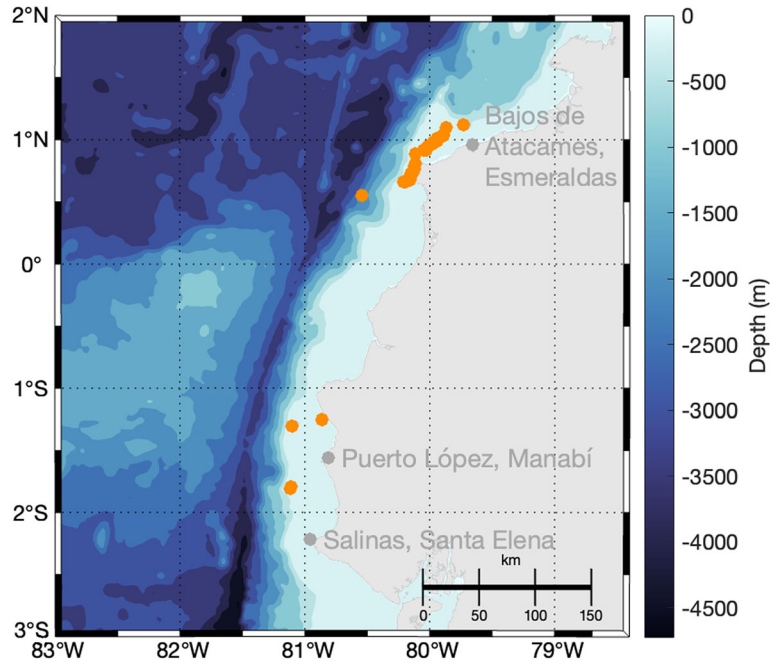

FIGURE 1 Bathymetric map with recording locations (orange dots) along the Ecuadorian coast.

Acoustic recordings were carried out mainly through a nonsystematic ad hoc acoustic sampling effort with acoustic stations every 25 to 30 min or during opportunistic encounters of singers identified by visual behavioral signals (e.g., sighted close to the surface with the tail in the air close to a second whale or when a pair was sighted while courting with tail and flipper displays) or the audibility of song above the surface. We sampled three to four acoustic stations in shallow and offshore waters throughout the breeding ground, which were placed at a minimum distance of 10 km from each other (see example of acoustic stations in Oña et al., 2017). Acoustic stations during offshore sailing surveys were conducted at a distance of approximately 25 km or more along the coast of Ecuador (see Denkinger et al., 2023). Also, the recordings were collected from different days in each season. This allows us to assume independent recordings of different singers.

2.3 | Song analysis

Humpback whale vocalizations were viewed and manually logged within spectrograms with a window size of 2,500 samples, discrete Fourier transform (DFT) size of 4,096 samples, a Hann window, and 80% overlap, generated in Raven Pro version 1.6.3 (Yang and Center for Conservation Bioacoustics, 2019). Logged vocalizations were manually classified into distinct unit types (identified by a preceding "CT" for "call type" and a number) according to the following criteria: (1) differentiation of tonal or broadband characteristics, (2) duration (within a range), (3) bandwidth (within a range), and (4) time-frequency slope (i.e., constant, downsweeping, upsweeping, or variable).

Within a humpback whale song, phrases were logged and classified according to unit repetition following the recommendations of Cholewiak et al. (2013), identifying first subphrases (consisting of a single unit type) and the start and end of a respective theme and then dividing the whole theme into separate phrases ensuring that no "hanging" phrases were created. Transitional phrases were either assigned to the preceding or following phrase type, depending on the level of similarity to one or the other, except for if the transitional phrase was repeated more than

once, because then, it was considered as a new phrase type and consequently a new theme. Phrase types were identified with an uppercase letter (indicating the first unit type), a lowercase letter (indicating the combination of following unit types), and a sequence of numbers (indicating the number of repetitions of each unit) in order to be able to isolate the original unit sequence during downstream analysis (Figure 2). The song sequence analysis in this study followed the same identification and classification of song structure (e.g., units, phrases, and themes) used in a recent Southern Hemisphere humpback whale song comparison (Schall et al., 2022).

The robustness of the manual subjective analysis of the unit repertoire was tested with a random forest supervised classification approach on 44 acoustic metrics computed on a subset of units as described in Schall, Thomisch, et al. (2021). The subset of units was extracted from recordings from the feeding ground in the Atlantic sector of the Southern Ocean, and the respective analysis could not be repeated for the recordings of this study due to time constraints (i.e., only phrases were logged in the spectrograms and not units, see examples in supplemental material 1). However, the described machine learning approach still proofs the robustness of the manual subjective analysis as it contained a large part of the same unit types (i.e., 12 out of 18) and because the manual classification has been conducted by the same analyst (E. S.). The level of agreement between the manual unit classification and the result of the supervised machine learning approach was high with a correct classification rate of 84% indicating a robust differentiation of units (Schall, Thomisch, et al., 2021b).

2.4 | Song metrics

For the following quantitative comparisons of song extension and acoustic richness within a song of individual singers (i.e., the entire vocalization period by one singer that was analyzed), the recorded song sequences had to be separated into single songs. Song sessions are commonly defined as all song elements sung until a gap of silence of

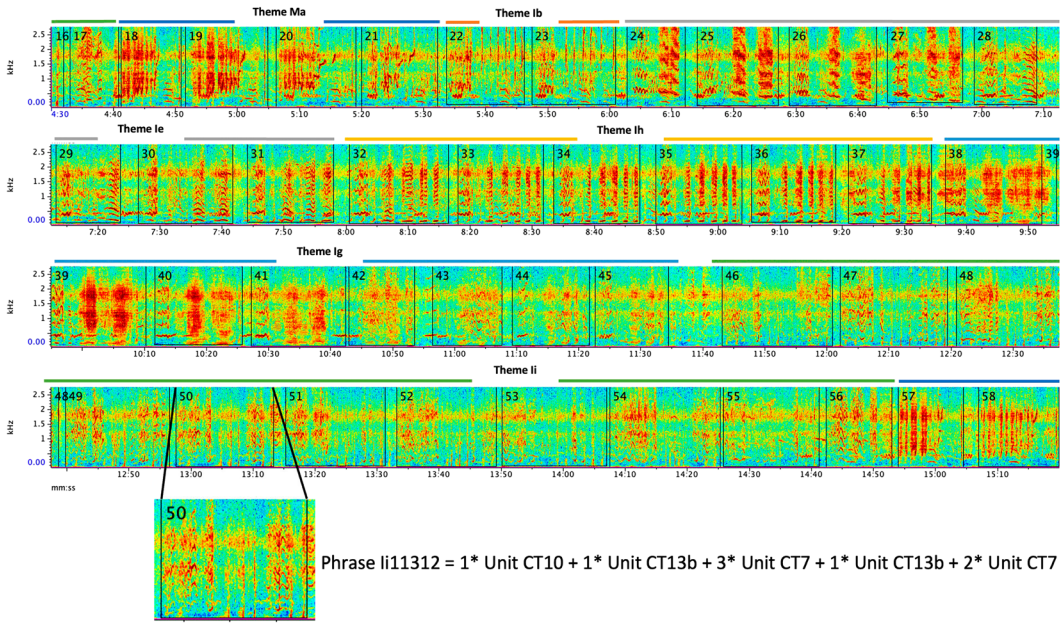

FIGURE 2 Example of song analysis method. The first four lines of spectrograms illustrate the phrase and theme delineation. The spectrogram in the bottom line illustrates the phrase nomenclature (e.g., Phrase "Ii11312") that contains the information of the original unit sequence (e.g., 1* Unit CT10 + 1* Unit CT13b + 3* Unit CT7 + 1* Unit CT13b + 2* Unit CT7').

more than 1 min occurs (Payne & McVay, 1971). Consequently, song sequences were first separated into single song sessions wherever applicable. The definition of the start and end of an explicit song within a session can be problematic due to the numerous distinct attempts defining a song in different studies. Inspecting our song sequence data for common patterns, the most sensible definition for song was the complete rendition of all unique theme types per song sequence to form an explicit humpback whale song (Cholewiak et al., 2013, see supplemental material 1).

To quantitatively compare the songs between years, we calculated the song extension as the number of units per song and three metrics for the acoustic richness of the song. The metrics of unit and phrase richness was adapted from studies on bird and humpback song (Boogert et al., 2008; Schall, Roca, & van Opzeeland, 2021a; Templeton et al., 2014; Woodgate et al., 2012; Zann & Cash, 2008). Unit richness was defined as the number of unique unit types divided by the total number of units per song. The phrase richness metric was defined as the number of unique phrase types divided by the total number of phrases per song. To adapt an overall measure of song richness, the unit richness was multiplied by phrase richness. Therefore, the three metrics range between 0 and 1, with 1 being that every unit or phrase used would be a unique unit or phrase type, corresponding to the most complex as possible. The song extension and richness metrics were then statistically compared among years by testing for significant variation in these metrics with a nonparametric Kruskal–Wallis test.

2.5 | Song repertoire and composition comparison

The phrase repertoires of all individual singers combined for each year was compared by applying the Dice Coincidence Index (DCI) with a custom-written script in R (Dice, 1945; R Core Team, 2018):

$$DCI = 2A/(B+C),$$

with A being the number of shared phrase types between a pair of singers and B and C being the number of phrase types of each singer, respectively. The resulting similarity matrix was supplied to a hierarchical cluster analysis in R (R Core Team, 2018) using the "nearest neighbor" method, and the output was visualized in a dendrogram. Hierarchical clustering was bootstrapped (1000 times) with the R function "pvclust" (Suzuki et al., 2019) to generate approximate unbiased (AU) values with AU values exceeding 95% indicating dendrogram divisions that are likely to occur.

To compare the song composition among years, the sequences of phrases were transcribed to sequences of themes (i.e., ignoring the repetition of phrases) and a set median string was chosen for each individual singer, and then, a set median string was chosen for each year. The set median string was defined as the sequence of themes that had the highest similarity to all sequences of themes of a given set (i.e., all songs of an individual singer or all set median strings of 1 year of recordings). The similarity between songs was calculated by applying the Levenshtein Distance Similarity Index (LSI) in MATLAB (Garland et al., 2012; Kohonen, 1985):

$$LSI(a,b) = 1 - \min(I+D+S)/\max[L(a),L(b)],$$

with a and b being the two songs, I being insertions, D being deletions, S being substitutions, and L being the length of the respective sequence. In the following step, the set median strings of all individual singers were compared by applying the LSI to pairs of individuals with the R function "stringdist" (van der Loo, 2014). The resulting similarity matrix was supplied to a hierarchical cluster analysis using the "nearest neighbor" method, the output was visualized in a dendrogram, and hierarchical clustering was bootstrapped (1,000 times) (R Core Team, 2018; Suzuki et al., 2019). All codes used for the analyses within this manuscript are available with open-access under https://gitlab.awi.de/eschall/humpback-whale-song-analysis.

3 | RESULTS

Off the Ecuadorian coast during the humpback whale breeding seasons from 2012 to 2019, a total of 26 recordings with 378.66 min of song sequences from three to four individual singers of each season were explored, and each year, an average of 14.49 min of song per singer was analyzed (Table 1, see DOI: 10.6084/m9.figshare.25259947 for open-access publication of the full recordings and accompanying Raven Pro selection tables that provide details on the unit, phrase, and theme compositions of each individual singer). The analysis revealed that some seasons were characterized by low interindividual variability in song patterns, and others by high interindividual variability. During the three breeding seasons of 2012, 2013, and 2019, singers displayed a low inter-individual variability in the order of themes, and consequently, there was a high intraseasonal similarity among song patterns of individual singers. In

TABLE 1 Overview of song sequences recorded from a total 26 individual singers off Ecuador between 2012 and 2019.

Date	mm:s	Number of songs	Number of units	Unit richness	Phrase richness	Song richness	Median string
June 27, 2012	20:27	3	270.50	.07	.21	.02	Dj Ja Ia Ic Cg As Ar Au
August 02, 2012	23:21	3	202.00	.10	.19	.02	Dj Ja Ia Ic Cg Ar As Au
August 13, 2012	23:02	3	232.67	.10	.24	.03	Dj Ja Ic Ia Cg Ar As Au
July 30, 2013	12:38	2	196.50	.12	.54	.10	Ec Ed Gb Ga Dj
August 05, 2013	11:38	2	163.50	.08	.09	.01	Ec Ed Gb Ga Dj Ha
August 06, 2013	18:13	3	232.00	.06	.10	.01	Ec Ed Gb Ga Dj Ha
July 14, 2014	18:29	5	80.80	.21	.25	.07	Ar Kc Av Fb Ja Jb Id
July 16, 2014	18:13	3	140.67	.10	.11	.01	Ar Kc Av Fb Jb Ja Id Ia
July 23, 2014	25:31	3	179.00	.09	.08	.01	Ar Av Kc Fb Jb Ja Ia Id
June 22, 2015	10:18	1	233.00	.09	.11	.01	Ar Ja La Aw Ax Kd Fc Jb Id Ia
June 25, 2015	7:18	1	149.00	.12	.16	.02	Ar Aw La Ax Kd Fc Jb Id Ia
June 26, 2015	9:37	1	161.00	.11	.13	.01	Ar Aw La Ax Kd Fb Jb Id
July 08, 2016	18:18	4	64.25	.26	.33	.10	Ar Gl Ay Na Lb Ma Ia Kd
July 21, 2016	12:00	2	91.00	.09	.12	.01	Ar Lb Ma Ia
July 23, 2016	9:37	2	71.00	.22	.23	.05	Ar Gl Ay Na Lb Ma Ic Ia
July 25, 2017	9:55	1	169.00	.11	.14	.02	Ma Ib Ie Ih Ig Ii
August 02, 2017	18:05	2	378.00	.05	.10	.01	Ma Ib Ie Ih If Ig Ii
August 10, 2017	11:28	1	320.00	.06	.15	.01	Ma Ib Ie If Ih Ig Ii
July 05, 2018	3:71	1	84.00	.10	.14	.01	Ij Ik
July 2018	11:59	2	86.50	.16	.08	.01	Dm Il
August 03, 2018	7:64	2	98	.16	.23	.04	Ij Il Ib Ic Dm
September 11, 2018	29:53	5	244.75	.10	.17	.02	Ee Dm Ij Dc
July 03, 2019	19:30	3	153.67	.17	.19	.03	Ic Dm Dg Lc Ld Dl Ib
July 17, 2019	9:55	2	104.50	.19	.18	.03	Ic Dm Dg Lc Ib
July 18, 2019	11:28	2	133.50	.17	.24	.04	Ic Dm Dg Lc Ld Dl Ib
July 19, 2019	16:38	2	195.50	.12	.15	.02	Ic Ib Dm Dg Lc Ld Dl

Note: For each individual singer, the table lists the date of recording, the minutes of song analyzed, the number of analyzed songs, average number of song units, average unit richness (N unit types/N units), average phrase richness (N phrase types/N phrases), average song richness (unit richness * phrase richness), and the median string of theme sequences.

contrast, during the remaining seasons, the interindividual variation among theme orders of individual singers was higher, especially during the 2014, 2015, and 2016 seasons (Table 1). From 2012 to 2014 most singers sang between six and eight themes, while in the seasons 2015 and 2016, singers sang from eight to 10 themes but one singer in 2016 displayed a sequence of four themes only. Furthermore, songs of the 2017 and 2019 seasons were composed of five and seven themes, respectively. In 2018, some song samples were of poor quality (short recordings with sometimes low signal-to-noise ratios resulting in only one to two analyzed songs per individual) leading to most likely incomplete theme sequences and therefore highly variable song patterns (two to five themes; Table 1).

3.1 | Song repertoires and composition

A total of 9217 song units were classified into 18 unit types (14 distinct unit types, plus four subtypes that were similar in the four defined classification criteria tonal/broadband, duration, bandwidth, and time-frequency slope but were located in a different frequency range), and 42 distinct phrase types (2,319 phrases classified) were identified in sequences of humpback whale songs between the 2012 and 2019 seasons (Figure 3). Of the 18 unit types, unit type 10 was most frequently used by all individual singers during all seasons, followed by unit types 4a, 1, and 12 (i.e., seven, six, and six out of eight seasons, respectively; Figure 3a). Between the 2014 and 2015 seasons, 44% of the unit types were shared, while among all other seasons, only between 17% and 33% of the unit types were shared.

Of the 44 phrase types identified, 13 were shared by the individual singers among two or more seasons. Eight phrase types were shared between two seasons (i.e., "Dg," "Dj," "Dm," "Fb," "Id," "Jb," "Kd," "Ma"); one phrase type was shared among the three seasons 2017, 2018, and 2019 (i.e., "Ib"); one phrase type was shared among the three seasons 2012, 2014, and 2015 (i.e., "Ja"); one phrase type was shared among the four seasons 2012, 2016, 2018, and 2019 (i.e., "Ic"); and two phrase types were shared among the four seasons 2012, 2014, 2015, and 2016

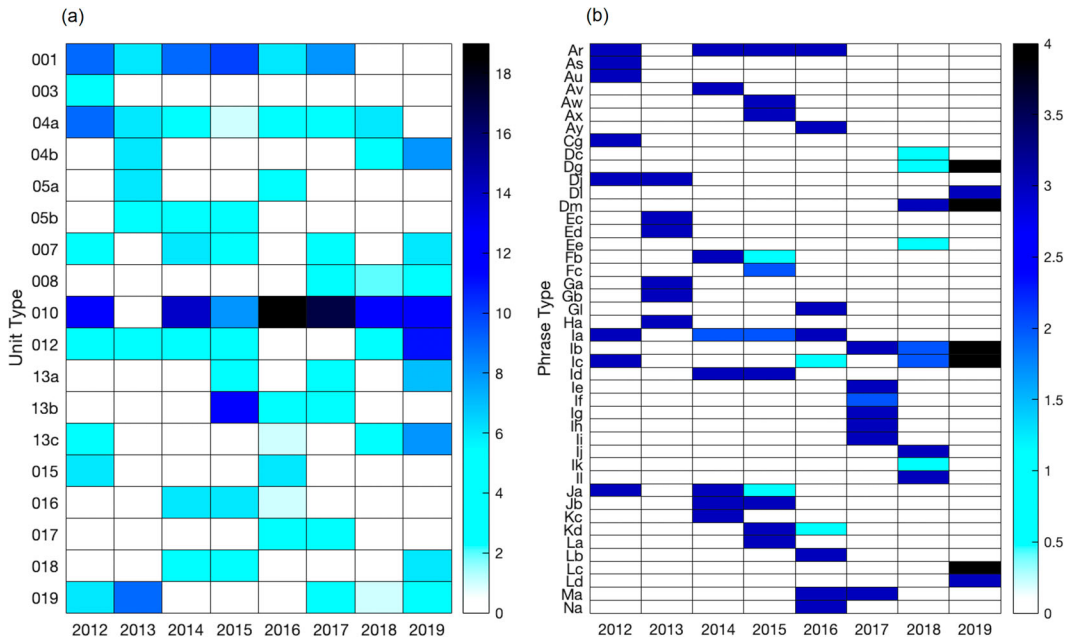

FIGURE 3 Heatmaps of unit (a) and phrase repertoires (b) per year. Color represents the number of individual singers using a phrase type in the case of phrase types and number of phrase types per individual singer containing unit type in the case of unit types.

(i.e., "Ar" and "Ia"). Between the 2014 and 2015 seasons, the highest percentage of phrase types was shared (14%), followed by the seasons 2018 and 2019 and 2012, 2014, and 2016, between which still 9.5% and 7% of the phrase types were shared, respectively (Figure 3b). Additionally, some themes reoccurred among seasons, but not necessarily in successive seasons. For example, the "Ar" and "Ia" themes, were first registered in the 2012 season, did not appear in 2013 but reappeared in 2014 and remained as part of the song pattern until 2016 (Figures 3b and 4). The "Ic" theme that was recorded for the first time in the 2012 season reappeared similar acoustic material sporadically in 2016 and 2018 and reappeared in all the recordings of all singers in the 2019 season (Table 1, Figures 3b and 4; supplemental material 1).

The observed percentage of shared phrase types between seasons is also represented in the phrase repertoire comparison among seasons (Figure 3b). Humpback whale phrase repertoires from the 2014 and 2015 seasons were highly similar (58%, AU > 95%) (Figure 5a). The phrase repertoires of humpback whale songs from the 2012 season were clustered together with the repertoires from 2014, 2015, and 2016, while the phrase repertoires of 2017, 2018, and 2019 were clustered together, with 43% similarity between 2018 and 2019. One exception was the phrase repertoire of the 2013 songs that had very low similarity with the repertoires of all other seasons.

The interseasonal similarities of theme sequences indicated by the LSI did not result in a clear temporal pattern. Some similarity among theme sequences was observed between songs from the 2012, 2014, 2015, and 2016

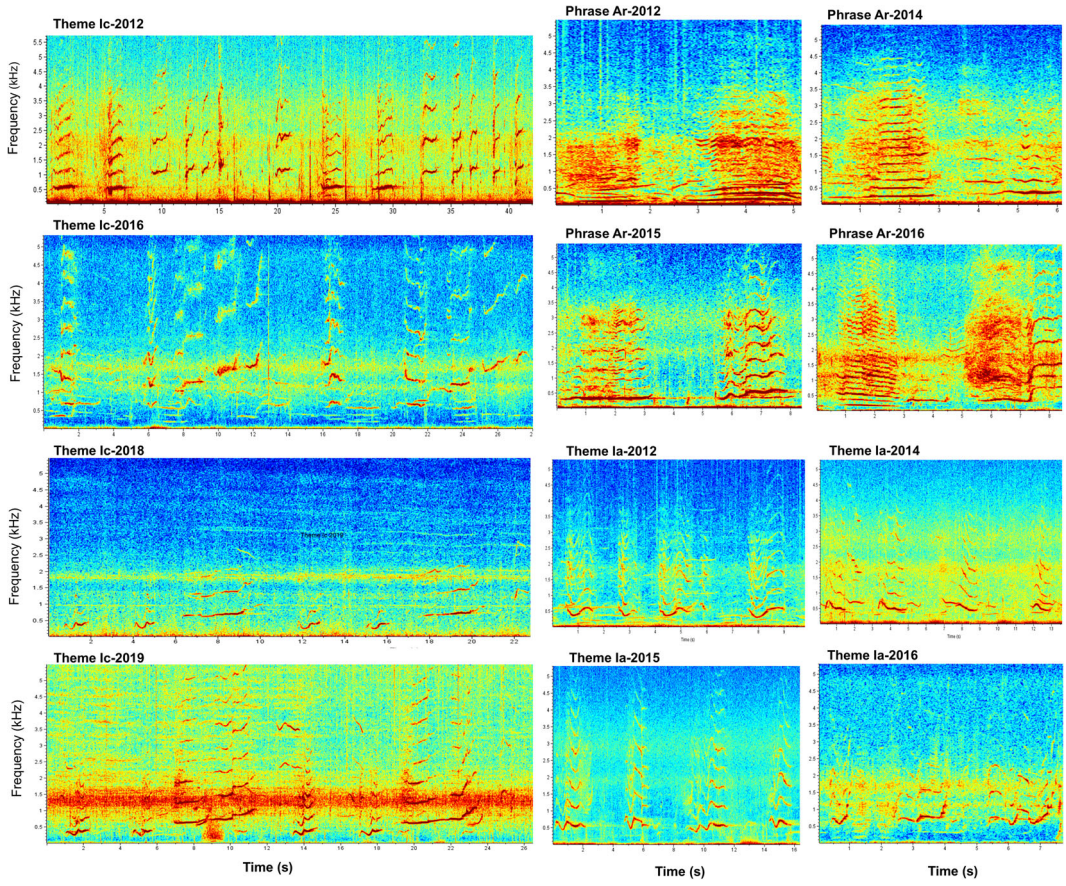

FIGURE 4 Example spectrograms of the irregularly recurring phrase "Ar," and themes "Ia" and "Ic." The spectrogram titles indicate in which years the phrases and themes were recorded. Spectrograms created in MATLAB with a Hamming Window, 3,528 window size, 63% overlap, 3500 DFT size. See supplemental material 2 with spectrograms and files of phrase and theme samples. DFT, discrete Fourier transform.

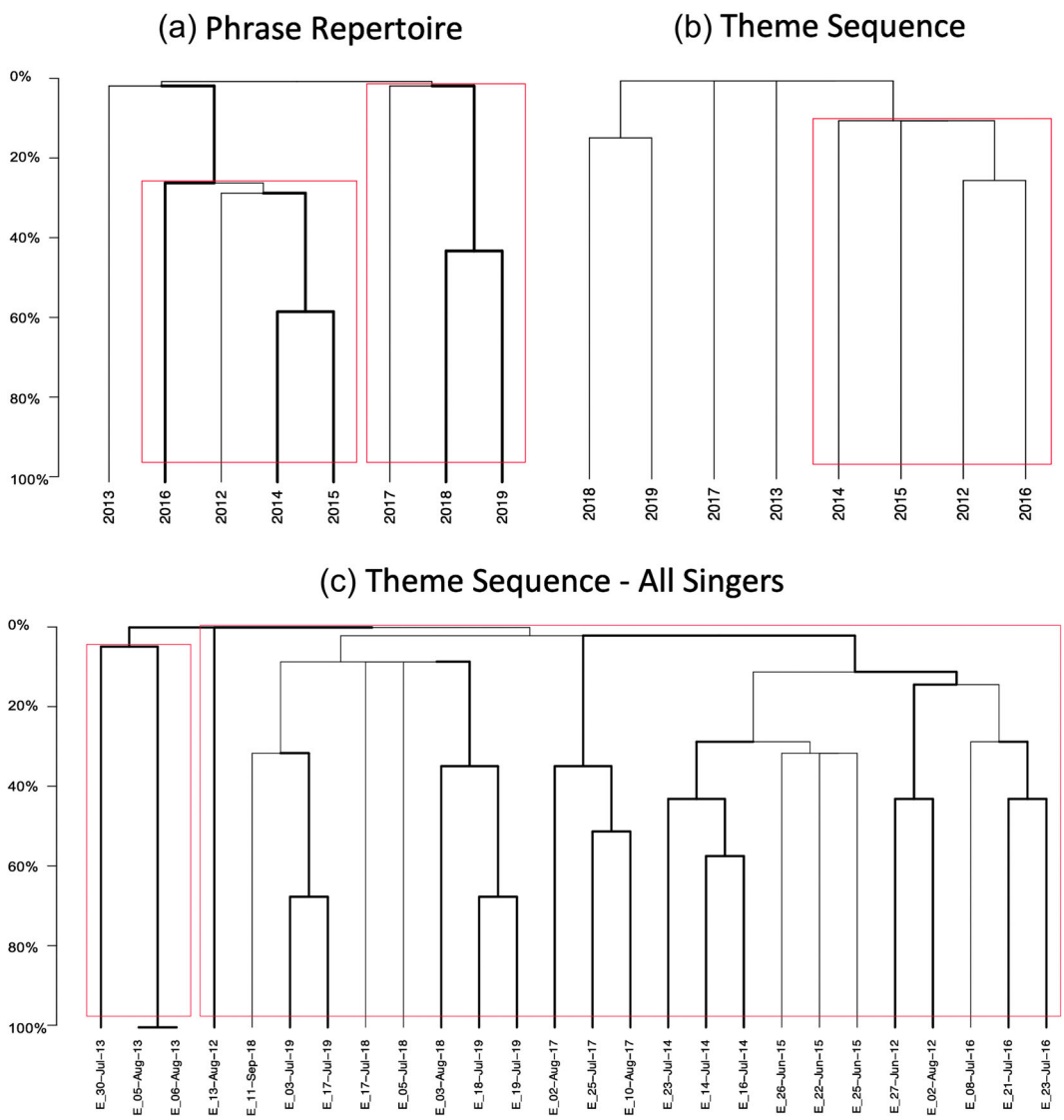

FIGURE 5 Bootstrapped dendrograms from hierarchical clustering of yearly phrase repertoires based on DCI analysis (a), of yearly set median song strings of theme sequences based on LSI analysis (b), and of per-individual-singer (identified by the capital letter "E" for "Ecuador" and the date of the recording) set median song strings of theme sequences based on LSI analysis (c). Bold lines indicate divisions that were likely to occur (i.e., AU >95%), and red boxes indicate clusters that are strongly supported by the data. DCI, Dice Coincidence Index; LSI, Levenshtein Distance Similarity Index.

seasons (cluster strongly supported by the data), with the highest similarity of theme sequences between the 2012 and 2016 season being only 23% (Figure 5b). Theme sequences from 2018 and 2019 had a low similarity of 17%. The theme sequences from 2013 and 2017 had 0% similarity with the theme sequences from all other seasons. These overall findings can also be confirmed when clustering the song similarities of the set median song strings of theme sequences from all individual singers (Figure 5c). Additionally, within year outliers can be identified, such as the song from one individual singer from 2012 that had 0% similarity with the rest of the songs from 2012 or the songs from any other year.

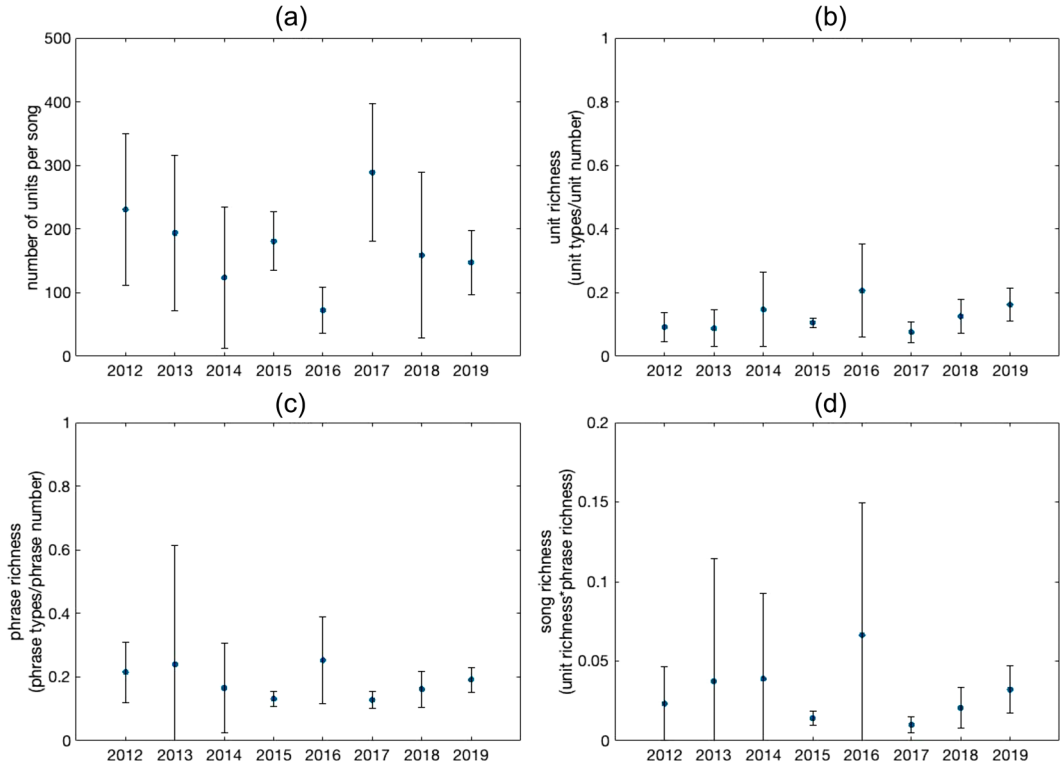

FIGURE 6 Number of units per song (a) and three metrics for acoustic richness (b–d) plotted against the year of recording. Dots represent averages, and error bars represent standard deviations from the distribution of all songs recorded during the respective year independent from the individual singers recorded (i.e., bias towards individuals with more songs recorded is therefore not accounted for in order to show the complete picture of variability captured here).

3.2 | Song metrics

During the eight breeding seasons from 2012 to 2019 off the northern coast of Ecuador, a temporal pattern was observed for number of units, unit, phrase, and song richness that resembled a periodic oscillation. The number of units per song slightly decreased between 2012 and 2016, drastically increased in 2017, and decreased in the 2018 breeding season (Figure 6a).

In 2016, song richness reached a maximum but was also characterized by a high intraannual variability. Unit and phrase richness variables presented a similar interannual pattern between 2012 to 2019, except for in the year 2013 when phrase richness was exceptionally high but unit richness was not (Figure 6b,c). Overall song richness decreased between 2014 and 2015 and between 2016 and 2017 (Figure 6d). The variation based on phrase richness (Kruskal–Wallis, $X = 7.62$, d.f. $= 7$, $p = .6$) and unit richness was nonsignificant ($X = 10.33$, d.f. $= 7$, $p = .11$). The changes in number of units per song among all seasons were significant ($X = 17.17$, d.f. $= 7$, $p = .01$). However, these statistical results must be interpreted with caution due to the small sample size available for this study.

4 | DISCUSSION

Song patterns of the southeastern Pacific region humpback whale population breeding off the Ecuadorian coast showed that songs of different singers were more similar within each season than between seasons (Payne &

Guinee, 1983; Payne & Payne, 1985; Winn et al., 1981; Winn & Winn, 1978). The observed interseasonal variations between 2012 and 2019 in song repertoire, composition, extension, and acoustic richness metrics contains signs of well-described evolution and revolution events (Garland et al., 2021; Noad et al., 2000) while not all the observed variability can be explained by these phenomena.

4.1 | Intraseasonal pattern in song repertoire

During one breeding season, all singers usually adopt the same song type, while some intra and interindividual variation within songs is normal (Payne & McVay, 1971; Payne & Payne, 1985). General interindividual variability of songs has been observed in different breeding areas such as Oceania (Noad et al., 2000), Hawaii and Mexico (Cerchio et al., 2001), the Caribbean (Payne & Payne, 1985; Winn & Winn, 1978), and South Africa (Hawkey et al., 2020). For the humpback whale breeding stock G, our results give first insights into the intraseasonal similarity of theme sequences and intraseasonal variation in the order and number of themes displayed by each singer, especially within songs during the 2014, 2015, and 2016 seasons. Even though, this variation in the order and number of themes is common especially at the beginning of the season or as a feature of hybrid songs (i.e., the combination of the song from the previous season and a newly introduced revolutionary song; Garland et al., 2017; Kowarski et al., 2022). In the present study, we could not confirm the development of song at the beginning of the breeding season nor could we confirm that these higher intraseasonal variations in theme order were related to clear revolution events. Alternatively, immature singers could display song structures with a different order, even omitting certain themes (Frumhoff, 1983; Winn & Winn, 1978). For the Ecuadorian breeding ground of the breeding stock G, one possible explanation for the high intraseasonal variability of songs in certain years could be the accumulation of immature singers during certain years (Herman et al., 2013; Lamoni et al., 2023).

In comparison to other Southern and Northern Hemisphere populations, the Ecuadorian song on average has the same number of theme types as for example populations from the western South Pacific Ocean (Murray et al., 2012), eastern Australia, New Zealand, and the central Pacific (Warren et al., 2020); South Africa (Hawkey et al., 2020); and the North Atlantic Ocean (Payne & Payne, 1985). However, in 2015, we registered an exceptionally high number of theme types ($N = 10$). This higher number of theme types could be influenced by the immigration of male humpback whales from other breeding populations or an increased acoustic contact with other populations during migration or on the feeding grounds (Garland et al., 2011, 2015; Mcloughlin et al., 2018; Noad et al., 2000; Owen et al., 2019; Schall, Djokic, et al., 2022; Schulze et al., 2022; Zandberg et al., 2021). In other studies, carried out in 2006, 2007, 2013, 2016, and 2017, a total of three, four, and six themes have been described for different breeding areas in the southeastern Pacific region such as the Gulf of Tribugá off Colombia, the Gulf of Panamá, and the Caño Island off Costa Rica (Chereskin et al., 2019; Oviedo et al., 2008; Perazio et al., 2018). These differences among the number of themes described in this and other studies could be driven by rapid progressive evolution events during migratory stop-overs (Owen et al., 2019; Tyarks et al., 2022). However, the differences in the number of theme types can also be influenced by the quality of samples and/or differences in acoustic analysis protocols and researcher expertise to identify acoustic structures (Jäckel et al., 2021). The acoustic analysis methods used here have been proven to be reliable in the structural characterization of humpback whale song and to be adequate for intra and interpopulation comparisons of song repertoire from both breeding and feeding grounds (Schall et al., 2022; Schall, Roca, & van Opzeeland, 2021a). Therefore, sample quality was maximized and differences in acoustic analysis protocols were minimized. Other analytical methods that include the manual classification of units and automatic transcription of theme sequences have been successfully applied in recent Latin American humpback whale song studies (Djokic, 2021; Gonçalves et al., 2023; Malige et al., 2021). In the long run, a global standardized classification method is imperative to provide more robust comparisons and allow for collaborative studies on humpback whale song composition and acoustic connectivity.

4.2 | Changes in song repertoire and composition

Humpback whale singers progressively transmit their acoustic material from season to season, gaining, losing, or replacing new or old elements (i.e., both single units and entire phrases/themes; Payne & Payne, 1985). Off Ecuador, singers often reused identified theme types in consecutive years; however, some theme types disappeared from 1 year to the next and reappeared again after one or two seasons (however, these results must be interpreted with caution because the small sample size available for this study might not be representative of the entire breeding population). Additionally, it has to be pointed out that any manual analysis of song is heavily affected by the subjectivity of classifying song units into the same or different categories. Even within the songs of a single individual, the acoustic characteristics of a unit type can be on broad scale, which overlaps as a continuum with the scale of another unit type (Kershenbaum et al., 2016; Mercado III & Perazio, 2022). Therefore, the downstream process of matching themes is also subject to this perception of the analyst (Cholewiak et al., 2013). To overcome this issue, here again, it is imperative to develop a global standardized classification method that at best would rely on the objective classification of song units through, for example, unsupervised learning methods (Stowell, 2022).

However, in case this reuse of certain themes after multiple years of disuse can be confirmed by alternative methods or more data, it would suggest a complex long-term memory capability in humpback whales as has been suggested to be also the cognitive basis for song evolution in general (Guinee & Payne, 1988). Studies on the acoustic memory capacity in birds have shown that the memorization of a song can lead to the reappearance of acoustic material from this song during their entire lifespan (Marler, 1997; Marler & Peters, 1982). For example, if juvenile swamp sparrows (*Melospiza georgiana*) get exposed to conspecific sounds, they will not immediately reproduce the taught repertoire but may reach adulthood before emitting what they had learned in the past (Marler & Peters, 1982). Both immature and mature humpback whale singers produce learned songs during the breeding seasons (Herman et al., 2013; Winn & Winn, 1978). Especially immature singers could learn a certain structure of these songs but display this learned structure later implementing a different order or even omitting certain themes (Frumhoff, 1983). In this sense, singers could learn as many song elements as possible and reproduce them during their entire lifespan in a more flexible fashion than strict song evolutions or revolutions.

Both song evolutions and revolutions have been related to the acoustic exchange among different humpback whale breeding populations, with the amount of acoustic exchange depending on the distances between breeding areas. The smaller the distance between adjacent breeding grounds, as for example Eastern Australia and New Caledonia (1250 km distance), the more similar the song structures (Allen et al., 2018). Between distant areas, as for example, the Babuyan Islands in the Philippines and Mexico (12,500 km distance), song structures have been observed to be less similar in terms of unit and phrase types (Darling et al., 2019). The Ecuadorian breeding population (stock G from Ecuador, Colombia, and Panama) appears to be often in acoustic contact with a number of other breeding populations. An analysis of acoustic exchange among humpback whales recorded in the Southern Ocean, off Ecuador, Chile, Brazil, Namibia, and South Africa revealed that all these populations show signs of acoustic contact with each other and that the contact most likely occurred on the feeding grounds in the Atlantic sector of the Southern Ocean (Schall et al., 2022). Accordingly, a rare unstructured theme type (i.e., a pattern-less sequence of units, not forming phrases between normally structured themes) from a novel song first recorded from singers and associated as an¨abrupt change of songë of the Atlantic breeding ground off Brazil during the 2018 season was recorded in the following breeding season in the eastern tropical Pacific off Panama in 2019 (Djokic, 2021; Gonçalves et al., 2023) and thus reveals that singers of breeding population G (Ecuador, Colombia, and Panama) had acoustic contact with Brazilian singers from 2018 onwards. Individual exchange of south eastern pacific humpback whales with the Atlantic humpback whale population through feeding grounds at the Antarctic Peninsula and South Orkney Islands is supported by whales photographically identified as PAN-1834 in Esmeraldas in 2015 and in Panama in 2019 and another individual (PAN-1055) identified in the Gulf of Panama in 2014 and at Gorgona in 2012 and both observed at the South Orkney Islands in 2020 (Marcondes et al., 2021). On the other hand, songs recorded between 2016 and 2018 in the western South Pacific off French Polynesia were recorded off Ecuador

during the 2018 season confirming a horizontal cultural transmission from west to east over a distance of 14,000 km (Schulze et al., 2022). Similar acoustic materials were found in the songs recorded in French Polynesia in 2016 and 2018 and the Ecuadorian songs from 2012, 2016, 2018, and 2019 (see example of themes 6 and 7a–b in supplemental material of Schulze et al., 2022 and theme Ic in the present study Figure 3 and supplemental material 1), which indicates an even earlier or more frequent contact between these two populations. In addition, the inter-populational contact of the Ecuadorian humpback whales has also been confirmed in genetic studies (Marcondes et al., 2021; Rizzo & Schulte, 2009). For example, similar mitochondrial haplotype sequences from Ecuadorian humpback whales have been identified in populations off Western Australia, New Caledonia, and French Polynesia, as well as in breeding areas located in the western (e.g., Brazil) and eastern South Atlantic Ocean (e.g., south Africa), and the Indian Ocean (e.g., Mozambique) (Dalgo, 2013; Rojas, 2014). Furthermore, similar haplotype sequences between Alaskan and Ecuadorian humpback whales support the genetic connection between humpback whales from the Northern and Southern Hemisphere (Medrano-González et al., 2001; Rojas, 2014). The repeated and nonsystematic (acoustic) contact between breeding populations might explain the different song developments in Ecuador. Similarities in song repertoires and compositions of Ecuadorian songs were not generally higher in consecutive years than in non-consecutive years (typical for song evolutions). Instead of continuous evolutions and rapid and complete revolutions, we partly see evolutions in combination with incomplete revolutions (from 2012 to 2013, 2016 to 2017, and 2017 to 2018 all theme types got replaced, except one; the song development from 2013 to 2014 is an exception when all theme types got replaced that might represent a complete revolution; however, the "new" 2014 song contained two themes that were also registered in 2012 already). The level of cultural transmission of acoustic material during different breeding seasons probably influences song dynamics of all Southern Hemisphere humpback whale subpopulations (Djokic, 2021; Schall et al., 2022; Schulze et al., 2022). The reason for the observed individual variation and adoption of previous acoustic material or learned from other subpopulations is yet unclear. To better understand social learning and cultural processes in baleen whales, our results highlight the need for future studies in subpopulations with frequent migratory contact, as evidenced on the Ecuadorian coast.

4.3 | Patterns in song richness

Eight years of recordings off the coast of Ecuador showed that humpback whale song from this subpopulation in some seasons displayed little variation in acoustic richness metrics among singers while other years showed high intraseasonal variation of song richness equivalent to the variation that is observed interseasonal. Recently, Murray et al. (2018) evidenced unique sequences of phrase repetitions, "variants," inside themes composed by singers of the east Australian population. This variant acoustic material has been observed to be maintained during interpopulation transmission. This might explain why the introduction of new acoustic material from other populations into the repertoire of the Ecuadorian population did lead to the high intraseasonal variability in acoustic richness that overshadows an interseasonal pattern that could have been indicative of the timing of evolution and revolution events (Allen et al., 2018).

5 | CONCLUSIONS

Off Ecuador, humpback whales seem to follow a notyet described and fully understood temporal song dynamic in terms of acoustic richness and changes in the repertoire composition. These findings indicate how different cultural transmission strategy can be among subpopulations in the southern Pacific region. In the case of Ecuador, a recent multuidirectional exchange from the Atlantic and western Pacific might be the cause for these diverse cultural scenarios such as song evolutions with partial revolution events. To improve our understanding and the interpretation of these complex cultural processes characterized by high intraseasonal variabilities, further long-term studies on the

acoustic composition of humpback whale songs in breeding areas in the southeastern Pacific region are necessary. On the larger scale, as a next step, circumpolar comparisons of song repertoire should be addressed with a standardized classification method and extended by global comparisons wherever possible to understand the functionality of song dynamics in humpback whales as well as the vulnerability of song in the context of constantly rising anthropogenic underwater noise levels.

AUTHOR CONTRIBUTIONS

Javier Oña: Conceptualization; data curation; funding acquisition; investigation; project administration; writing – original draft; writing – review and editing. **Judith Denkinger:** Conceptualization; funding acquisition; project administration; writing – review and editing. **Elena Schall:** Conceptualization; data curation; formal analysis; methodology; writing – review and editing.

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SUPPORTING INFORMATION

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