
Global cultural evolutionary model of humpback whale song

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Summary

Humpback whale song is an extraordinary example of vocal cultural behaviour. In northern populations, the complex songs show long-lasting traditions that slowly evolve, while in the South Pacific, periodic revolutions occur when songs are adopted from neighbouring populations and rapidly spread. In this species, vocal learning cannot be studied in the laboratory, learning is instead inferred from the songs' complexity and patterns of transmission. Here, we used individual-based cultural evolutionary simulations of the entire Southern and Northern Hemisphere humpback whale populations to formalise this process of inference. We modelled processes of song mutation and patterns of contact among populations and compared our model with patterns of song theme sharing measured in South Pacific populations. Low levels of mutation in combination with rare population interactions were sufficient to closely fit the pattern of diversity in the South Pacific, including the distinctive pattern of West-to-East revolutions. Interestingly, the same learning parameters that gave rise to revolutions in the Southern Hemisphere simulations gave rise to evolutionary patterns of cultural evolution in the Northern Hemisphere populations. Our study demonstrates how cultural evolutionary approaches can be used to make inferences about the learning processes underlying cultural transmission and how they might generate emergent population-level processes.

1. Introduction

Social learning underpins a wide variety of behaviours in many species of animal. Social learning (from the observation of, or interaction with, others) can lead to innovations spreading through a population (e.g., [1–4]) or could, on longer timescales, potentially lead to the emergence of local cultures (e.g., [5–9]). One example of social learning, vocal production learning has been extensively studied in birds and to some extent mammals. Birdsong is the most studied example of vocal learning, with all species of songbird that have been tested experimentally having been shown to socially learn the (components of) songs that function in resource defence and breeding [10]. But only a small proportion of species have been studied experimentally in laboratory conditions. Instead, evidence for the ubiquity of vocal learning within the songbirds has been augmented by field studies that infer vocal learning from patterns of geographic variation in song, or changes in the frequency of song-types over time. Such studies of cultural transmission and evolution have been carried out in numerous species [11] (e.g., corn buntings, *Emberiza (Miliaria) calandra* [12]; white-crowned sparrow, *Zonotrichia leucophrys* [13]; village indigo birds, *Vidua chalybeata* [14,15]; song sparrows, *Melospiza melodia* [16]; indigo buntings, *Passerina cyanea* [17,18]; savannah sparrows, *Passerculus*

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47 *sandwichiensis* [19]; chaffinches, *Fringilla coelebs* [20] and swamp sparrows, *Melospiza georgiana* [21]). Like in
48 songbirds, captive studies of smaller cetacean species have demonstrated that they are capable of vocal pro-
49 duction learning, where as a result of experience with signals of other individuals, an individual modifies
50 their own signal [22]. But just as with songbirds, not all cetacean species have been or could be studied in
51 the lab or are amenable to field experiments. Included in this category is a species whose complex [22],
52 evolving [23,24] song displays represent an extraordinary example of vocal cultural behaviour, the hump-
53 back whale (*Megaptera novaeangliae*) [23].

54
55 Male humpback whales sing, at any timepoint, a single long, stereotyped, complex, and hierarchically struc-
56 tured song [24–26]. Although the exact details are still debated (see [27]), song in humpback whales is
57 thought to function in sexual selection. The song is arranged in a nested hierarchy: on the most fundamental
58 level is the ‘unit’, representing an individual sound; a few units sung in a stereotyped sequence comprises a
59 ‘phrase’; phrases are repeated one to many times to make a ‘theme’; and finally, a sequence of different
60 themes comprise a song [24,28]. Within a population, at any point in time, most males will sing the same
61 song (known as a ‘song type’) [29,30]. At the same time, however, the song is also constantly evolving
62 [7,30,31]; males incorporate changes to the population song in their own display to maintain the observed
63 conformity. Slow, progressive song evolution is a key feature of all humpback whale populations world-
64 wide. What processes (e.g., production errors, innovation, etc.), learning biases or individual(s) may be driv-
65 ing this evolutionary change, and how this may relate to fitness, female choice and reproductive success,
66 remains elusive [23].

67
68 Another key feature of humpback whale song is at the scale of oceans: within oceans, populations sing sim-
69 ilar songs but the degree of similarity depends on the geographic distance and also appears to depend on
70 the extent of interchange among populations [32–34]. Humpback whales spend the summer months feeding
71 in high latitudes before undertaking one of the longest migrations of any mammal to their low latitude win-
72 ter breeding and calving grounds, where they aggregate around islands and banks [35–39]. They show
73 strong maternally directed site fidelity to breeding and feeding grounds, with occasional movement among
74 locations [40–43]. Song sharing among populations is suggested to occur due to three mechanisms [32],
75 which have been demonstrated to varying degrees around the world [40,43–50]. Song sharing between pop-
76 ulations can occur through males visiting more than one wintering ground in consecutive years, by males
77 visiting more than one wintering ground within a breeding season, and finally through song sharing on
78 shared feeding grounds and/or on shared or partially shared migratory routes [32]. This can result in a
79 common (single), ocean-wide song type that has varying degrees of similarity (based on ‘matching’
80 themes/phrase types), as epitomised by studies in the North Pacific (see [34]).

81
82 However, in 1996 and 1997, a cultural phenomenon was recorded for the first time that represented a very
83 different pattern of variation. Song from the west Australian humpback whale population, located in the
84 Indian Ocean appeared in the east Australian population, in the South Pacific, and rapidly replaced the very
85 different existing song [51]. This process, in which the song in a population is rapidly replaced by a com-
86 pletely novel song, was termed a ‘song revolution’, to distinguish it from the much slower process of song
87 evolution [51]. The new song first appeared in low numbers and then increased in frequency until the old
88 song was completely gone; a process that took two years [51]. The authors hypothesized that the movement
89 of a small number of whales from the west Australian population to the east Australian population may
90 have initiated the cultural transmission of the song between the oceans [51]. Further work demonstrated the
91 expansion of this phenomenon where multiple song types and thus revolutions have been horizontally
92 transmitted east from the east Australian population across the populations in the South Pacific, in a series
93 of cultural waves spanning a decade [7,44,52,53]. Multiple song types are thus present in the South Pacific
94 Ocean at any point in time in contrast to the single ocean song type characteristic of the Northern Hemi-
95 sphere oceans. This pattern of not only population-wide concerted song evolution but also revolution in
96 humpback whales is unique among non-human animals [23].

97
98 To date, the only event that appears to trigger a song revolution is the appearance of a new song type in a
99 population that can be traced to come from another [7,51]. We hypothesize that novel songs are rapidly and
100 preferentially learned [51,54]. This might result from a sexually selected drive for novelty [31,51]. However,
101 if this is the case that raises a problem: what constrains songs within populations from diverging from each
102 other [55]? It is not clear whether a neutral process of cultural mutation and transmission could also give

103 rise to revolutionary dynamics. We speculate that song revolutions occur throughout the Southern Hemi-
104 sphere [23], with recent hints of directional transmission also emerging around Africa [56]. This may be
105 facilitated by geographical structure: the large circumpolar feeding grounds lead to low rates of contact be-
106 tween neighbouring populations, while providing no landmasses to impede movement at high latitude.
107 Moreover, the west to east direction of the song revolutions observed in the South Pacific is hypothesized to
108 occur due to the relative differences in population sizes. Novel song types appear to spread from large to
109 small populations [7,53]. On the other hand, the fact that revolutionary dynamics are empirically absent in
110 Northern Hemisphere populations (primarily located in the North Pacific and North Atlantic) may be due
111 to differences in learning biases, or alternatively could be due to differences in geography that affect the
112 patterns of population interactions. The Northern Hemisphere populations are constrained by continents on
113 each side of the oceans, which prevents interaction between Atlantic and Pacific meta-populations, while at
114 the same time encourages multiple populations to interact within an ocean by funnelling populations into
115 comparatively small areas (see figure 1a) [23]. Experimentally testing such hypotheses is unfeasible; hump-
116 back whales cannot be kept in captivity, as they are 14 m long, weigh 30 tonnes and undertake long migra-
117 tions across half the globe. They can also be less than amenable to field experiments, notwithstanding the
118 ethical considerations surrounding attempting to modify a vocal cultural display that may spread at the
119 Hemispherical scale [57]. A viable way forward is to use cultural evolutionary models in combination with
120 empirical data to infer which processes could underlie these broad-scale patterns of cultural transmis-
121 sion. Recent work using spatially explicit agent-based models of fine-scale song evolution, taking into ac-
122 count the spatial movements of individual whales, suggested that production errors (rate = 0.01%) led to the
123 pattern of gradual song evolution observed in the wild [58]. To produce a song revolution which mirrored
124 the empirical data from the west-east Australian song revolution, a song memory was included [59]. These
125 fine-scale models on song transmission within and between the west Australia and east Australia popula-
126 tions explored learning processes and biases to understand, at the level of the individual, what factors may
127 facilitate song evolution and revolution.

128
129 Here, we modelled humpback whale song transmission, not at a population scale, but at the global Hemi-
130 sphere scale to understand what broad-scale processes may initiate, stop, and spread song evolutions and
131 revolutions. Using individual-based simulations (based on [21]), we explored how past population trajec-
132 tories [60] in combination with connectivity and geographic location may interact to create conditions that
133 promote cultural dynamics. As any model has necessary simplification, we compared our model with data
134 from published South Pacific humpback whale research (e.g., [7,52,61]), using Approximate Bayesian Com-
135 putation to find parameter values that were statistically most consistent with the empirical data. We also
136 compared our model more informally with patterns of song sharing in other oceans ([24,30,34,56,62,63]). By
137 using models to explore likely scenarios, targeted future field studies can be designed to empirically test
138 hypotheses.

139

140 2. Methods

141
142 **Empirical song data**
143 Empirical song data was drawn from published studies of humpback whale song transmission in the South
144 Pacific Ocean. Detailed descriptions of field locations, data collection methods, song transcription, and quan-
145 titative analyses can be found in [7,52,61]. Briefly, 211 singers were recorded singing 798 songs from 1998 to
146 2008 across the western and central South Pacific populations [52]. Units were transcribed and then grouped
147 in stereotyped themes; 'matched' themes were given the same label, and a sequence of themes made up each
148 song. Songs with similar themes were grouped into song types [7]. Here, the presence of themes per singer
149 was collated regardless of whether those themes were common or not. Song length ranged between 2-11
150 themes with 6.84 ± 1.73 (mean \pm SD) themes per song.

151
152 **Cultural evolutionary model of song learning**
153 We constructed an individual-based simulation model of song learning and cultural evolution. For a sum-
154 mary overview of all models see table 1.

155
156 ***Model 1 – Southern Hemisphere***
157 *Population structure*

158 We simulated all humpback whale populations in the Southern Hemisphere: 11 populations in a circular
159 chain. Each population had a population to its left and a population to its right (figure 1b); all distances
160 between populations were the same for ease of modelling. We based the size of the populations on [60], with
161 the exception of Oceania which we divided into four smaller populations (New Caledonia, Tonga, American
162 Samoa/Niue/Cook Islands and French Polynesia) to be able to compare these with the empirical data. All
163 population size estimates were divided by two to represent only the males in these populations. We simu-
164 lated cultural evolution over a period of 50 years, starting at a whaling-induced population ‘bottleneck’ in
165 1960. For each population, i , we estimated three different population sizes: $N_{i,min}$ (estimated minimum abun-
166 dance during the bottleneck), $N_{i,2015}$ (estimated abundance in 2015) and $N_{i,K}$ (estimated carrying capacity),
167 based on estimates in [60]. Each simulation ran for 50 years during which populations were allowed to grow
168 from $N_{i,min}$ to their $N_{i,2015}$ with a population dependent logistic growth rate estimated from the three popula-
169 tion sizes. See table S1 for all population size estimates used in the models (electronic supplementary mate-
170 rial S1).

171 172 *Songs and song memory*

173 In the simulation model, songs were characterised by a string of 11 units representing the themes in a song.
174 Some theme locations in the array could be left ‘empty’ representing the absence of a theme, to allow for
175 differences in song lengths: ranging between 2-11 themes per song. Each individual whale in the model at
176 any timepoint (epoch) only sang one song: its ‘current song’. Whenever an individual learned a new song,
177 this song was stored in its song memory. The length of the song memory in epochs, L_{SM} , was drawn from
178 the priors. When learning a new song, the oldest song in the memory was replaced by the new song. Only
179 current songs were sung at any timepoint, with the memory only serving as a repository of old songs against
180 which tutor songs were compared (see Song selection and song learning). At the start of each simulation, all
181 individuals within a given population started with the same song consisting of seven different themes,
182 which differed for each population. As our models measure theme sharing (see Summary statistics), a revo-
183 lution was deemed to occur when the within population theme sharing with the previous year was very
184 low. This suggested that within a year the old themes (and thus the old song type) were rapidly replaced by
185 new themes.

186 187 *Learning epochs*

188 Humpback whales predominantly sing during the breeding season, although some song has also been heard
189 during migration and on the feeding grounds [49,64]. Here, during migration and on the feeding grounds,
190 rare interactions between individuals of different populations may provide opportunities for exposure to
191 song from neighbouring populations [45,46]. To mimic these patterns of singing behaviour and interactions
192 in our model, each year individuals went through ten song learning events (‘learning epochs’). Of these ten
193 epochs per year, nine epochs corresponded with the breeding season, during which individuals only inter-
194 acted with individuals from their own population as a potential tutor. Each year one of the learning epochs
195 corresponded with the migratory / feeding season during potential interactions with other populations and
196 tutors could be selected from a neighbouring population.

197 198 *Song selection and song learning*

199 During a learning epoch a focal individual randomly selected N_T tutors. In the nine breeding season learning
200 epochs, these tutors were randomly drawn from the focal’s own population. In the single migratory / feeding
201 season epoch each tutor was drawn randomly with a probability P_N for each tutor to come from a neigh-
202 bouring population. Individuals only selected novel songs for learning (songs that were not already present
203 in their memory): each of the songs sung by the selected tutors was compared to each of the songs in the
204 memory of the focal individual. For each of these comparisons, if a given tutor’s song contained one or more
205 themes that were not present in a given focal song, it was considered a different song. Only when all songs
206 in the focal individual’s song memory were different from the tutor’s song – and it was considered a novel
207 song – could it be learned. If one or more novel songs were sampled by a whale during a learning epoch,
208 one was selected at random and copied by the focal individual into its song memory. Copying of songs did
209 not always happen faithfully: deletions, insertions and theme substitutions occurred. Firstly, for each theme
210 in the chosen song there was a probability P_{learn} for each theme that it was learned (and not deleted from the
211 song). This probability was dependent on the number of times k that the theme was present in the tutor
212 songs it heard during that epoch, and a parameter for deleting themes P_d : $P_{learn} = 1/(1 + 0.5^{(k+P_d)})$. When a
213 theme was deleted, this location in the song array was left empty. Secondly, for each empty location in the

214 song array, a new theme could be invented and inserted with a probability calculated as: $P_{\text{insert}} = e^{-1 * P_d * P_i}$,
 215 where P_i was drawn from the priors. Lastly, theme substitutions occurred with a substitution rate μ , in which
 216 a theme was substituted by a new theme. In cases where all tutor songs were already present in the focal
 217 individual's song memory, no new song was learned. Instead, only new theme substitutions were intro-
 218 duced in the old song with substitution rate μ , similar to newly learned songs. These changes – insertions,
 219 deletions and substitutions – broadly mirror humpback song evolution processes. To prevent an effect of the
 220 order in which the populations go through their learning epochs, each individuals' current song was only
 221 replaced by a newly learned song after all individuals had gone through the song selection and song learning
 222 phases in that epoch.

223 224 *Summary statistics*

225 To compare the empirical data to the simulated data we measured seven summary statistics, averaged over
 226 all populations and the last 11 simulated years. We compared these to the same statistics measured on the
 227 empirical data. The sample sizes measured for each population and year followed the sample sizes in the 11
 228 years of the empirical data: each sample represented one year of one particular population. All summary
 229 statistics were calculated on the basis of the song that each particular individual in that population sample
 230 sang in that particular epoch (not on the basis of its memory). Summary statistics consisted of: (1) Singleton
 231 themes: average number of theme types that were sung by only one individual in a sample population (sp);
 232 (2) the unweighted average of the average song length in a sp ; (3) the within population standard deviation
 233 of the song lengths. Statistics (4-7) were derived from theme sharing between different populations and / or
 234 timepoints. Theme sharing was calculated following formula 1, where ns_A is the sample size of the sp , and
 235 ns_B the sample size for the population it is compared to. $T_{A,i}$ indicates the themes for individual i in the sp ,
 236 and $t_{B,j}$ the themes of individual j in the population it is compared to.

237 (1)

$$238 \quad TS_{A,B} = \left(\sum_i^{ns_A} \left(\sum_j^{ns_B} |t_{A,i} \cap t_{B,j}| / |t_{A,i}| \right) ns_B^{-1} \right) ns_A^{-1}$$

239
 240 Summary statistic (4) was the average of theme sharing within the sp (TS_{FC}): calculated as formula (1), where
 241 population $B =$ population $A -$ individual i . Summary statistic (5) was the average of the theme turnover
 242 within the sample population, calculated as the change in average theme sharing within the sp between the
 243 current year and the previous year: $TS_{sp,sp} - TS_{sp,sp(year-1)}$. Summary statistic (6) was the average of the
 244 absolute difference in theme sharing between the sample population and both neighbouring populations
 245 (western population wp and eastern population ep), in the previous year: $TS_{sp,sp(year-1)} - TS_{sp,ep(year-1)}$. Fi-
 246 nally, summary statistic (7) was the average of the maximum theme sharing between the sp and both neigh-
 247 bouring populations in the previous year ($Max TS_{wp}, TS_{ep}$). We square root transformed summary statistics
 248 1, 3, 5 and 7. We then normalised each summary statistic by dividing it by the standard deviation of this
 249 statistic in a set of 3,000 simulations sampling from the priors.

250 251 *Approximate Bayesian Computation*

252 We used Approximate Bayesian Computation (ABC) to obtain the posterior distribution of the model pa-
 253 rameters by comparing the summary statistics of the empirical data with the summary statistics of the sim-
 254 ulated data [21,65]. Simulations were carried out with parameter values drawn from the prior distributions
 255 (see below). For each simulation we then calculated the Euclidian distance across the normalised summary
 256 statistics of the simulated data and the empirical data. Parameter values were accepted when the summary
 257 statistic values of the simulated data were within threshold ϵ from the empirical summary statistic values.
 258 By using a Population Monte-Carlo approach to the ABC model (PMC-ABC; [65]) we were able to reduce
 259 the number of simulations needed to obtain a sufficient number of simulations within the final threshold ϵ .
 260 PMC-ABC achieves this by carrying out subsequent sets of simulations in which the threshold ϵ is stepwise
 261 decreased. We used the following values for ϵ : {6, 5.5, 5, 4.5, 4, 3.5, 3, 2.75, 2.5}. We ran each set until 1,000
 262 accepted parameter sets were produced.

263 264 *Prior distributions*

265 We set the prior distributions for N_T , P_N , μ and L_{SM} as log-uniform distributions with limits N_T {1, 20}; P_N
 266 {0.0000001, 0.25}; μ { 1×10^{-10} , 0.001}; L_{SM} {1, 100}. P_d and P_i were given a uniform distribution with limits P_d
 267 {1, 20}; P_i {0.2, 6}.

268
269 *Validation of ABC*
270 To validate that our ABC design was producing unbiased parameter estimates we carried out a leave-one-
271 out cross validation analysis. We used the 73,600 samples from the adjusted priors in the last round of the
272 PMC method, and for each one of these, estimated its parameter values using the remaining samples. We
273 describe these results in the electronic supplementary information (S2).
274

275 ***Model 1a-c – Population size and direction of revolutions***

276 To test the hypothesis that relative differences in the population sizes underlie the west-to-east direction of
277 the revolutions, we further explored the effects of population size, and population growth on the direction
278 of revolution transmission. We ran 1,200 simulations for each of three different scenarios (a-c: see also table
279 1) using song learning parameters sampled from the posterior distribution of the Southern Hemisphere in
280 *Model 1*. **a)** We reran the simulations for the Southern Hemisphere, because, due to stochasticity, we did not
281 expect the same parameter settings to always generate the same theme sharing patterns. For this simulation
282 we used the original population sizes N_{min} , $N_{i,2015}$ and $N_{i,K}$ as described in *Model 1*. **b)** To explore the role of
283 relative differences in population sizes on the direction of the revolutions we ran the same model but with
284 all population sizes set to equal values, to see whether the pattern of eastward revolutions would disappear.
285 All populations started with $N_{min}=100$, and grew to $N_{i,2015}=1,000$ and $N_{i,K}=5,000$. **c)** Finally, we also explored
286 the role of the population size bottleneck on the direction of the revolutions. For this we reran the simulations
287 for the Southern Hemisphere but only fixed the $N_{i,2015}$ for all populations to 1,000 individuals, and the $N_{i,K}$ to
288 5,000 individuals, while the N_{min} was kept at the empirical values. For each model we selected the simulations
289 with $\epsilon < 3$, and calculated the proportion of revolutions that ran from east to west (opposite to the direction
290 found in the empirical data).
291

292 ***Model 2 – Projecting cultural evolution into the future***

293 In the second model we explored what would happen to the patterns of song evolution and revolution in
294 the future, if population sizes were to increase and approach carrying capacity. In this model we ran the
295 simulations for 500 years (starting during the 1960 bottleneck, and projecting ~450 years into the future),
296 and allowed populations to grow to their carrying capacity. For this model we sampled with replacement
297 1,000 parameter settings from the posterior distribution of *Model 1* – i.e., settings that generated summary
298 statistics that were a close fit to the empirical data. For each simulation we calculated average theme sharing
299 within the focal population, and between the focal population and each of the neighbouring populations in
300 the previous year.
301

302 ***Model 3 – Northern Hemisphere***

303 In the third model we compared the differences in patterns of theme sharing between the Northern Hemi-
304 sphere and the Southern Hemisphere humpback whale populations. For this we ran 1,000 simulations for
305 both the Northern and the Southern Hemisphere populations using song learning parameters sampled from
306 the posterior distribution of the Southern Hemisphere in *Model 1*. We reran the simulations for the Southern
307 Hemisphere, because, due to stochasticity, we did not expect the same parameter settings to always generate
308 the same theme sharing patterns. For the Northern Hemisphere simulations, we used the exact same model
309 as for the Southern Hemisphere (see *Model 1*), but only changed the number of populations, population size
310 estimates and the pattern of interactions between the populations to match those observed in the Northern
311 Hemisphere (figure 1b, table S1). We used current population size estimates for the different populations in
312 the Northern Pacific and Atlantic Oceans [66], and, since these are not as readily available as for the Southern
313 Hemisphere, we roughly estimated bottleneck and carrying capacity population sizes. Interaction patterns
314 between populations on the feeding grounds were based on [66,67]: both populations in the Atlantic Ocean
315 and most populations the Pacific Ocean were allowed to interact with each other, but there was no interac-
316 tions between Atlantic and Pacific populations. For the interaction rate between the populations, we used
317 the estimate obtained from *Model 1*. While there is no reason to expect that this parameter value is the same
318 in the Northern Hemisphere as the Southern Hemisphere, we chose to use this value out of conservatism.
319 For each simulation we calculated within population theme sharing and turnover. We also calculated aver-
320 age theme sharing between the focal population and each of the neighbouring populations in the previous
321 year, and the difference in theme sharing with the eastern and western neighbouring populations ($\text{Diff TS}_{\text{WP-}}$
322 $\text{TS}_{\text{EP}}: \text{TS}_{\text{sp,sp}(\text{year}-1)} - \text{TS}_{\text{sp,ep}(\text{year}-1)}$).
323

324 3. Results

325

326 ***Model 1 – Southern Hemisphere***

327 With relatively simple learning rules we were able to create a model with signatures of both evolution and
328 revolution of songs. Within year, within-population theme sharing was high (TS_{FC} median: 0.67, 95% credi-
329 ble interval: 0.53-0.82), whereas within population theme sharing with the previous year was low (TS_{FP} me-
330 dian: 0.15, CI: 0.03-0.37), suggesting a high rate of turnover of themes present in the population. Theme
331 sharing with neighbouring populations in the previous year was higher than within population sharing in
332 the previous year, with maximum theme sharing (regardless of which neighbour) of 0.32 (Max $TS_{WP,TS_{EP}}$ CI:
333 0.24 – 0.45), suggesting revolutionary changes. By calculating the difference in theme sharing with the focal
334 population between the eastern and western neighbours, we found that the majority of the revolutions ran
335 from west to east (Diff $TS_{WP}-TS_{EP}$ median: 0.21, CI: -0.21-0.34). Out of 1,000 simulation runs, 552 showed a
336 signature of revolutionary waves running from west to east (Diff $TS_{WP}-TS_{EP} \geq 0.2$), whereas only 37 simula-
337 tions showed revolutionary waves running from east to west (Diff $TS_{WP}-TS_{EP} \leq -0.2$). Individual themes
338 were transmitted from population to population through the years. Themes were usually only found in a
339 population for one or two years before they were replaced with new themes. Although the direction of the
340 majority of theme transmissions was from west to east resulting in the larger patterns of eastward waves of
341 revolutions, some themes were still transmitted from east to west (figure 2a). Moreover, due to these revo-
342 lutions, average theme sharing probability between the focal population and the population to the west in
343 the previous year was high, which decreased stepwise when going a year back in time and moving a popu-
344 lation further westward relative to the focal population (figure 2b). This pattern of sharing faded after
345 around five years, after which the songs had evolved to such an extent that the theme sharing probability
346 with the focal population in the current year was not higher than for other populations.

347

348 From our simulations we estimated that individual humpback whales learned their songs with a high pre-
349 cision (substitution rate per individual per theme per learning epoch – median: $\mu=1.60 \times 10^{-7}$, CI: 4.10×10^{-10} -
350 8.24×10^{-6}). Similar to the low substitution rates, insertion and deletion probabilities were also estimated to
351 be low (median: $P_d=6.42$, CI: 3.34-22.73); median: $P_i=3.69$, CI: 0.56-5.84), resulting in a deletion probability of
352 0.006 for a theme only heard once in that learning epoch by a focal individual. We estimated that the length
353 of an individual's memory was 54.59 epochs long (CI: 21.36-97.5). Individuals sampled 5.11 tutors to select
354 their new songs from (CI: 1.57-17.95). In the feeding grounds, individuals rarely encountered and learned
355 from neighbouring populations, with a probability of $P_N=0.001$ (CI: 8.02×10^{-5} - 2.90×10^{-2}). The number of tutors
356 sampled and the probability for a tutor to be selected from a neighbouring population were negatively cor-
357 related ($r=-0.23$), which is due to the fact that the more tutors an individual samples, the greater the proba-
358 bility that one of these comes from another population.

359

360 ***Model 1a-c – Population size and direction of revolutions***

361 For the three models exploring the effects of relative population sizes and growth rates, we found that the
362 differences in size between the populations around the moment of measuring (the simulated year 2015)
363 determined whether or not the simulations resulted in a situation with revolutions running from east to west
364 (opposite to direction of the patterns found in the empirical data). In *model 1a* with the empirical population
365 size estimates we found that of all the simulations with a signature of revolutionary waves (Diff $TS_{WP}-$
366 $TS_{EP} > |0.21|$) only a very small proportion (0.05) of these revolutions ran from west to east, mirroring the
367 patterns found in the empirical data. In *model 1b*, all population sizes at N_{min} , $N_{i,2015}$ and $N_{i,K}$ were set to the
368 same values for all populations, we found that a proportion of 0.54 of the revolutions waves ran from west
369 to east. This suggests that when the relative differences in population sizes are removed, the direction of
370 revolutions is almost equally likely to run from east to west as from west to east. We then explored the effect
371 of the bottleneck N_{min} on the direction of revolutions in *model 1c*, by only setting the $N_{i,2015}$ to 1,000 individuals,
372 and the $N_{i,K}$ to 5,000 individuals, while keeping the N_{min} at the empirical values. Similar to model 1b, the
373 probability for revolutions to run eastward or westward was almost equal (proportion east to west=0.47),
374 suggesting that the bottleneck did not play a role in the direction of the revolutions in the current day.

375

376 ***Model 2 – Projecting Southern Hemisphere cultural evolution into the future***

377 When we allowed models to keep running for 500 years from the bottleneck, we found that, on the basis of
378 our model and the range of parameter settings, there was a wide range of possible future outcomes (figure
379 3). In a number of simulation runs, revolutionary waves could still occur, including when populations grew

380 and approached carrying capacity. However, in most models, periods with revolutionary waves were inter-
381 spersed with periods without them. When waves occurred, their direction tended to be from west to east,
382 although some waves running from east to west were also observed (figure 3a). Among the predictions of
383 our model there were also simulations where the variation in themes within (figure 3d) and between popu-
384 lations (figure 3c) increased to such an extent that there were no more population-wide revolutionary waves.
385

386 *Model 3 – Northern Hemisphere vs Southern Hemisphere*

387 When comparing the model outcomes for the Northern and the Southern Hemispheres we found very dif-
388 ferent patterns of theme sharing (summarised in figure 4). The Northern Hemisphere had slightly higher
389 levels of within population theme sharing than the Southern Hemisphere in the current year (TS_{FC} : NH 0.76,
390 SH 0.64; figure 4a). This difference between Hemispheres was far more pronounced in the level of within
391 population sharing with the previous year. The Southern Hemisphere had a much lower level of within
392 population sharing with the previous year (TS_{FP} : NH 0.44, SH 0.17; figure 4b). This resulted in a higher theme
393 turnover in the Southern Hemisphere (Turnover: NH 0.30, SH 0.45), suggesting more abrupt changes in
394 themes sung by the Southern Hemisphere populations. Moreover, Southern Hemisphere theme sharing was
395 more directional than in the Northern Hemisphere. In the Northern Hemisphere, theme sharing was similar
396 for eastern (TS_{EP}) and western neighbours (TS_{WP}) (TS_{EP} : 0.27; TS_{WP} : 0.28; figure 4c). In the Southern Hemi-
397 sphere, however, focal populations showed a higher level of sharing with western neighbours in the previ-
398 ous year (TS_{EP} : 0.17; TS_{WP} : 0.22; figure 4d). This difference in sharing with the eastern and western popula-
399 tions (figure 4e), resulted in revolutionary waves in 69 of the 1,000 simulations in the Southern Hemisphere
400 ($Diff\ TS_{WP}-TS_{EP} > |0.2|$), whereas in the Northern Hemisphere, only two simulations were found showing a
401 signature of revolutions.
402

403 4. Discussion

404
405 With simple song learning rules we have been able to replicate the patterns of cultural evolution of hump-
406 back whale song as found in the Southern Hemisphere. Here, we found that rare interactions between pop-
407 ulations combined with a song memory and a tendency to learn novel songs was sufficient to create patterns
408 of song evolution and revolutions. As long as learning was precise and population interactions were suffi-
409 ciently rare, the tendency to learn only novel songs, not present in the song memory, lead to the patterns of
410 song conformity within populations. We found that similar to the empirical data, the majority of our simu-
411 lations resulted in revolutions running in an eastward direction which was related to the size differences
412 among populations. When projecting into the future we found that there was a wide range of possible future
413 outcomes for patterns of song transmission, including both the persistence and disappearance of revolution-
414 ary waves. Moreover, with the same song learning parameters as the Southern Hemisphere whales, we
415 found mainly song evolution for the Northern Hemisphere, and that revolutions were extremely rare.
416

417 *Population interactions and direction of revolutions*

418 As previously observed in [58,59], our models confirm that the pattern of rare interactions between
419 populations during the non-breeding season is a key determinant as to whether or not song transmission
420 and revolutions occur. The direction of revolutions running west to east in the Southern Hemisphere popu-
421 lations, which were observed both in empirical studies as well as in our simulations as an emergent property
422 in our models, is likely to be a result of these rare interactions between populations in combination with the
423 size differences among the populations. Novel songs are more likely to spread from larger to smaller popu-
424 lations (as hypothesised in [7]), resulting in eastward revolutions for the populations in the South Pacific
425 where population sizes decrease from west to east. This is illustrated by the results from models 1a-c in
426 which the proportion of westward revolutions increased when the different populations were equal in size,
427 in particular shortly before and during the year that was sampled. In model 1, the population size of the
428 focal population automatically had an effect on the number of interactions with neighbouring populations.
429 However, in estimating interactions between neighbouring populations we took a conservative approach,
430 by not including the effects of the population sizes of the neighbouring populations on interaction probabil-
431 ities.
432

433 Our models identify the pattern of interaction between populations during the non-breeding season as being
434 a key determinant as to whether or not revolutions occur. In these models, however, interactions are simply

435 modelled as fixed probabilities, which is certainly an oversimplification. To move beyond this, the dynamic
436 relationship between an individual, its conspecifics and its environment could be captured using spatially
437 explicit agent-based models [59]. Furthermore, testing the collective effects of these individual spatial inter-
438 actions can be useful to provide increasingly realistic predictions. For example, this type of model has been
439 helpful to evaluate the effectiveness of conservation measures [68] as well as the impact of habitat degrada-
440 tion on individual fitness [69,70]. The modelling approach of [59] simulated both long range humpback
441 whale migratory movements and short-range interactions between conspecifics mediated by singing activ-
442 ity. An extension of this model, which includes song memory [57], is ideal to investigate the effects of pop-
443 ulation densities and individual movements on the occurrence of song revolutions between contiguous pop-
444 ulations.

445 446 *Continuation of revolutions through time*

447 When projecting into the future we found that there was a wide range of possible future outcomes for pat-
448 terns of song transmission, including both the persistence and disappearance of revolutionary waves. Rev-
449 olutions could emerge, starting a particular direction of song transmission, which would persist for a num-
450 ber of decades before the pattern disintegrated (figure 3a). The presence of cultural waves in some decades
451 and the absence in others are likely the result of stochasticity in the levels of between population interactions
452 in the model. Nevertheless, our results suggest that during a revolutionary period, song revolutions occur
453 throughout the Southern Hemisphere, as speculated in [23]. Further, it suggests we are in a current revolu-
454 tionary transmission time period in the Southern Hemisphere, as observed in empirical South Pacific song
455 data where multiple song types and thus revolutions have been horizontally transmitted eastward from the
456 east Australian population across the populations in the South Pacific, in a series of cultural waves spanning
457 a decade [7,44,52,53]. There is also a hint of directional transmission emerging around Africa [56]. Whether
458 these cultural dynamics persist into the future will depend on the interaction with population size, carrying
459 capacity and mixing. Overall, we hypothesise that once a revolution starts, it will continue to spread from
460 one population to the next, and this could occur in any of the Southern Hemisphere populations. In theory,
461 a full circumpolar transmission of a song type is possible, however further modelling using fine-scale spa-
462 tially explicit models including population density (as outlined above) may provide the key to understand-
463 ing whether song transmission from small to large population sizes is possible. Regardless, a Southern Hem-
464 isphere-wide comparison of empirical song data is timely given we are currently in a time period of revolu-
465 tionary dynamics.

466 467 *Difference between the Northern and Southern Hemispheres*

468 Geography matters. The Southern Hemisphere is modelled as a circumpolar ring of populations due to the
469 circumpolar feeding grounds around Antarctica [60], creating the potential for individuals to interact with
470 populations on both sides (eastern and western neighbour). Two aspects of this appear critical for the emer-
471 gence of revolutions: first, the lack of geographic barriers to movement between oceans, and second the
472 spacing out of populations so that interactions only occur between neighbouring populations. In contrast,
473 both oceans in the Northern Hemisphere are constrained by continents on east and west sides, creating no
474 contact between the two oceans. Moreover, within an ocean, land-masses funnel populations into a compar-
475 atively small area during the summer feeding season, allowing greater interaction between the multiple
476 populations that are distant during the breeding season. Together, these factors resulted in few song rev-
477 olutions emerging, high levels of song sharing among populations, and lower rates of turnover within popu-
478 lations. Humpback whales are vocal production learners – as a result of experience with signals (e.g., songs)
479 of other individuals, an individual modifies their own signal [22]. The only event to date that appears to
480 trigger a song revolution is the appearance in an ocean of a new song type that can be traced to come from
481 another [7,51]. Here we have shown song revolutions occurred in the Southern Hemisphere models but only
482 emerged in two (of 1,000) rare occasions in the Northern Hemisphere suggesting they are theoretically pos-
483 sible but highly unlikely. Simply put, without geographic barriers to whale movement song revolutions can
484 spread through many populations until the song evolves so much it is unrecognisable compared to the orig-
485 inal song. Without such fluid contact, as characterised by the Northern Hemisphere, new, novel song mate-
486 rial must evolve or be generated *de novo* within each population or ocean.

487 488 *General points to take away about models of cultural evolution*

489 Models can help clarify our understanding of evolutionary processes. In the case of cultural evolution, they
490 can connect individual processes of learning to cultural processes at the level of populations. Applying

491 techniques like ABC now allows one to fit complex computational models to empirical data, and draw sta-
492 tistical inferences from them too. In this case, we were able to draw conclusions about population sizes and
493 the geographic factors that promote revolutions, as discussed above. We were also able to make inferences
494 about the individual parameters that appear to underlie vocal learning in humpback whales. “All models
495 are wrong” [71], and in this case, refinements to our model might examine whether biases in learning (such
496 as conformist biases) lead to a better fit between model and data. In addition, since our model only considers
497 themes to be the same or different, we were only able to determine the upper limit to the mutation rate and
498 not a lower limit. Future models could overcome these limitations by also modelling the acoustic structure
499 of themes and how they are sequenced more explicitly to gain more informative predictions about mutation
500 rates and how novelty is introduced in whale songs. Nevertheless, we believe that this model is useful in
501 establishing that a simple mutation/drift model might be sufficient to accurately model learning in hump-
502 back whales and suggesting a range of mutation rates that are congruent with empirical patterns of diversity.
503

504 The humpback whale song transmission patterns, as found in the Southern Hemisphere, are unique
505 among non-human animals. While song cultural evolution and local dialects are widely documented in
506 birds [13,15,72,73], to our knowledge, no other species shows a dynamic in which a whole population rap-
507 idly and concertedly replaces their song for a different version. Some bird species such as the corn bunting
508 and the village indigobird show a similar pattern of concerted change among all males of a local song dia-
509 lect [12,72]. In corn buntings, from year to year, all males concertedly make changes to the details of their
510 local song dialect [12]. Although these song changes are evolutionary, unlike the humpback whales’ song
511 revolutions, similar processes may be driving the patterns of conformity in combination with rapid change
512 (see [23] for a recent review). In both species many questions remain, such as: Who or what is the source of
513 song variation? What is the role of sexual selection in the evolution of these learning processes? And how
514 do human induced changes, in for instance population size, affect the patterns of cultural evolution? Tak-
515 ing a comparative approach in studying these questions will increase the possibilities for experimental ap-
516 proaches and may greatly enhance our understanding of the processes underlying cultural evolution.
517

518 To conclude, here we have found that a low level of mutations in combination with rare interactions be-
519 tween neighbouring populations were sufficient to closely fit the pattern of song sharing in the South Pa-
520 cific, including the distinctive pattern of west-to-east revolutions. The direction of these revolutions was
521 consistent with the relative differences in population size. Moreover, we have shown that the same learn-
522 ing parameters that give rise to these revolutions in the Southern Hemisphere can give rise to the evolu-
523 tionary patterns of cultural evolution as found in the Northern Hemisphere. These results demonstrate the
524 potential of models of cultural evolution to make inferences about the processes underlying vocal learning
525 and cultural transmission. Future empirical work investigating fine-scale song transmission from small to
526 large population sizes in conjunction with extended modelling approaches including geographic distances
527 among populations are needed to further unravel the learning processes underlying this striking pattern of
528 cultural transmission.

529

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 542

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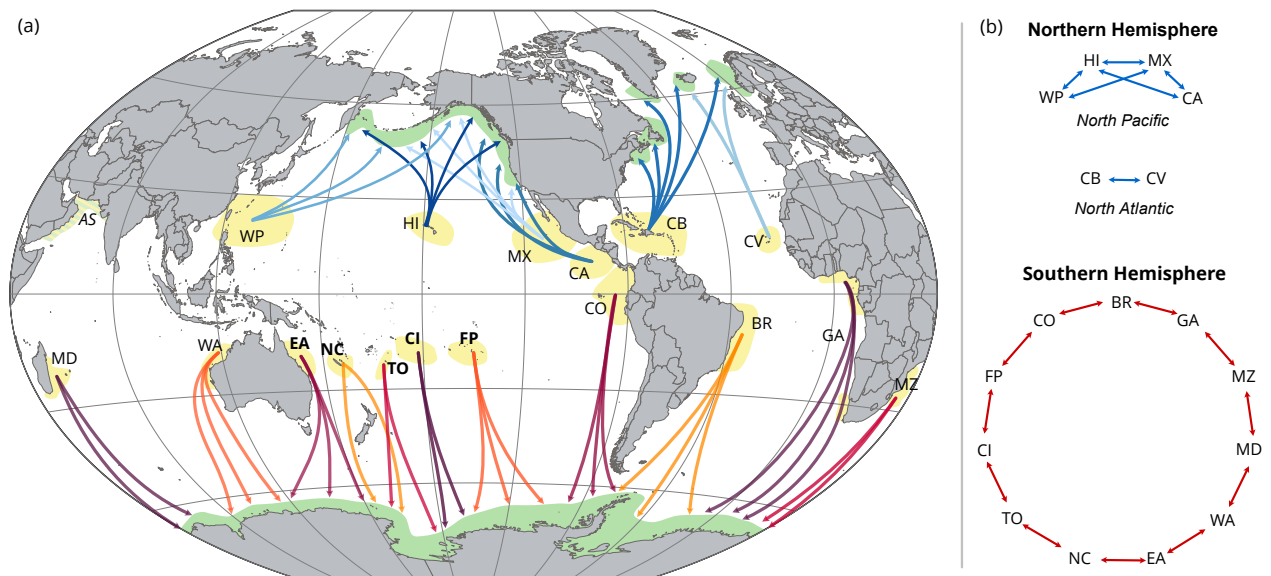
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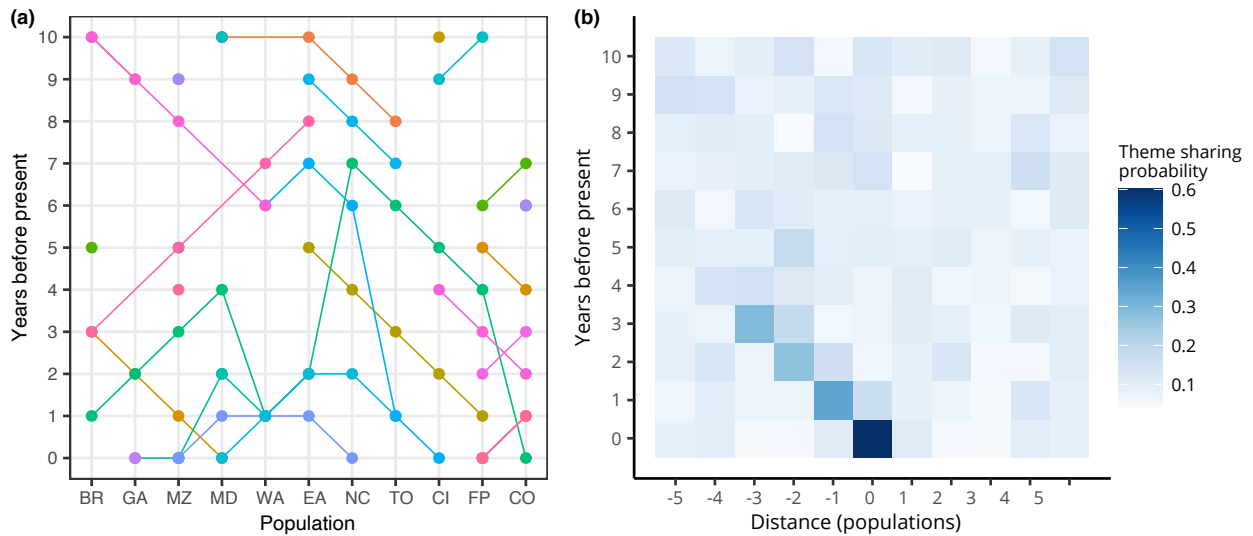
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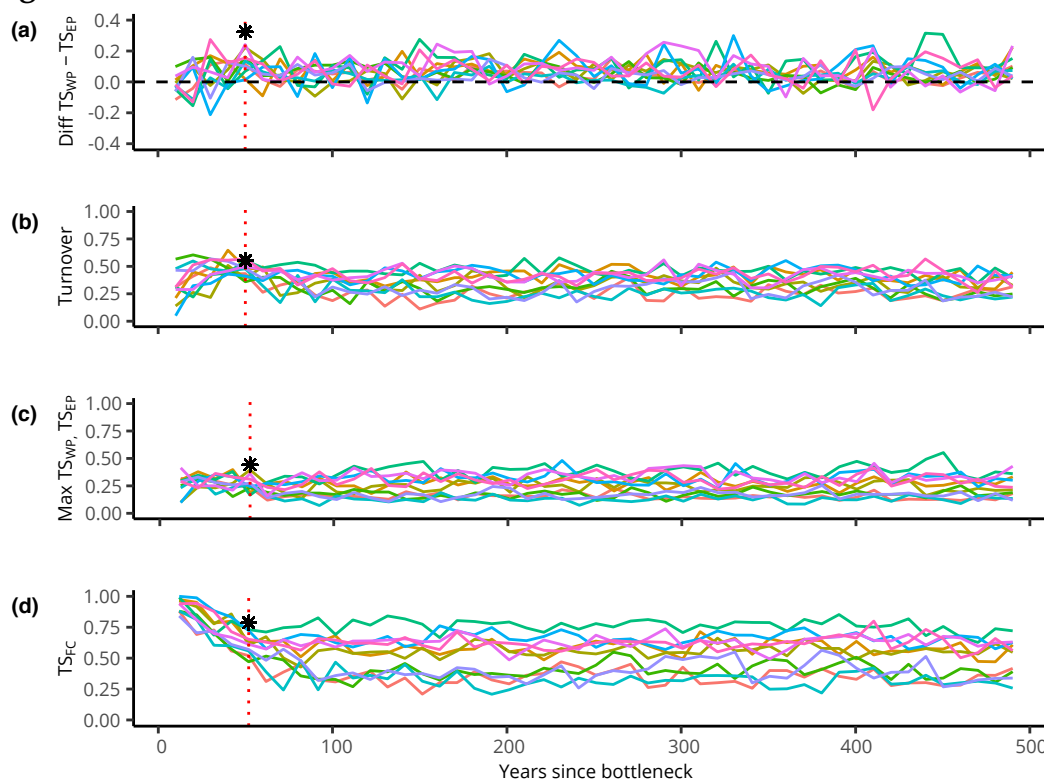
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1075 **Figure 1.** (a) World map showing suggested breeding and feeding areas of humpback whales [60,66,74].
 1076 Arrows indicate to which general feeding areas whales from the different breeding stocks migrate, with blue
 1077 shades representing the Northern Hemisphere populations and red shades indicating the Southern Hemi-
 1078 sphere populations (arrows are not intended to indicate exact migratory routes). It is highly unlikely that
 1079 whales from the Northern and Southern Hemisphere populations come into contact with each other, due to
 1080 the alternate seasons between the two Hemispheres (winter = low latitude breeding areas, summer = high
 1081 latitude breeding areas). Northern Hemisphere breeding populations: WP – West Pacific, HI – Hawaii, MX
 1082 – Mexico, CA – Central America, CB – Caribbean, CV – Cape Verde. AS - Arabian sea (non-migratory pop-
 1083 ulation, not included in model). Southern Hemisphere breeding populations: BR – Brazil, GA – Gabon and
 1084 West South Africa, MZ – Mozambique, MD – Madagascar, La Réunion, WA – West Australia, EA – East
 1085 Australia, NC – New Caledonia, TO – Tonga, CI – Cook Islands (possibly migratory), FP – French Polynesia,
 1086 CO – Colombia, Costa Rica, Panama, Ecuador. Populations from which the empirical data was collected are
 1087 indicated in bold. (b) Interaction patterns as implemented in the model. Arrows represent presence of inter-
 1088 actions. In the model the Southern Hemisphere populations were evenly spaced and connected only with
 1089 the neighbouring populations on either side. The Northern Hemisphere populations in the model were al-
 1090 lowed to interact with, depending on the population, all or almost all other populations within their respec-
 1091 tive oceans.



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 1098 **Figure 2.** Southern Hemisphere model theme sharing. (a) Theme trajectories in the different populations and
 1099 over the different years, with years before. Year 0 represents the last year in the simulation (or the current
 1100 year), and the 10 years before that. Different colours indicate different themes. (b) Theme sharing profile
 1101 with the focal population = 0, and the populations west (negative values) and east (positive values) of the
 1102 focal population. Y-axis represents the years before the last simulated year (current = 0 years before). Colour
 1103 intensity indicates the average probability of theme sharing between the focal population in the current year
 1104 and the population and year indicated by the x and y axes.
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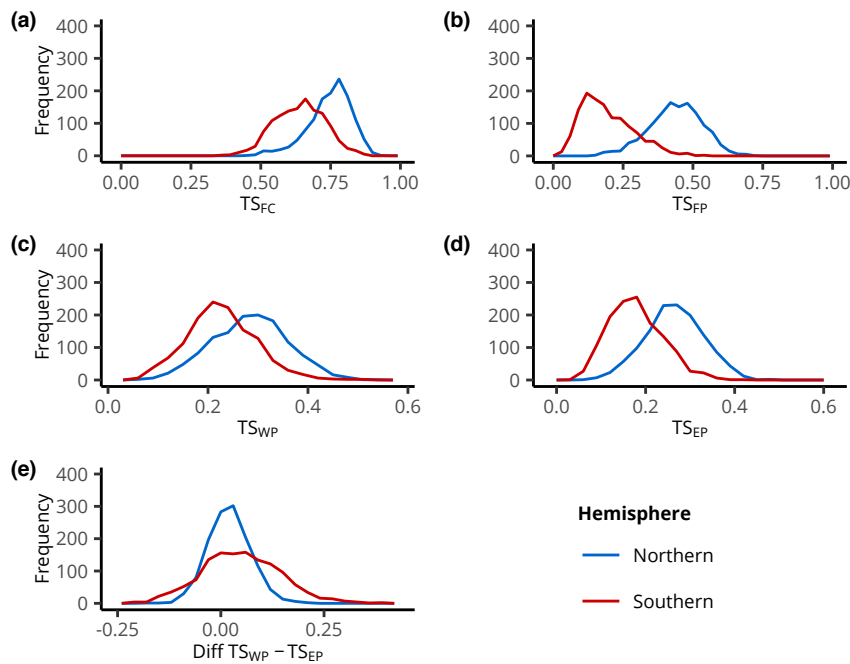
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1109 **Figure 3.** Southern Hemisphere model projecting cultural revolutions 500 years into the future, results from
 1110 10 simulation runs (each shown in a different colour). The red dotted line indicates 50 years after the bottle-
 1111 neck (2015) and the asterisk indicates the values for the empirical dataset. Statistics were sampled once every
 1112 10 years. (a) Difference in theme sharing with the focal population between the western and eastern neigh-
 1113 bouring population in the previous year ($Diff\ TS_{WP} - TS_{EP}$). Positive values indicate easterly transmission,
 1114 while negative values indicate westerly transmission. (b) Theme turnover. (c) Maximum theme sharing be-
 1115 tween the focal population and the neighbouring populations in the previous year ($Max\ TS_{WP}, TS_{EP}$). (d)
 1116 Within population theme sharing within year (TS_{FC}).

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 1121 **Figure 4.** Difference in theme sharing between the Northern and Southern Hemisphere populations. Each
 1122 panel shows the distribution of the different theme sharing statistics resulting from 1,000 simulations. (a)
 1123 Within population theme sharing (TS_{FC}). (b) Within population theme sharing in the previous year (TS_{FP}). (c,
 1124 d) Theme sharing with western and eastern neighbour, respectively, in the previous year (TS_{WP} and TS_{EP}).
 1125 (e) Difference in theme sharing with the focal population between the western and eastern neighbouring
 1126 population in the previous year ($Diff\ TS_{WP} - TS_{EP}$). Positive values indicate higher theme sharing with a west-
 1127 ern population, while negative values indicate higher theme sharing with an eastern population.
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Model		Description
1	Southern Hemisphere	Full model of song learning and cultural evolution in the 11 Southern Hemisphere (SH) populations with the associated population size estimates. Using ABC we obtained the posterior distribution of the model parameters by comparing the model outcomes with the empirical data. All other models use song learning parameters sampled from this posterior distribution.
1a-c	Population size and direction of revolutions	Exploring the effect of relative population sizes in the SH on the direction of revolutions by varying the different population size estimates:
	a) Rerun of SH: empirical population sizes	Due to stochasticity re-running the simulation with the same parameters doesn't always give the same results. We used the original population sizes N_{min} , $N_{i,2015}$ and $N_{i,K}$.
	b) Equal population sizes	To test the hypothesis that relative differences in population size determine the direction of the revolutions, we set the N_{min} , $N_{i,2015}$ and $N_{i,K}$ for all populations to the same values ($N_{min}=100$, $N_{i,2015}=1000$ and $N_{i,K}=5000$)
	c) Bottleneck: N_{min} empirical size, $N_{i,2015}$ and $N_{i,K}$ equal	To explore whether the bottleneck in population sizes affected the direction of the revolutions, we only set the $N_{i,2015}$ and $N_{i,K}$ to equal values, and kept the N_{min} the same as the empirical N_{min} .
2	Projecting cultural evolution into the future	To explore what would happen to the patterns of song evolution and revolution we reran model 1, but in this case let it run for a total of 500 years, while allowing the populations to reach carrying capacity.
3	Northern Hemisphere	To test whether the SH learning parameters would also lead to patterns of song transmission as found in the Northern Hemisphere (NH), we reran <i>Model 1</i> using the NH populations, their population sizes and patterns of interaction.