

A multilevel study of the demographic drivers of cultural evolution in bird song

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SUMMARY

Social learning within communities can lead to shared behavioural patterns that persist over time, which we know as culture. Examples of culture include bird and whale songs, cetacean feeding techniques, and avian and mammalian migratory routes. Shaped by neutral and selective forces, animal cultures evolve dynamically and form cultural traditions that vary greatly in their diversity and stability. These cultural traits can influence individual and group survival, population structure, and even inform conservation efforts, underscoring the importance of understanding how population processes interact with social learning to shape culture. Although the impact of social learning mechanisms and biases has been extensively explored, the role of demographic factors—such as population turnover, immigration, and age structure—on cultural evolution has received theoretical attention but rarely been subject to empirical investigation in natural populations. Doing so requires very complete trait sampling and detailed individual life history data, which are hard to acquire in combination. To this end, we compiled a multi-generational data set containing over 109,000 songs from >400 repertoires in a population of great tits (*Parus major*), trained a deep metric learning model to re-identify individuals and quantify song similarity, and fit spatially explicit regression models of cultural diversity and turnover at the individual and neighbourhood scales. We show that demographic variation within the small spatial scales at which learning takes place has the potential to impact the diversity and pace of change of animal vocal cultures. In particular, longer natal dispersal distances within the population reduce cultural diversity and uniqueness, while immigrant birds seem to acquire local song types rather than introducing new ones, but tend to have larger repertoires and so increase the absolute diversity of neighbourhoods. Birds of the same age tend to have more similar repertoires, and neighbourhoods comprising a mix of ages tend to have more cultural diversity. Individual turnover is the primary driver of cultural change. However, several factors slow this change: dispersal, a higher proportion of immigrant birds, and an older population. Our analyses support theoretical expectations regarding a key role of demographic processes in cultural evolution, while highlighting their interaction with species-specific factors such as the timing of song acquisition.

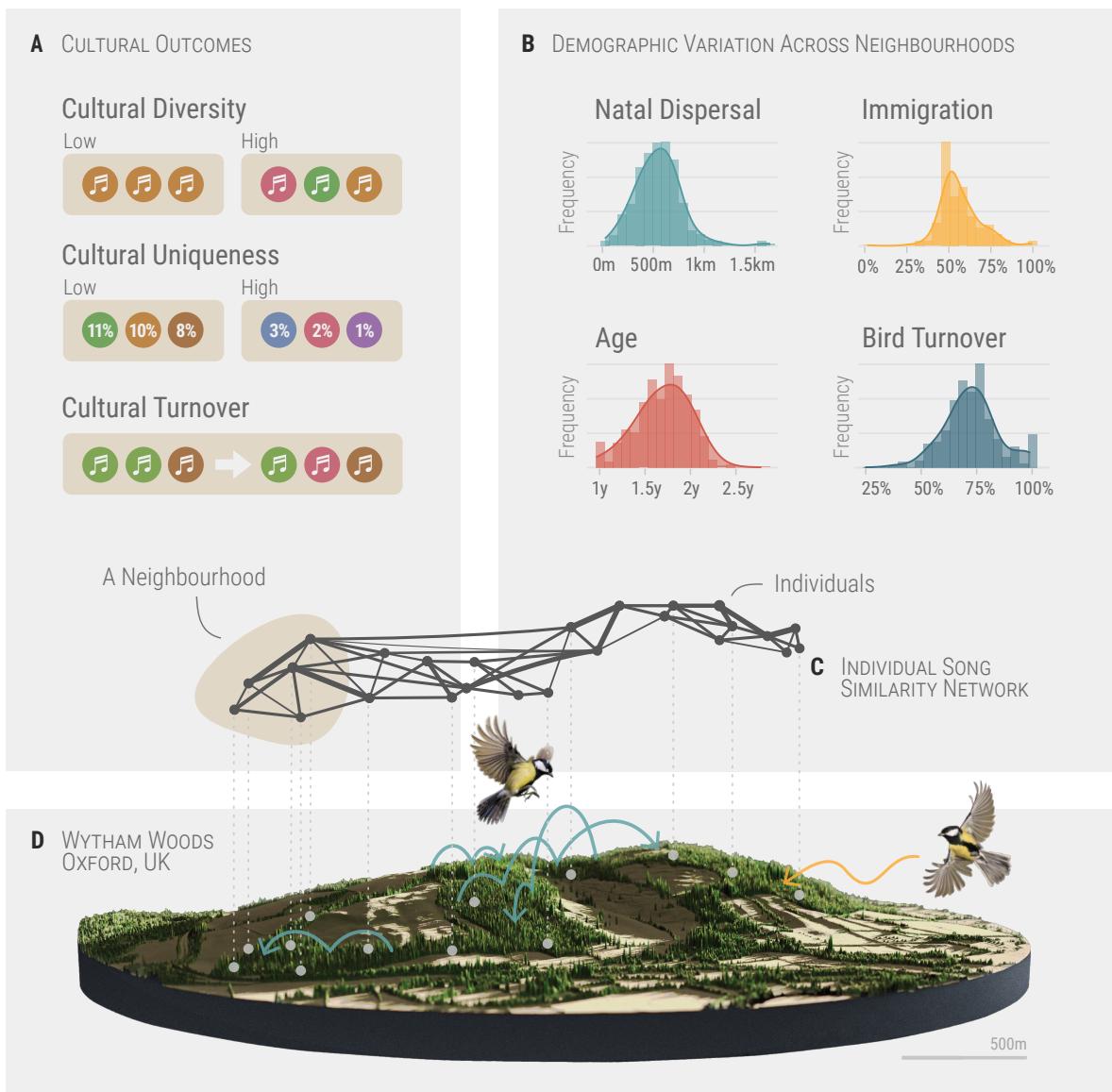
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RESULTS AND DISCUSSION

Some behavioural traits are shared and persist within communities due to social learning.¹ We refer to these behaviours as 'animal culture', exemplified by tool use in capuchin monkeys,² the learned songs of oscine birds,^{3–5} migration routes,^{6–8} and the feeding techniques of some cetaceans.^{9,10} Animal cultures are not static: neutral and selective mechanisms influence the frequency of cultural traits,^{5,11} leading to a process of cultural evolution. The resulting cultural traditions differ considerably in their diversity and stability,¹² determined by both learning biases and mechanisms and the demographic structure of populations.^{13,14}

While the role of social learning strategies and biases—frequency dependence, tutor biases, etc.—has been extensively studied,^{3,15–18} there exists a substantial gap in our understanding of how demography contributes to the emergence and persistence of distinct cultural traits within wild populations. Processes such as the recruitment of juveniles, immigration, emigration, mortality, and variation in age structure are likely to strongly affect an individual's opportunities for learning and exposure to different cultural variants, which has been amply emphasized by theoretical work.^{13,19–28} However, translating theoretical expectations into empirical evidence remains a challenge (see^{29–31} for exceptions).

Culture is increasingly recognized as both a fundamental aspect of many animals' lives and a valuable tool in monitoring and conservation efforts.^{34,35} Cultural traits play a role in the survival and reproduction of individuals and social groups; they reflect or even shape the structure of the population,³⁴ and can be lost when habitat fragmentation and population decline lead to reduced learning opportunities.^{36,37} A comprehensive understanding of cultural change and loss, then, requires that we have the ability to detect and study not just intrinsic factors—social, cultural, cognitive—but also extrinsic, ecological and demographic processes. This entails identifying the relevant spatial and temporal scales at which these processes manifest within natural

**Figure 1. Study system and main variables in our analysis.**

(A) Cultural variables measured at the neighbourhood level. Higher values of cultural diversity indicate that there are more distinct song types in the neighbourhood relative to the total song output. Higher cultural uniqueness indicates that the songs in the neighbourhood are on average less common in the population, and higher cultural turnover indicates that the neighbourhood's song repertoire has changed more from one year to the next. See [definitions](#) for full definitions.

(B) Variation in the demographic properties and composition of neighbourhoods across the population. See [demographic variables](#) for full definitions.

(C) Cartoon representation of the pairwise continuous repertoire similarity network used in our individual level analyses. Each node represents an individual bird, and the edges represent the similarity between their song repertoires. The network is based on the similarity of the songs produced by each bird during the dawn chorus, and is used to estimate the cultural similarity between individuals.

(D) 3D render of our study site, Wytham Woods, seen from the East. Image based on first return LiDAR data³² and made with rayshader.³³ Elevation is exaggerated. Aquamarine (darker) arrows represent natal dispersal within the population, and the yellow (lighter) arrow represents immigration into the population, two of the variables used in this work. Age and bird (individual) turnover are not depicted.

52 populations, as well as their relative importance.

53 To contribute to this goal, we built a comprehensive data set that spans three years and documents the dawn
 54 songs produced by male great tit birds during 454 breeding attempts in a single population located in Wytham
 55 Woods, UK. The population's marked variation in individual turnover, postnatal dispersal distances, age struc-
 56 ture, and immigration across space—known through ongoing long-term monitoring³⁸—allowed us to estimate
 57 their effects on song cultural repertoires at both individual and group levels. First, we assigned more than
 58 109,000 songs in 330 song repertoires to 242 individual birds through a combination of direct physical capture,
 59 radio frequency identification microchips, and a novel song-based re-identification method using a deep metric
 60 learning model. Then, we quantified individual and group-level traits and analysed variation in song cultural
 61 similarity, diversity, and turnover (see [definitions](#)) using network and spatially explicit Bayesian multilevel re-

62 gression models. See Figure 1 for a visual abstract of the study.

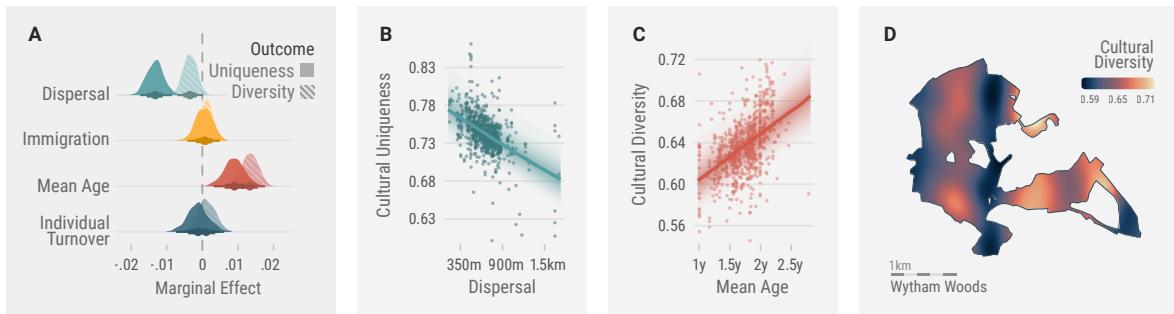


Figure 2. Influence of demographic variables on cultural diversity and uniqueness within neighbourhoods.

(A) Marginal effects at the mean of neighbourhood characteristics including mean dispersal distance, proportion of immigrant birds, average age, and individual turnover. See methods for full definitions. (B) Adjusted predictions and partial residuals of the effect of mean neighbourhood dispersal distance on cultural uniqueness. Low-dispersal neighbourhoods are those in which birds hatched in the same area. (C) Adjusted predictions and partial residuals of the effect of the mean age of the neighbourhood on cultural diversity. A neighbourhood with a mean age of 1 would be one where all birds are breeding for the first time. (D) The average distribution of cultural diversity in the population across space during the study period (2020–2022). This map captures the residual variation in cultural diversity after taking into account the demographic variables in (A). The map is based on a Gaussian process model with an exponentiated-quadratic kernel covariance function, which allows us to interpolate between the locations where we have data.

63 Our results reveal an interplay of demographics and song cultural dynamics that, albeit complex, largely
 64 matches theoretical expectations, as discussed below. This work also demonstrates that bird song, which already
 65 provides what is perhaps the largest body of evidence for cultural change in animals,³⁹ also has the potential to
 66 help us shed light on the impact of other population processes on animal cultures, owing to the fact that we can
 67 sample individual song repertoires with relative ease.

68 Reduced dispersal, higher immigration and and age associated with higher cultural diversity

69 Population genetics provides robust evidence supporting the notion that high dispersal rates facilitate gene
 70 flow, which, in turn, reduces the efficacy of selection and diversification. Conversely, low dispersal facilitates genetic differentiation through mechanisms such as mutation and drift, leading to allopatric population
 72 divergence.^{40–42} Were we to adhere to an analogy from genetics to culture, we would anticipate that reduced
 73 dispersal rates will decelerate the diffusion of cultural traits.²⁵ This, in turn, should result in the maintenance
 74 of distinct behavioural patterns within populations if learning is somewhat accurate, leading to a greater num-
 75 ber of cultural variants unique to a neighbourhood or region.^{43,44} Our analysis indeed indicates that neigh-
 76 bourhoods (see here more birds have remained in proximity to their natal areas harbour greater and more
 77 unique cultural diversity (*diversity*: $P(\beta_{disp(\bar{m})} < 0|D) = 1$, $mem = -0.018$, $CI_{95\%} [-0.023, -0.012]$; *unique-*
 78 *ness*: $P(\beta_{disp(\bar{m})} < 0|D) = 0.96$, $mem = -0.005$, $CI_{95\%} [-0.01, 0]$; Figure 2A&B, Table S3; see section), in line
 79 with prior research at a much coarser grain.³⁰

80 The analogy breaks down as soon as we consider the underlying individual-level mechanisms, however,
 81 due to complex interactions between the timing of dispersal and learning mechanisms that are specific to the
 82 cultural domain. Some species only learn songs from their parents and early in life, in a manner reminiscent
 83 of genetic inheritance, while others learn continuously from their neighbours, or only after dispersal (see⁴⁵ for
 84 an overview of different strategies). In the case of our study species, the great tit, these learning mechanisms
 85 are thought to involve selective retention or modification of songs encountered early in life, while they disperse,
 86 and up until before they begin breeding for the first time—a process that results in crystallized repertoires of 1
 87 to $\simeq 10$ different song types.^{46–48} In our individual-level analysis, we see that birds that dispersed over longer
 88 distances tend to have learned repertoires composed of songs that are more common within the population
 89 (*uniqueness*: $P(\beta_{disp(m)} < 0|D) = 1$, $mem = -0.2$, $CI_{95\%} [-0.3, -0.09]$; Figure 3B, Table S3), and possibly smaller
 90 repertoires as well (*rep.size*: $P(\beta_{disp(m)} < 0|D) = 0.91$, $mem = -0.2$, $CI_{95\%} [-0.44, 0.05]$; Figure 3B; Table S3). We
 91 hypothesize that birds with more extensive movements are more likely to sample and acquire a larger proportion
 92 of common cultural variants, simply because they are exposed to more songs across their learning period. This
 93 finds support in a spatially explicit simulation of song learning with dispersal, which shows this pattern would
 94 emerge under positively frequency-dependent learning or a process leading to similar acquisition curves (see
 95 Figure S10; note that we do not currently know which learning strategies are employed by great tits).

96 Building on our understanding of cultural dynamics in relation to dispersal we expect that, when song learn-
 97 ing is relatively precise and dispersal is limited, cultural differences between populations will accumulate, and
 98 immigration will introduce cultural novelty to the recipient population. However, the extent to which immigra-
 99 tion introduces new cultural variants also hinges on an interplay between the species' learning programme, the

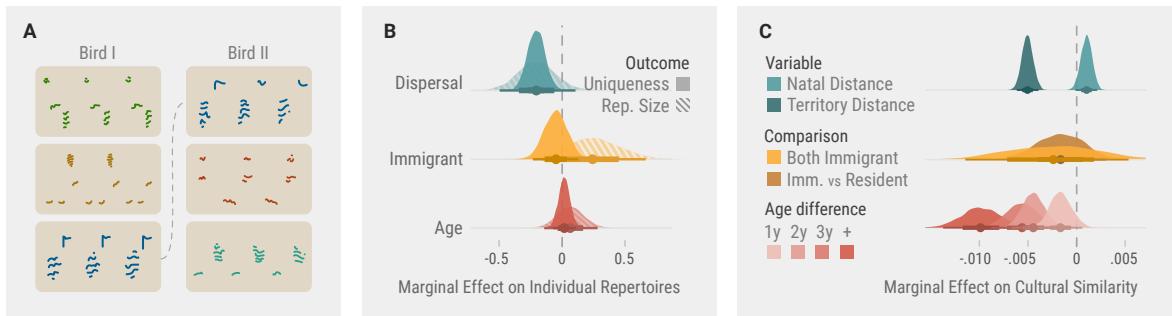


Figure 3. Individual and dyadic analysis of cultural diversity and similarity.

(A) Illustrative example showing the repertoires of two different birds in the population, with three songs in each, one of which is shared. Each sub-panel shows a cartoon spectrogram, with time in the horizontal axis and frequency in the vertical. Units not shown. (B) Marginal effects of dispersal, immigration status, and age on individual song repertoires, described in terms of their absolute size (the total number of distinct song types sung by that bird) and their uniqueness (how rare, on average, the song types are in the population within that year). (C) Marginal effects of dispersal, immigration status, and age on song repertoire similarity between individuals. Dispersal: Birds that are close neighbours are more culturally similar, regardless of where they hatched, whereas natal distance may have a weak positive effect on cultural similarity. Immigration: There is no strong evidence that birds that hatched outside the population are dissimilar from resident birds. Age difference: Birds are less culturally similar the greater the difference in their birth years, which evidences cultural change.

100 timing of dispersal, and the spatial movements of individuals. Animals that learn first and then disperse, for example, may bring cultural novelty with them. But this is not the case for great tits, whose young disperse in late summer and autumn, shortly after achieving independence, learn their songs until the end of their first winter,⁴⁷ and become chiefly sedentary as adults.^{49–51} In this species, then, we anticipate that immigrant birds will learn or retain songs they encounter upon arrival, either before or during the establishment of their territories.^{52,53}

105 Indeed, in our population, we find no evidence that the repertoires of birds originating from outside the population significantly differ acoustically from those of resident birds ($mem = -0.002$, $CI_{95\%} [-0.006, 0.002]$; Figure 106 3C). This, in conjunction with the observation that song repertoire similarity between individuals is predicted 107 by the distance between breeding territories ($mem = -0.005$, $CI_{95\%} [-0.006, -0.004]$; Figure 3C; Table S3), supports 108 the hypothesis that great tits are critical period learners that learn primarily from territorial neighbours 109 after dispersal.^{46,47}

110 However, immigrant birds, while not acoustically distinct, tend to have larger repertoires compared to their 111 resident counterparts (Figure 3B; $P(\beta_{imm.} > 0 | D) = 0.87$, $mem = 0.24$, $CI_{95\%} [-0.098, 0.593]$; Table S3). At the 112 group level, this small and uncertain effect amplifies, such that neighbourhoods with a higher proportion of 113 immigrant birds do not have increased cultural diversity relative to the total number of songs ($mem = 0.002$, 114 $CI_{95\%} [-0.004, 0.007]$; Figure 2A); but they do have a higher absolute cultural diversity—above what would be 115 expected based solely on the number of birds ($P(\beta_{imm.} > 0 | D) = 0.98$, $mem = 0.47$, $CI_{95\%} [0.1, 0.84]$; Figure S9, 116 Table S3).

117 Previous research⁵⁴ has revealed that most birds arriving from outside the population disperse over two 118 kilometres, significantly farther than the typical distances observed within the population (median for males 119 = 558 metres⁴⁹). This extended dispersal may have qualitative consequences for cultural diversity, through 120 a combination of factors: first, an initial exposure to songs from the source population; then, a heightened 121 pressure to adopt vocalisations similar to those of territorial neighbours to avoid any social or reproductive 122 costs associated with non-local signals, as seen in other species.^{55–59}

123 Finally, we find that individual turnover does not significantly affect cultural diversity or uniqueness, and we 124 uncover an association between age structure and cultural diversity and uniqueness. Individuals of the same 125 generation share the most similar song repertoires, and while age itself does not directly relate to changes in the 126 repertoires of individual birds (Figure 3B), the acoustic similarity between pairs of individuals decreases as the 127 age gap between them widens (Figure 3C; Table S3). This is expected in birds that cease to learn new songs as 128 they age, and has detectable consequences for neighbourhoods: those with a higher proportion of older 129 individuals have heightened levels of cultural diversity and uniqueness (Figure 2A&C, Figure S9). Conversely, in 130 areas where the majority of the population comprises younger birds surrounded by similar-aged peers, individual 131 birds tend to sing fewer song types, and those song types tend to be more common within the population 132 (diversity: $P(\beta_{age} < 0 | D) = 1$, $mem = 0.021$, $CI_{95\%} [0.014, 0.027]$; uniqueness: $P(\beta_{age} < 0 | D) = 0.99$, $mem = 133 0.012$, $CI_{95\%} [0.005, 0.019]$; Figure 2A&C, Table S3).

135 Demographic processes moderate the rate of cultural change at small spatio-temporal scales

136 We now shift our focus from static measures of cultural diversity to cultural turnover, examining how quickly 137 song types disappear from neighbourhoods and the consequences this has for their cultural makeup. The pri-

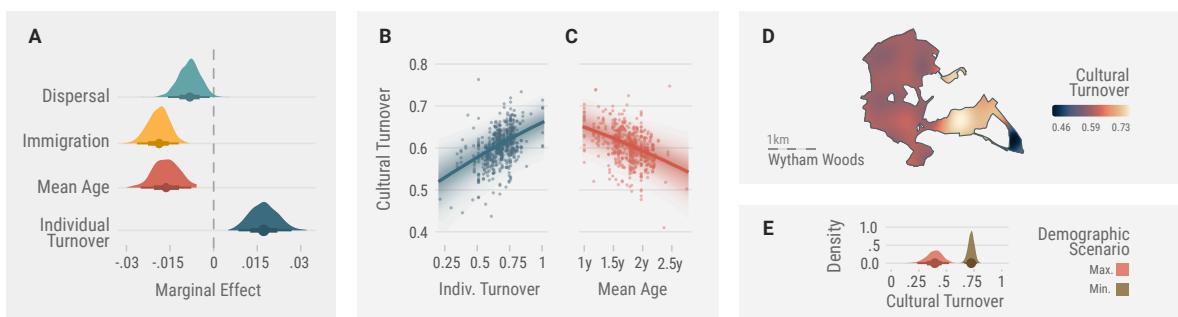


Figure 4. Influence of demographic variables on cultural turnover within neighbourhoods.

(A) Marginal effect at the means for mean dispersal distance, proportion of immigrant birds, average age, and individual turnover on the rate of cultural turnover within neighbourhoods (B and C) Adjusted predictions and partial residuals of the effects of the proportion of individual turnover on cultural turnover (B) and the effect of mean neighbourhood age on cultural turnover within neighbourhoods (C). (D) The population's average distribution of cultural turnover across space during the study period (2020–2022). (E) Posterior counterfactual predictions for two scenarios: all variables at their maximum (Max.) and minimum (Min.) observed values in the population, holding turnover constant at its mean value. Cultural turnover is expected to be over two times higher if neighbourhood dispersal, immigration and age are low, as they slow down cultural change.

mary driver of cultural turnover within neighbourhoods is individual turnover (total effect $mem = 0.072 CI_{95\%} [0.051, 0.093]$). When birds leave or die, many song types disappear with them and, as modelling suggests, the young birds that replace them might speed up the adoption of new song types.²⁷ Across the three-year study period, now considering the entire population, cultural turnover between consecutive years averages 0.45 (0.47 and 0.44; note that specific values are contingent on the granularity of song type definitions, see [manual categorization](#)). If all variants faced an equal chance of disappearing, this would quickly lead to complete cultural replacement. However, after a two-year gap (2020 – 2023), turnover only slightly increases to 0.59 (compared to an expected 0.7; estimating the variance around these figures would require longer-term data). We anticipate this rate to taper further over longer periods, as rare variants encounter greater stochasticity while common songs endure, likely placing a ceiling on the long-term rate of cultural turnover ([Figure S8A](#)). Indeed, some common song types documented over four decades ago persist within the population.^{46,52} This persistence might be due to different factors, like accurate learning based on song frequency, or strong tendencies to converge on certain song types.^{17,18,60,61}

After factoring in individual turnover, we examine how mean natal dispersal distance, the proportion of immigrant birds, and mean neighbourhood age affect cultural change within a neighbourhood. We find that higher levels of these factors correlate with slower cultural change ([Figure 4A](#); [Table S3](#)). Specifically, when individuals have dispersed over greater distances to get to their breeding neighbourhood, there is a high influx of immigrants, and the distribution of age is skewed towards older individuals, the model predicts slower cultural change, at less than half the rate compared to the converse scenario ($[0.66, 0.77] 0.39 CI_{95\%} [0.24, 0.51]$ vs. 0.72 $CI_{95\%}$, as illustrated in [Figure 4E](#)). This twofold difference in cultural turnover, based on realistic parameter values, is likely to significantly influence the cultural composition of neighbourhoods over time if it persists, highlighting the importance of the demographic structure of populations in also moderating the pace of cultural change.

The observed slowdown in cultural change due to dispersal and immigration aligns with our findings that dispersal homogenizes song repertoires and that immigrants tend to adopt the existing population's variants rather than introducing new ones (see [Figure 2A](#) and [Figure 3A](#)). At the same time, our estimate for the effect of neighbourhood age ($P(\beta_{age} < 0 | D) = 1$, $mem = -0.044, CI_{95\%} [-0.063, -0.026]$; [Figure 4C](#)) aligns with modelling work suggesting that learning from older individuals should slow down cultural change.²⁴ Indeed, age may serve as a brake on change, as older birds continue to sing song types that are becoming less frequent in the population, an idea supported by the observation that individual birds' repertoires are least similar when there is a large age difference ([Figure 3C](#)). The differences between the older and younger birds' repertoires also increases cultural diversity and uniqueness within neighbourhoods that include many older birds, as discussed above, suggesting an important role of age structure in shaping both cultural diversity and turnover.

Consequences for cultural structure, stability and diversity

Cultural traits, learnt bird song in this case, are shaped by many factors: some external, such as those discussed here, others intrinsic to learning and culture, and yet others that arise from selective processes driven by preference and function. Even within the confines of a relatively small population—Wytham Woods spans a mere four kilometres—we have been able to document associations between heterogeneity in the demographic composition of neighbourhoods and cultural outcomes using a large data set of song repertoires. These outcomes

177 are most likely driven by differences in individual learning and exposure to cultural variants. In particular, we
 178 find that dispersal within the population reduces cultural diversity and uniqueness. Birds that hatched outside
 179 the population seem to adopt existing song types rather than introduce new ones, but tend to have larger repertoires and so increase the absolute diversity of neighbourhoods. Birds of the same age tend to share similar song
 180 types, while neighbourhoods comprising both older and younger birds are more likely to have a broader array
 181 of song types. Additionally, such neighbourhoods are more likely to host a greater number of birds singing rare
 182 song types, perhaps because, as we also find, older-age neighbourhoods have slower cultural turnover. The
 183 main driver of cultural turnover is individual turnover, while longer postnatal dispersal distances, a higher
 184 proportion of immigrant birds, and an older population slow it down.

185 Our study explores how demographic processes influence cultural diversity and the pace of cultural change
 186 on small spatial and temporal scales. We show that these factors can significantly shape cultural dynamics
 187 within a wild bird population, though their effect on long-term cultural diversification and stability remains
 188 uncertain. Both empirical studies and modeling efforts on cultural dynamics should consider the population's
 189 demographic characteristics and their variability across time and space, as these factors determine individuals'
 190 exposure to cultural variants and learning opportunities, ultimately affecting emergent group-level cultural
 191 dynamics.

193 METHODS

194 Resource availability

195 The complete Wytham great tit song data set is available in osf.io/n8ac9, and documented [here](#). The main
 196 repository with code and data to reproduce the analysis and figures in this article can be found at [birdsong-](#)
 197 [demography](#).

198 Data collection

199 Study system and fieldwork

200 Great tits are small, short-lived birds—average lifespan: 1.9 years—that sing acoustically simple yet highly diverse songs. Each male great tit has a repertoire of one to over 10 song types, also referred to as syllable types,
 201 which are repeated multiple times in short bursts separated by longer periods of silence. Although detailed
 202 studies on how individual great tits learn their songs are limited, existing evidence suggests several key points.
 203 First, it appears that great tits do not learn their song repertoires from their fathers.⁴⁶ Instead, their song development is influenced by the songs they encounter during their early life until they establish a territory and breed
 204 for the first time. We do not currently know how precisely great tits learn songs, or how social interactions affect
 205 the process. At 10–11 months of age, before their first breeding season begins, vocal learning culminates in a
 206 final crystallised song repertoire that remains relatively stable afterward⁴⁷—a process known as critical period
 207 learning.^{62,63} Additionally, while there is evidence that birds can continue to learn to recognize new songs later
 208 in life (that is, learning for discrimination, as opposed to learning for production), this ability seems to be limited
 209 compared to their early learning experiences.⁶⁴ Furthermore, females are able to individually recognize males
 210 based on their songs⁶⁵ and, even across a large population, individual song renditions can accurately indicate
 211 the identity of the bird producing them.⁴⁸

212 During the breeding season, from March to June, great tit pairs are socially monogamous and defend territories around their nests.⁶⁶ In Wytham Woods, Oxfordshire, UK ($51^{\circ}46'N, 1^{\circ}20'W$), a population of these birds
 213 has been the focus of a long-term study since 1947.³⁸ Wytham Woods is a semi-natural, predominantly deciduous and partly discontinuous woodland that spans an area of approximately 385 hectares and is surrounded
 214 by farmland. Most great tits in this population breed in nest boxes with known locations, and the majority of
 215 individuals are marked with a unique British Trust for Ornithology (BTO) metal leg ring as either nestlings or
 216 adults. The birds were not provided with supplementary sources of food during the study.

217 We collected data from late March to mid-May during the 2020, 2021, and 2022 breeding seasons. Every year,
 218 fieldworkers checked each of the 1018 nest boxes at least once a week before and during the egg-laying period,
 219 which typically lasts from one to 14 days,⁶⁷ and recorded the identities of breeding males and females, the
 220 dates of clutch initiation and egg hatching, clutch size, and fledgling number and condition under standardized
 221 protocols. We found the first egg date by assuming that one egg is laid every day and counting back the number
 222 of eggs present on the day of observation. In cases where we did not observe the chicks on their day of hatching,
 223 the hatching date was determined by assessing the weight of the heaviest chicks and extrapolating their age
 224 from established growth curves.^{68,69}

225 Nest box occupancy and breeding density vary across the study area, with some areas having a higher density
 226 of nest boxes and a higher proportion of occupied boxes, which we account for in some of our analyses as
 227 described in the sections below. In the years of our study, 261, 289 and 278 nest boxes were occupied by pairs

232 of great tits, with 173, 184 and 184 that led to successful breeding attempts where at least one chick fledged. See
 233 [Figure S1](#) for a map of the study site and sampling locations.

234 To record the vocalisations of male great tits we took advantage of their behaviour during the reproductive
 235 period, when they engage in continuous singing near their nests at dawn before and during egg laying.⁷⁰ Col-
 236 lectively, this vocal display is referred to as the dawn chorus, and has been demonstrated to yield a reliable
 237 estimation of the song repertoire of individuals when recorded in full.^{71,72} As soon as we suspected that a pair
 238 of great tits were using a nest box—based on nest lining materials, egg size if present, or other signs of activity—
 239 we deployed an autonomous sound recorder nearby. The microphone faced upwards and slightly away from
 240 the nest box, aligning with the nest box entrance hole's direction. The birds sang near the recorder: although we
 241 did not gather data on the singer's location, our anecdotal observations were in line with a different population
 242 where the average distance to the nest box while singing was 10 metres.⁷³

243 This approach is supported by previous studies on great tit dawn song,^{52,74–77} as well as our observations
 244 that: (a) recordings from consecutive days contain renditions of the same song types clearly sung by a single
 245 individual cycling through its repertoire, (b) performances of the same song types across different days can be
 246 assigned to a single individual by our deep metric learning model (see [deep metric learning model training](#)), and
 247 (c) when we recapture the same bird in a different field season (often in the same location due to high adult site
 248 fidelity), we can easily match its songs to the ones on record, which would not happen if we were misattributing
 249 songs to individuals. To further ensure that we were recording the correct birds, we discarded recordings with
 250 more than one vocalizing bird unless one was distinctly louder than the others during the segmentation process.
 251 Additionally, we excluded all songs with a maximum amplitude below -16 dB, calculated as $20 \log_{10} \left(\frac{A}{A_0} \right)$, with
 252 $A = 5000$ and $A_0 = 32767$ (the maximum value for 16-bit digital audio). This threshold was established based
 253 on observations showing that an amplitude cutoff greater than 4000 unambiguously differentiated the focal
 254 bird from its closest neighbours when simultaneous recordings from nearby spatial locations captured multiple
 255 birds. It is important to note that these values are not calibrated and are relative to our recording equipment and
 256 settings, as well as other factors like sound directionality and vegetation cover. Although variation in sound
 257 amplitude due to distance and direction of the singer could affect which songs were recorded clearly enough to
 258 analyse, we did not observe any systematic bias that might have resulted in low signal-to-noise ratios causing
 259 exclusion of song types.

260 Our recording efforts captured song repertoires from birds belonging to approximately half of all breeding
 261 attempts [Figure S2](#), including both successful and unsuccessful attempts, as well as individuals with and without
 262 linked data. This song sampling density, while high for this kind of field study, could theoretically result in
 263 some rare song types being undersampled—particularly if rare song types are primarily sung by unsuccessful
 264 or late-breeding individuals—but we have no evidence suggesting that this is the case. A related potential issue
 265 is that birds that sing more frequently might be more likely to be recorded, but as these individuals are also
 266 the primary contributors to the local song pool due to their higher song output, we are confident that our data
 267 provides a representative sample of the song repertoire of the breeding population in each area. Importantly,
 268 the birds that we recorded are representative of the neighbourhood's composition in terms of breeding density,
 269 dispersal distances, contribution of immigration, and age distribution (see [Figure S2](#)).

270 For this study, we calculated postnatal dispersal distance as the straight line distance from the natal site to
 271 the breeding site. The dispersal distances of birds classed as immigrants (not ringed as chicks in the population)
 272 are not known, but most are thought to come from other populations at least 1 km, and likely more than 2.5
 273 km, away.^{54,78} We determined age based on the year of hatching for birds hatched in the population and using
 274 plumage characteristics for immigrants, which are most often caught as yearlings (76%)—allowing us to age
 275 them accurately.⁷⁹

276 All work involving birds was subject to review by the University of Oxford, Department of Zoology, Animal
 277 Welfare and Ethical Review Board (approval number: APA/1/5/ZOO/NASPA/ Sheldon/TitBreedingEcology).
 278 Data collection adhered to local guidelines for the use of animals in research and all birds were caught, tagged,
 279 and ringed by BTO licence holders (NMR's licence: C/6904).

280 ***Recording equipment and schedule***

281 We used 60 (30 in 2020) AudioMoth automated recorders,⁸⁰ which were housed in custom-built waterproof
 282 enclosures. Recording began approximately one hour before sunrise (05:36 – 04:00 UTC during the recording
 283 period) and consisted of seven consecutive 60-minute-long recordings with a sample rate of 48 kHz and a depth
 284 of 16-bit. To sample as many birds as possible, we left each recorder at the same location for at least three
 285 consecutive days before moving it to a different nest box. We relocated 20 recorders (10 in 2020) every day
 286 throughout the recording period.

287 **Data processing and annotation**

288 We processed and annotated the song recordings, 109,963 in total, from 299 repertoires belonging to 242 known
 289 birds, using custom software and scripts written in Python 3⁸¹ and the open source package `pykanto`.⁸² These
 290 are available from github.com/nilomr/great-tit-hits-setup.⁸³ Our annotated data set and a detailed description
 291 of the process can be found in Merino Recalde et al.⁴⁸ Below we provide a narrative summary of the subsequent
 292 characterisation of song similarity and song types.

293 **Characterizing repertoire similarity**

294 Our analyses require i) a measure of the acoustic similarity between any two birds for the individual-level analy-
 295 ses, and ii) a way to identify categorical song types for the neighbourhood analyses. The underlying assumption
 296 is that two song repertoires will be more similar if one bird has learned his repertoire at least in part from the
 297 other, or if they have both learnt from other individuals who are themselves similar due to intergenerational cul-
 298 tural descent. There is no single optimal solution for this problem, both due to technical challenges and because
 299 we do not know enough about song perception and learning mechanisms in this species. There are three main
 300 possible approaches, each with its own advantages and disadvantages, which we describe below.

301 ***Continuous similarity (individual-level analyses)***

302 Traditional methods used to compare bird vocalisations include visual inspection of spectrograms and mea-
 303 surement of hand-picked acoustic features. However, these approaches have limitations in dealing with noise
 304 and variations in performance, and can be extremely time-consuming. So, instead, we adopted a data-driven
 305 approach by training a Vision Transformer (ViT) model for feature extraction in a metric learning task on spectro-
 306 gram representations of great tit songs. Our goal was to create a similarity space based on inherent variation in
 307 the data, using categorical labels of song types sung by individual birds, which we know to be perceptually and
 308 behaviourally significant.⁶⁵ Further details, data, and code to reproduce this process are available at⁸² and;⁴⁸ we
 309 include a summary here.

310 We optimized model performance using Triplet loss, a loss function that ensures the projection of a positive
 311 sample (belonging to the same class as the anchor point) is closer to the anchor's projection than that of a
 312 negative sample (belonging to a different class) by a specified margin.^{84,85} During training, we mined hard
 313 triplets—where the negative sample is closer to the anchor than the positive—and used the Adam optimizer
 314 with a fixed learning rate of 1×10^{-5} .

315 To prevent the model from overfitting to irrelevant features within localized portions of the training data or
 316 learning background noise, we applied various data augmentation techniques during model training.^{86–88} These
 317 included random cropping in the time domain, dropping out parts of the spectrogram, adding Gaussian and
 318 multiplicative noise, equalization, sharpening, changes to brightness and contrast, blurring, and slight shifting
 319 in both time and frequency domains. This leads to a more robust model that can generalize better and is not
 320 influenced by differences in background noise.

321 Finally, we used the resulting model to calculate feature vectors for each song in the data set (109,963 samples
 322 \times 384 dimensions), which serve as compressed representations that can be used to compare them. Great tits
 323 have variable repertoire sizes and there is no evidence that they learn them en bloc.^{46,89} Therefore, the simplest
 324 continuous measure (an average Euclidean distance between all pairs of songs) would mask any signatures of
 325 learning if the average repertoire similarity is similar across the population, and does not take into account the
 326 asymmetry in total repertoire size. To improve on this, we defined repertoire similarity as the average minimum
 327 Euclidean distance (AMED), given by

$$\text{AMED} = \frac{1}{|A|} \sum_{a \in A} \min_{b \in B} |a - b|_2 \quad (1)$$

328 where we compared each song feature vector a in set A with all song feature vectors b in set B and computed
 329 their Euclidean distance $|a - b|_2$. We then retained the minimum distance for each element in set A and obtained
 330 the AMED by averaging these minimum distances over all elements in set A . The main advantage of this ap-
 331 proach is that it allows us to avoid imposing discrete population-wide song categories. We used the continuous
 332 similarity approach for all individual-level analyses in this paper.

333 ***Automated clustering (first step for neighbourhood analyses)***

334 If song learning is categorical and not very precise in terms of fine song structure, the continuous similarity
 335 method could underestimate or fail to detect similarities between repertoires. In addition, our neighbourood-
 336 level analyses require that we define discrete cultural units (population-wide song types). To do this, we first
 337 calculated the distances between all songs in the data set using the feature vectors obtained from the ViT model,
 338 as described above. Then we used UPGMA hierarchical clustering and dynamic tree-cut techniques to assign

339 the syllables to distinct types (since songs consist of repeated syllables, syllable and song types are synonymous
 340 in this species). We allowed a minimum cluster size of 1 to ensure the representation of rare song types. The use-
 341 fulness of this method depends on the global properties of the embedding space derived from the [continuous](#)
 342 [similarity](#) process. In a low-dimensional space where linear distances effectively capture meaningful variation,
 343 creating clusters by cutting the hierarchical tree at different heights yields varying cluster counts while maintain-
 344 ing meaningful groupings. However, in a high-dimensional space where global distances are not meaningful,
 345 only relatively small clusters of nearby points remain interpretable. This is the case with our data set and em-
 346 bedding space: we find that the method reliably groups song renditions by the same bird across different years,
 347 alone or together with other birds with highly similar songs, yet consistently splits songs that are similar by hu-
 348 man (and perhaps great tit⁹⁰) standards, ultimately leading to a very large number of clusters (the most stable
 349 clustering solutions were close to the total number of different individual song types, >1000). Due to these issues,
 350 we did not directly use song types defined by automated hierarchical clustering, but performed an additional
 351 manual categorization step.

352 **Manual categorization (second step for neighbourhood analyses)**

353 With over 100,000 songs, our data set is very large and would have been impossible to label entirely manually
 354 as is common in the field. Instead, we used the output of the automated clustering process described above,
 355 consisting of 1920 labelled song clusters assigned to 422 larger clusters of highly similar songs (making the prob-
 356 lem 57 times smaller), which we reviewed manually using the criteria followed by McGregor and Krebs^{46,91,92}
 357 and subsequent work.^{30,90,93,94} This process is both inevitable and partly subjective. However, despite its clear
 358 problems, human perceptual judgments might be our best available substitute for those of the birds for some
 359 tasks (but see recent work by Morfi et al.⁹⁵ and Zandberg et al.⁹⁶). Indeed, across fields, advanced classification
 360 algorithms are routinely evaluated against ground truth created by humans, and this is also the case in bird song
 361 research.

362 Following common practice in the field, we statistically validated our resulting 335 manually assigned labels
 363 to evaluate whether they represented quantitatively robust clusters. To do this, we retrained the ResNet50-based
 364 classifier described in Merino Recalde⁸² on a random subset of labelled song spectrograms data and obtained
 365 an accuracy of 0.87 on the validation set (see other metrics in the repository). For comparison, an equivalent
 366 process by Fayet et al.³⁰ was able to reach 0.71 accuracy for 374 songs. We further explored the result by creating
 367 a hierarchical clustering diagram (dendrogram) based on how often the model mistakenly classified one song
 368 type as another during evaluation. We then reviewed the song classes that weren't clearly distinguished by the
 369 model. Following Fayet et al.³⁰ (2014), this led us to combine seven poorly differentiated classes into two more
 370 distinct categories. With the caveats already mentioned, this means that our classification following McGregor
 371 and Krebs⁴⁶ is successful at finding song type clusters that reduce intraclass variation.

372 Most of the great tits in our population sing some variation of the well-known 'tea-cher, tea-cher' song. These
 373 are harder to assign to discrete classes than rarer songs with more complex structures, a problem that is not
 374 restricted to our data set: regions of the acoustic space with more data are harder to cluster because they often
 375 contain more variation and overlap, making it difficult for algorithms (or humans) to find clear boundaries. As
 376 mentioned in the main body of the article, the consequence of this for any analysis is that the absolute estimates
 377 of cultural turnover depend on the granularity of this clustering process. Were we to lump most 'tea-cher'
 378 songs together, as McGregor and Krebs⁴⁶ do, the estimates of turnover would become lower—but, crucially,
 379 any relative differences across time or space remain the same. Indeed, precisely quantifying turnover using
 380 categorical metrics might be altogether impossible in some species, because song categories are not likely to be
 381 natural kinds beyond the scale of interacting neighbours.

382 See [Figure S4](#) for examples of song types defined in this study. The exact code used to perform this song type
 383 validation process, along with the figures generated during it, can be found in [the main narrative notebook](#) and
 384 a dedicated repository.

385 **Re-identifying individuals from their songs**

386 In some cases, we failed to capture birds or identify them using PIT (Passive Integrated Transponder) tags, as
 387 tags sometimes malfunction, birds can be difficult to catch, or may have disappeared before their chicks were
 388 old enough for us to attempt capture at the next box. We were able to match an additional 31 song repertoires
 389 belonging to this subset of birds with existing individual IDs by using the deep metric learning model (ViT)
 390 described earlier to recognize individual songs. This increased the number of identified repertoires from 299 to
 391 330, belonging to the same 242 unique birds. We summarise the process here, but see also⁴⁸ for details on model
 392 design and training.

393 Briefly, we calculated pairwise song distances using the feature vectors obtained from a vision transformer
 394 on a metric learning task. This model achieved a mean average precision at 5 (mAP5) of 0.98 and a cumulative

395 matching characteristic at 1 (CMC1) of 0.98, which roughly means that in 98% of the queries made to the similar-
 396 ity space (on a held-out test data set of known songs) the candidate bird and song type returned by the model
 397 were correct. Given that the model was trained on almost 2000 classes, this means that there is enough indi-
 398 vidual information contained in each song type to distinguish between birds with very high confidence: even
 399 though many have likely copied tutor songs that were also in the data set, this model could still tell them apart.

400 We used the calculated song distances to determine if two song repertoires came from the same bird, even
 401 when the bird wasn't physically identified more than once. We set very conservative criteria for this: at least
 402 two songs in the repertoires had to be more similar than the 0.025 quantile of the distance distribution for songs
 403 from known different birds, or (distance score of 0.9), and the bird must be within 100 meters of the reference
 404 bird. When we applied the metric learning model to songs from the entire population, which increases the risk
 405 of false positives, we found that the percentage of wrongly assigned birds in our ground truth data (birds that
 406 we have physically re-identified across years) was 0.3%, or 34 out of 11,359 unique comparisons if we only used
 407 the acoustic distance criterion—further reduced to 0.04%, or 4 out of 11359, when we also added the spatial
 408 constraint (see [Figure S7](#) for a graphic explanation).

409 Quantification and statistical analysis

410 Modelling pairwise similarity and individual repertoires

411 It is common for analysis of song similarity to fit simple linear regression models using all pairwise comparisons
 412 in a population. However, this leads to very strong pseudo-replication and, therefore, an increased chance of
 413 Type I errors. To avoid this, we treated our song similarity data as a fully connected network and built Bayesian
 414 multilevel models with a multi-membership structure and the pairwise AMED described above as the response
 415 variable. The full model specifications can be found in the [main repository](#) for this project; also see a summary
 416 in [Table S2](#) and variable descriptions in [Table S1](#).

417 **Individual repertoires** We first modelled individual repertoire size using Poisson and negative binomial models,
 418 but this led to poor performance as assessed through posterior predictive checks (both underestimation of mean
 419 values and either under or over-estimation of very low repertoire sizes). Instead, we built continuation ratio
 420 models, a type of sequential ordinal model where reaching a particular level (number of song types in the reper-
 421toire) requires first reaching all lower levels.^{97,98} rep_{m_1} , $rep_{m_{1,1}}$, and $rep_{m_{1,2}}$ estimate the association between immi-
 422 grant status, distance dispersed, age, and repertoire size. Three further log-normal models, $repnov_{m_1}$, $repnov_{m_{1,1}}$,
 423 $repnov_{m_{1,2}}$, do the same for the average cultural uniqueness of individual repertoires, defined as one minus the
 424 mean of the relative frequencies of each song type present in the repertoire.

425 **Pairwise similarity** Our first model ($disp_{m_1}$) explored the interaction between natal distance, that is, the distance
 426 between the nests where two resident birds hatched, and the distance between the centre of their breeding
 427 territories, adjusting for year and absolute age difference. We do not have direct information on how long
 428 birds have spent around one another, so instead we estimated the effect of the interaction of the distance at
 429 which they hatched and the distance at which they subsequently breed: If both are small, they will have had
 430 more opportunities for interaction and learning. We extracted predictions for the interaction and calculated
 431 marginal effects at minimum distances, to answer the questions 'How does cultural similarity change with
 432 distance for birds that hatch nearby' and 'Does how close a bird hatched matter for birds that end up holding
 433 neighbouring territories'. We used a similar model structure (age_{m_1}) to estimate the marginal effects of the
 434 absolute age difference, this time adjusting for the natal and territorial distance between birds. Then, to study
 435 the effect of immigration, we fit a model (imm_{m_1}) with the possible combinations of immigration status (both
 436 immigrant, both residents, one of each) and adjusted for age difference and territorial distance.

437 Modelling group-level outcomes

438 **Defining neighbourhoods and their demographic properties** Song turnover, diversity, and uniqueness are group-level
 439 properties. However, our study lacks naturally occurring distinct subpopulations that we can use as units for
 440 analysis. Rather than partitioning the population using a discrete polygonal grid or non-overlapping areas, we
 441 opted to model neighbourhoods continuously across space, defining a radius of 200 m around each of 549 nest
 442 boxes that were occupied at least once during the study,³⁰ which we then sampled across the duration of the
 443 study. This radius is necessarily arbitrary but strikes a good compromise between capturing the relevant spa-
 444 tial scale at which vocal interactions occur, which extends up to around 180 metres,^{99,100} and maintaining an
 445 adequate sample size in areas of low density (neighbourhood sizes range from 7 to 60, mean 30.3 ± 14.9). Impor-
 446 ntantly, neighbourhoods defined in this way are highly non-independent, so we modelled both this methodolog-
 447 ical spatial dependence and other sources of complex spatial autocorrelation intrinsic to the study site (such as
 448 edges, nest box density, etc.) by including a 2D Gaussian process (GP), which estimates a length-scale parameter
 449 defining a variance-covariance matrix for the spatial locations based on their distance.^{101–103} We confirmed that

450 this eliminated the residual spatial autocorrelation via Moran's I tests. Note that we fitted a separate GP for
 451 each year, as treating the spatial dependence as fixed across the study duration, as is often done, risks further
 452 underestimating uncertainty.

453 We defined our predictor variables in the following way:

- 454 • Individual turnover is the proportion of birds that were not present in a neighbourhood during the pre-
 455 ceding year.
- 456 • Dispersal is the mean of the distances, in metres, that birds in the neighbourhood travelled to get from
 457 their natal territories to their current territories if they were hatched within the Wytham population.
- 458 • Immigration is the proportion of birds that were not ringed as nestlings in the population, and
- 459 • Neighbourhood age is the mean age of the birds within it.

460 Figure S2 illustrates that our sampling process did not introduce bias into any of these predictor variables: the
 461 birds from which we recorded song repertoires were, on average, representative of the true neighbourhood
 462 composition. Figure S3 shows the distribution of the 'raw' variables across the study site.

463 **Operational definitions of cultural diversity, uniqueness, and turnover** In this paper we use simple descriptions of
 464 cultural diversity, cultural uniqueness, and cultural turnover that intuitively capture relevant aspects of the
 465 collective song repertoires of neighbourhoods in relation to the rest of the population. We defined our outcome
 466 variables in the following way:

- 467 • Relative cultural diversity ('diversity'): the ratio of distinct song types recorded in a neighbourhood to the
 468 total number of songs recorded in that neighbourhood. Higher values indicate that there are more distinct
 469 song types in the neighbourhood relative to the total song output.
- 470 • Absolute cultural diversity: the number of distinct song types recorded in a neighbourhood. Higher values
 471 indicate that there are more distinct song types in the neighbourhood.
- 472 • Uniqueness index: the complement of the logarithm of the mean population-wide frequency of the song
 473 types present in a neighbourhood. Higher values indicate that the songs in the neighbourhood are on
 474 average less common in the population.
- 475 • Cultural turnover: the proportion of distinct song types recorded in a neighbourhood that were not present
 476 in the previous year. Higher values indicate that the neighbourhood's song repertoire has changed more
 477 from one year to the next.

478 In this way, 'diversity' describes the relative proportion of distinct songs in a neighbourhood, and 'unique-
 479 ness' refers to how uncommon, on average, the songs of the birds in a neighbourhood are. These two ways of
 480 characterizing cultural diversity are (as expected) anti-correlated in our study site due to the effect of sampling:
 481 more frequent songs are sampled more readily, causing larger sample sizes—neighbourhoods with more density
 482 and therefore songs—to yield lower average estimates of diversity and higher average estimates of uniqueness,
 483 in a nonlinear manner. Once this is adjusted for, which we did by including a GAM term capturing the nonlinear
 484 effect of the sample size, diversity and uniqueness are positively correlated, as expected (see Figure S5; models
 485 nov_{m_2} and $nov_{m_2,1}$; spatial distribution of these variables in Figure S6). All the relevant models adjusted for these
 486 effects of neighbourhood density and sampling.

487 **Models** To study the effect of dispersal and immigration on local cultural diversity and uniqueness, we built
 488 log-normal models (div_{m_1} , nov_{m_1}) and estimated the marginal effects of the proportion of immigrants, mean
 489 dispersal distance, and mean neighbourhood age, while also adjusting for individual turnover, year, and spatial
 490 dependence. Lastly, to examine whether the effects of immigration and dispersal on cultural diversity were
 491 related to individual differences in repertoire size and uniqueness, we fit two further models predicting the
 492 absolute number of distinct song types in a neighbourhood while also adjusting for the number of birds (div_{m_2})
 493 and the number of songs ($div_{m_2,1}$).

494 The rate of song cultural turnover was the response variable in two models: one ($turn_{m_1}$) trying to estimate the
 495 total effect of turnover and a second ($turn_{m_2}$) estimating the marginal effects of the proportion of immigrants,
 496 mean dispersal distance, and mean age while also adjusting for individual turnover, year, and spatial depen-
 497 dence. In both cases, we modelled the response distribution as a truncated log-normal with a hurdle (logistic)
 498 part to account for the zeroes.

499 **Model estimates and reporting**

500 We built the models and approximated the posterior distributions of the parameters of interest using brms,¹⁰⁴
 501 an interface to the Hamiltonian Monte Carlo engine Stan.¹⁰⁵ We then processed the posterior distributions with
 502 the help of the marginaleffects package.¹⁰⁶ We checked model convergence via the effective number of samples,
 503 visual inspection of the chain trace plots, and the Gelman-Rubin diagnostic. Estimation in a Bayesian framework

504 returns a posterior distribution of possible values instead of point estimates. By convention, we report posterior
 505 central estimates (means or medians) and their 95% credible intervals. Note that categorical predictors are
 506 dummy-coded and continuous predictors z-score transformed. Estimates in the text and tables are calculated
 507 as the posterior probability under a hypothesis (e.g., that a parameter estimate is greater than 0) against its
 508 alternative. Our figures include plots containing the posterior distributions of the marginal effect at the mean
 509 of each variable of interest. Regression plots show predicted values of the mean and their credible intervals, as
 510 well as partial residuals adjusted to the means or other relevant values of the explanatory terms included in the
 511 model.^{107,108} We have tried to build reasonable models, but even then our estimates should not be interpreted
 512 causally. Figure S11 shows posterior predictive checks for all models in the study. See the software section
 513 at the end for a complete list of libraries used in the various analyses and the code repository for full model
 514 specifications.

515 Software

516 Song processing and analyses were carried out using pykanto⁸² and rely on the following open-source scientific
 517 libraries or tools: numpy,¹⁰⁹ scipy,¹¹⁰ pandas,¹¹¹ numba,¹¹² pytorch,¹¹³ torchvision,¹¹⁴ pytorch lightning,¹¹⁵
 518 tqdm,¹¹⁶ ray,¹¹⁷ soundfile,¹¹⁸ umap,¹¹⁹ joblib,¹²⁰ hdbSCAN,¹²¹ seaborn,¹²² scikit-image,¹²³ librosa,¹²⁴ bokeh,¹²⁵
 519 ujson,¹²⁶ psutil,¹²⁷ attrs.¹²⁸ We also used R version 4.2.1¹²⁹ and the following R packages: bayesplot,^{130,131}
 520 box,¹³² brms,^{104,133} ClustGeo,¹³⁴ colorspace,¹³⁵ config,¹³⁶ devtools,¹³⁷ DHARMa,¹³⁸ fs,¹³⁹ ggdist,¹⁴⁰ ggraph,¹⁴¹
 521 httpgd,¹⁴² igraph,^{143,144} insight,¹⁴⁵ kableExtra,¹⁴⁶ languageserver,¹⁴⁷ marginaleffects,¹⁰⁶ modelsummary,¹⁴⁸
 522 patchwork,¹⁴⁹ progress,¹⁵⁰ renv,¹⁵¹ rprojroot,¹⁵² scales,¹⁵³ scico,¹⁵⁴ sf,^{155,156} svglite,¹⁵⁷ terra,¹⁵⁸ tidygraph,¹⁵⁹
 523 tidyverse,¹⁶⁰ viridis.¹⁶¹ See the code repositories for specific versions of these libraries.

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529 AUTHOR CONTRIBUTIONS

530 **Nilo Merino Recalde:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation,
 531 Writing - Original Draft, Writing - Review & Editing, Visualization. **Andrea Estandía:** Investigation, Data
 532 Curation, Writing - Review & Editing. **Sara C. Keen:** Writing – Review & Editing. **Ella F. Cole:** Supervision,
 533 Project Administration. **Ben C. Sheldon:** Supervision, Project Administration, Writing – Review & Editing,
 534 Funding Acquisition.

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871 SUPPLEMENTARY INFORMATION

Table S1. Model variable key

Variable	Description
repertoire_size	Number of distinct song types sung by an individual
immigrant	Immigrant status (hatched in the population / not hatched in the population)
sampling_effort	Total number of recordings obtained for this individual
year	Year in which the repertoire was recorded
father	ID of the male; BTO (British Trust for Ornithology) ring number
dispersal_distance	Postnatal dispersal distance, in metres, from the natal nest box to the breeding nest box
age	The age of the bird. This is exact if the bird was ringed as a pullus in the population, or approximate (based on plumage moult) otherwise
average_frequency	The mean of the frequency of each song in a bird's repertoire in a given year
mean_dist1	Average minimum Euclidean distance between the repertoires of two birds
natal_distance	Distance in metres at which two birds were born
nest_distance	Distance in metres at which two birds bred
year_born_diff	The absolute difference between the birth years of two birds
mm(...)	Multi-membership grouping term for the similarity network
resident_status	Origin of a pair of birds: both, one or neither were hatched in the population
prop_immigrant	Proportion of the birds in a neighbourhood that were not hatched inside the population
mean_dispersal_distance	Mean postnatal dispersal distance, in metres, of the birds in the neighbourhood
prop_same_birds	Proportion of the birds in a neighbourhood that were already there the year before
mean_age	Mean age of the birds in a neighbourhood
diversity	The ratio of distinct song types recorded in a neighbourhood to the total number of songs recorded in that neighbourhood
n_current_songs	Absolute number of songs in a neighbourhood, where each different song types is counted as many times as it appears. This variable correlates with neighbourhood size, and we use to more precisely adjust for the fact that some birds sing more song types
gp(x, y)	2D Gaussian process to model spatial dependency in the data
n_unique_current_songs	Number of distinct song types within a neighbourhood in a year, counting each different song type only once
uniqueness	Quantified as one minus the logarithm of the mean population-wide frequency of the songs in the repertoire of either a bird or an entire neighbourhood within a given year
recorded	Number of birds recorded singing in a neighbourhood, which is linearly correlated with neighbourhood size
prop_shared	Proportion of the song types in a neighbourhood that were already present. Reported as 1-prop_shared: 'song turnover'

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Table S2. Model information

Model	Formula	Family	N	Groups
Individual Repertoires				
rep_m_1	repertoire_size ~ 1 + immigrant + s(sampling_effort) + year + (1 father)	cratio	301	242
rep_m_1.1	repertoire_size ~ 1 + dispersal_distance + s(sampling_effort) + year + (1 father)	cratio	133	105

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Table S2. Model information (Continued)

Model	Formula	Family	N	Groups
rep_m_1.2	repertoire_size ~ 1 + age + s(sampling_effort) + year + (1 father)	cratio	256	205
repnov_m_1	average_frequency ~ 1 + immigrant + s(sampling_effort) + year + (1 father)	lognormal	300	242
repnov_m_1.1	average_frequency ~ 1 + dispersal_distance + s(sampling_effort) + year + (1 father)	lognormal	133	105
repnov_m_1.2	average_frequency ~ 1 + age + s(sampling_effort) + year + (1 father)	lognormal	256	205
Cultural Similarity				
disp_m_1	mean_dist1 ~ 0 + natal_distance + nest_distance + year_born_diff + year + (1 mm(father, father2))	Gaussian	8745	105
imm_m_1	mean_dist1 ~ 0 + resident_status + year_born_diff + nest_distance + year + (1 mm(father, father2))	Gaussian	11029	205
age_m_1	mean_dist1 ~ 0 + natal_distance + nest_distance + year_born_diff + year + (1 mm(father, father2))	Gaussian	8745	105
Cultural Novelty and Diversity				
nov_m_1	uniqueness ~ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(n_current_songs) + year + gp(x, y, by = year)	lognormal	791	GP
div_m_1	diversity ~ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(n_current_songs) + year + gp(x, y, by = year)	lognormal	791	GP
nov_m_2	uniqueness ~ 0 + diversity + s(n_current_songs) + year + gp(x, y, by = year)	lognormal	791	GP
nov_m_2.1	uniqueness ~ 0 + diversity + year + gp(x, y, by = year)	lognormal	791	GP
div_m_2	n_unique_current_songs ~ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(recorded) + year + gp(x, y, by = year)	Gaussian	791	GP
div_m_2.1	n_unique_current_songs ~ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(n_current_songs) + year + gp(x, y, by = year)	Gaussian	791	GP
Cultural Turnover				
turn_m_1	prop_shared ~ 0 + prop_same_birds + year + gp(x, y, by = year, k = 25, c = 5/4)	hurdle lognormal	544	GP
turn_m_2	prop_shared ~ 0 + prop_immigrant + mean_dispersal_distance + mean_age + prop_same_birds + year + gp(x, y, by = year, k = 25, c = 5/4)	hurdle lognormal	544	GP

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Table S3. Model estimates

Model	Hypothesis	Estimate ^a	Evid. Ratio	Post. Prob
Individual Repertoires				
rep_m_1	immigrant > 0	0.239 [-0.098, 0.593]	6.963	0.874
rep_m_1.1	dispersal distance < 0	-0.201 [-0.443, 0.045]	10.111	0.910
rep_m_1.2	age > 0	0.064 [-0.108, 0.241]	2.701	0.730
repnov_m_1	non-immigrant < 0	-0.049 [-0.2, 0.1]	2.401	0.706
repnov_m_1.1	dispersal distance > 0	0.203 [0.088, 0.316]	741.857	0.999
repnov_m_1.2	age > 0	-0.017 [-0.093, 0.058]	0.540	0.351

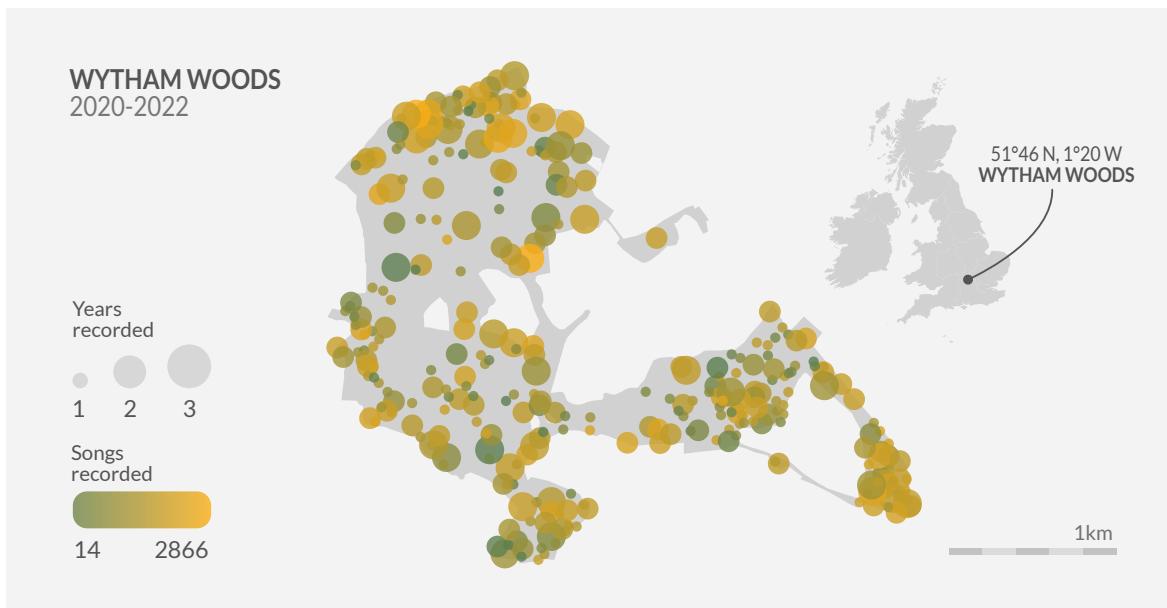
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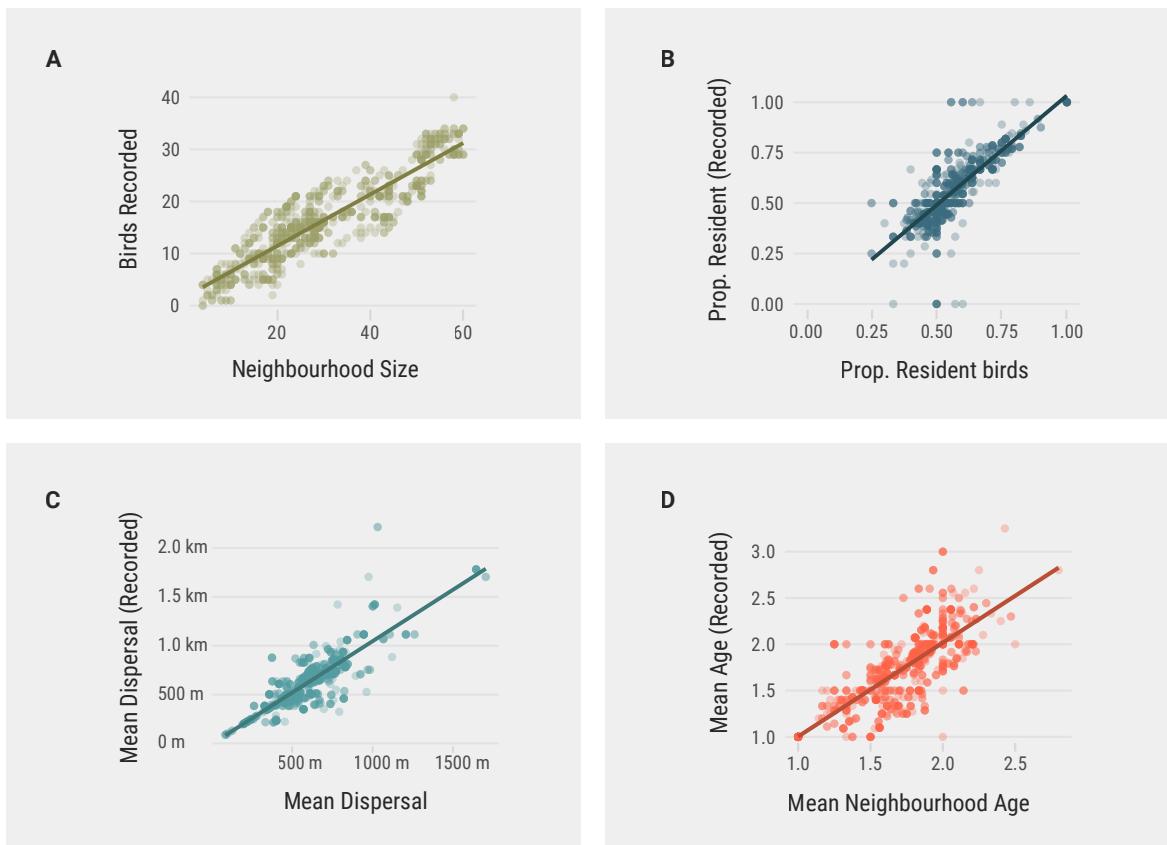
Table S3. Model estimates (Continued)

Model	Hypothesis	Estimate ^a	Evid. Ratio	Post. Prob
Cultural Similarity				
disp_m_1	natal distance > 0	0.001 [0, 0.002]	22.529	0.958
disp_m_1	nest distance > 0	-0.005 [-0.006, -0.004]	Inf	1
imm_m_1	both resident-both immigrant < 0	0.002 [-0.005, 0.01]	0.438	0.304
imm_m_1	both resident-one immigrant < 0	0.002 [-0.002, 0.006]	0.331	0.248
age_m_1	age difference 0-1 > 0	0.002 [0, 0.003]	12.289	0.925
age_m_1	age difference 0-2 > 0	0.004 [0.002, 0.006]	Inf	1
age_m_1	age difference 0-3 > 0	0.006 [0.003, 0.008]	1999	1
age_m_1	age difference 0-4+ > 0	0.01 [0.006, 0.013]	Inf	1
Cultural Novelty and Diversity				
nov_m_1	mean dispersal distance < 0	-0.018 [-0.023, -0.012]	Inf	1
nov_m_1	proportion immigrant < 0	0.001 [-0.005, 0.006]	0.752	0.429
nov_m_1	mean age < 0	0.012 [0.005, 0.019]	399	0.998
nov_m_1	individual turnover < 0	0.001 [-0.005, 0.008]	1.733	0.634
div_m_1	mean dispersal distance < 0	-0.005 [-0.01, 0]	26.65	0.964
div_m_1	proportion immigrant < 0	0.002 [-0.004, 0.007]	0.442	0.306
div_m_1	mean age < 0	0.021 [0.014, 0.027]	Inf	1
div_m_1	individual turnover < 0	-0.002 [-0.008, 0.005]	0.446	0.309
nov_m_2	diversity > 0	0.713 [0.629, 0.795]	Inf	1
nov_m_2.1	diversity > 0	-0.099 [-0.216, 0.018]	0.086	0.080
div_m_2	mean dispersal distance < 0	-0.658 [-0.999, -0.315]	570.429	0.998
div_m_2	proportion immigrant < 0	0.469 [0.1, 0.837]	62.492	0.984
div_m_2	mean age < 0	1.045 [0.576, 1.495]	Inf	1
div_m_2	individual turnover < 0	0.204 [-0.291, 0.683]	3.077	0.755
div_m_2.1	mean dispersal distance < 0	0.019 [-0.213, 0.249]	0.824	0.452
div_m_2.1	proportion immigrant < 0	0.072 [-0.168, 0.312]	2.259	0.693
div_m_2.1	mean age < 0	0.928 [0.599, 1.245]	Inf	1
div_m_2.1	individual turnover < 0	-0.031 [-0.349, 0.279]	0.726	0.421
Cultural Turnover				
turn_m_1	individual turnover > 0	0.072 [0.054, 0.09]	Inf	1
turn_m_2	mean dispersal distance < 0	-0.022 [-0.039, -0.006]	79	0.988
turn_m_2	proportion immigrant < 0	-0.051 [-0.065, -0.037]	Inf	1
turn_m_2	mean age < 0	-0.044 [-0.063, -0.026]	3999	1
turn_m_2	individual turnover < 0	0.047 [0.028, 0.066]	Inf	1

878 ^a Estimates are Medians and 95% Credible Intervals

**Figure S1. Map of the study site and sampling locations.**

This study was conducted in Wytham Woods, a 385-hectare semi-natural woodland surrounded by farmland. Data was collected during the breeding seasons of 2020, 2021, and 2022 by regularly checking 1018 nest boxes, documenting information such as breeding pair identities, clutch initiation and hatching dates, clutch size, and fledgling details according to standardized protocols, and recording the songs of the birds in the population using 60 AudioMoth acoustic logger. Each dot on the map shows the locations of a nest box where we recorded song repertoires.

**Figure S2. Demographic characteristics of recorded birds compared to those of all birds in the neighbourhood.**

Comparison between the actual neighbourhood properties and neighbourhood properties estimated from birds for which we have song recordings. (A) Neighbourhood size (number of individuals) and number of individuals for which we have song recordings in that same neighbourhood. (B) Proportion of resident birds calculated from monitoring data and only from those birds with song recordings. Residents are birds that were ringed as nestlings in the population. (C) Mean dispersal distance of the birds in a neighbourhood calculated from monitoring data and only from birds with song recordings. (D) Mean age of birds in a neighbourhood calculated from monitoring data and only from birds with song recordings.

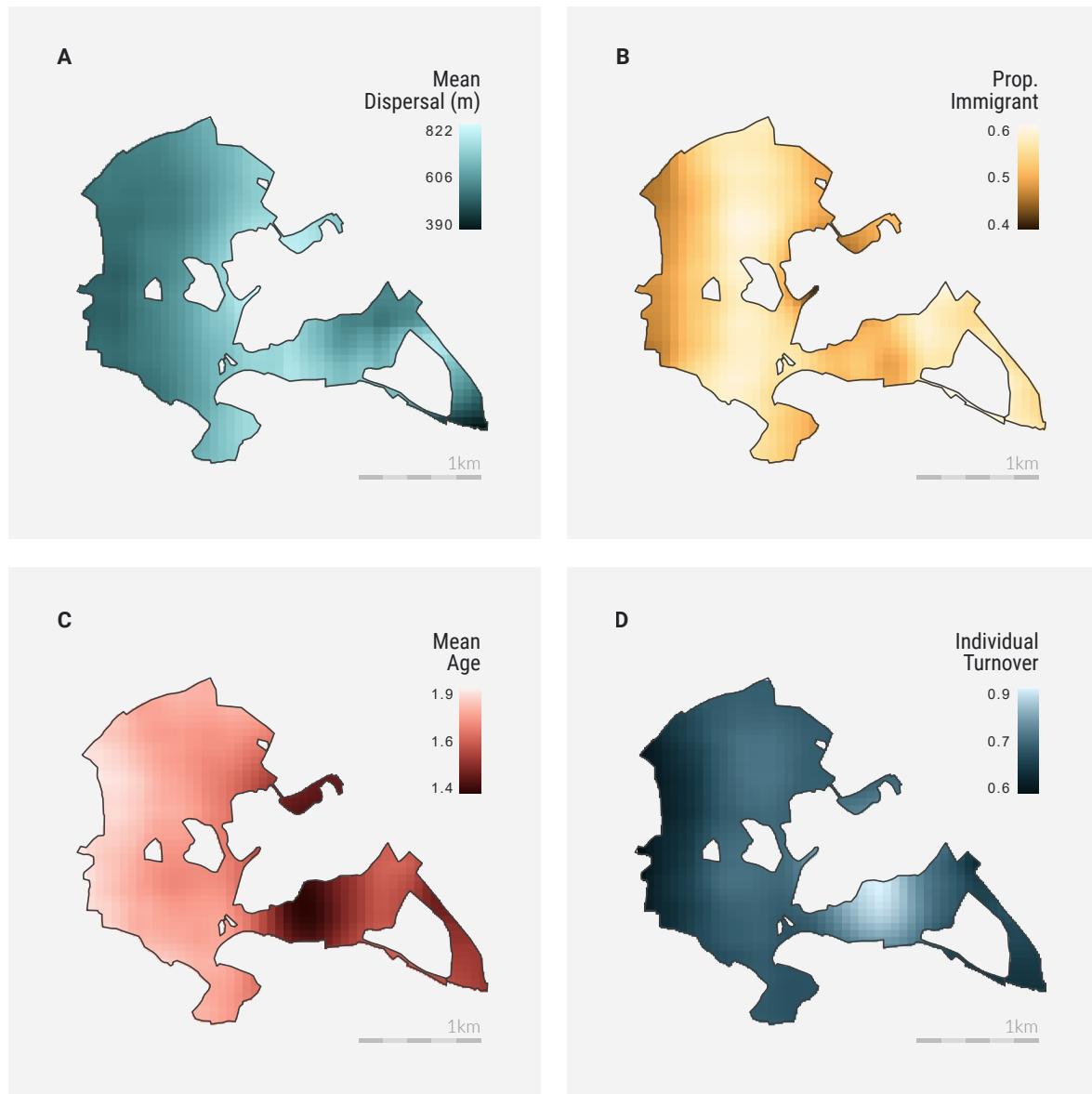
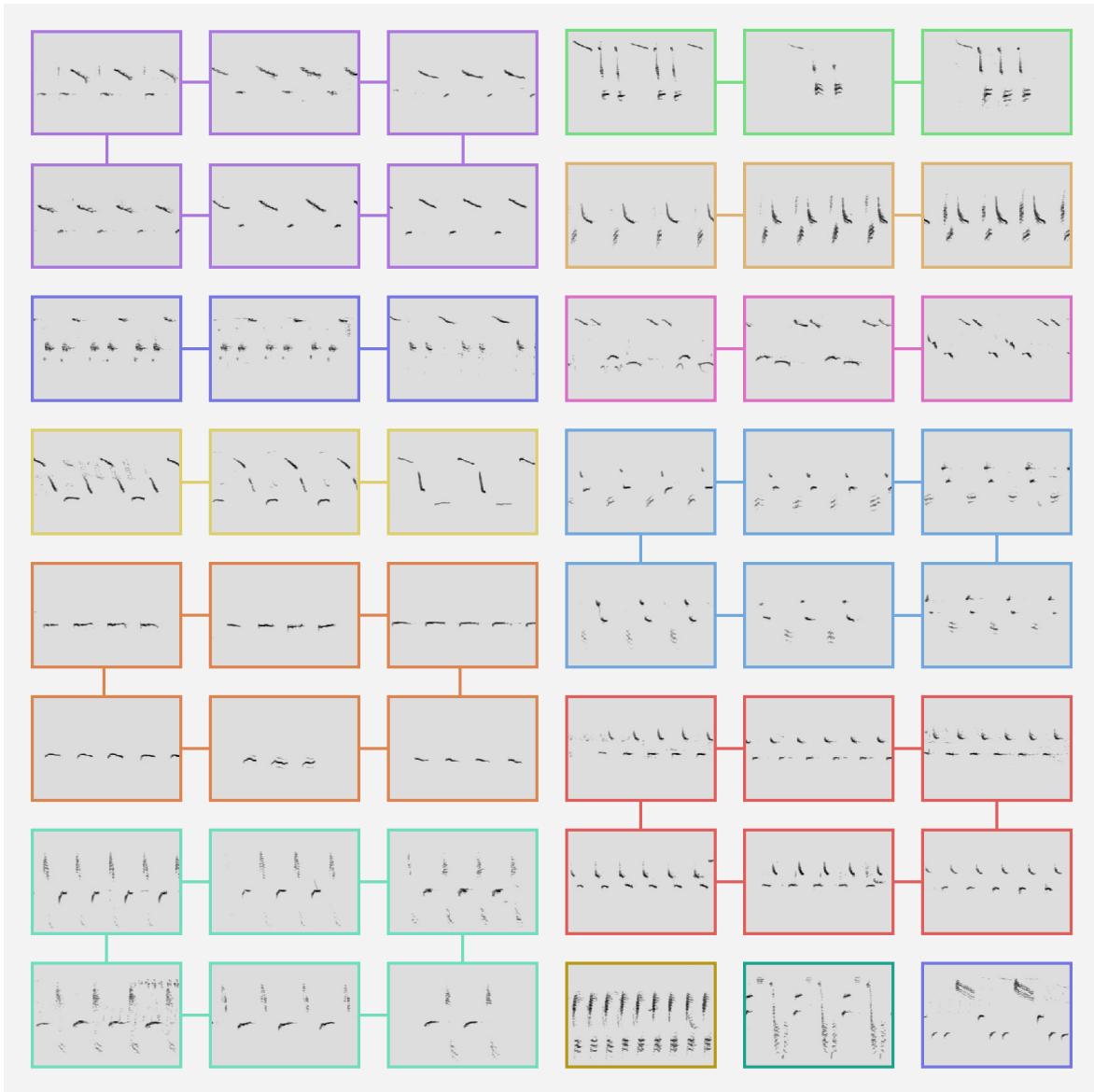


Figure S3. Spatial distribution of the neighbourhood-level predictor variables in the study.

(A) Mean natal dispersal distance, or the mean distance between the natal nest box and the breeding site for all birds in the neighbourhood. (B) Proportion of immigrant birds in the neighbourhood. (C) Mean age of birds in the neighbourhood. (D) Individual turnover, or the proportion of birds that were not already in a neighbourhood in the preceding year.

**Figure S4. Examples of song type clusters in the study population.**

Colours and connected lines represent the same song type cluster sung by different birds. Some song types are sung by many birds, while others are unique to a single bird. The clustering process is based on song similarity derived from a deep metric learning model and a manual categorization process following McGregor and Krebs.⁴⁶

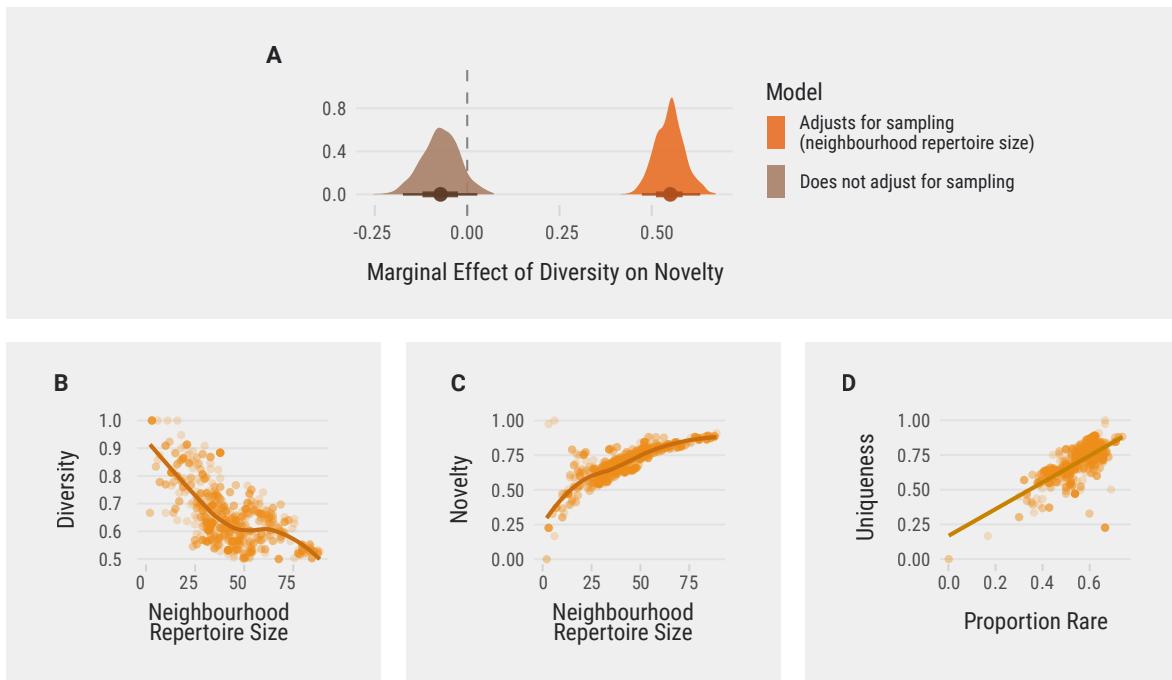


Figure S5. Estimates of cultural outcomes depend on the size of the neighbourhood repertoire.

(A) Marginal effect of diversity—which describes the proportion of distinct songs in a neighbourhood—on uniqueness, that is, how rare, on average, the songs of the birds in a neighbourhood are in the population. These two ways of characterizing cultural diversity are anti-correlated in our study site due to the effect of sampling: more frequent songs are sampled more readily, causing larger sample sizes (neighbourhoods with more birds and therefore songs) to yield lower average estimates of diversity (B) and higher average estimates of uniqueness (C), in a nonlinear manner. Once this is adjusted for, which we do by including GAM terms capturing neighbourhood song density or number of birds, diversity and uniqueness are positively correlated, as expected. (D) Our measure of cultural uniqueness (y-axis) has the advantages of being continuous and not using an arbitrary cut-off, but is nonetheless correlated with definitions traditionally used in the literature, such as ‘songs shared by fewer than 4 birds’,⁴⁶ here on the x-axis.

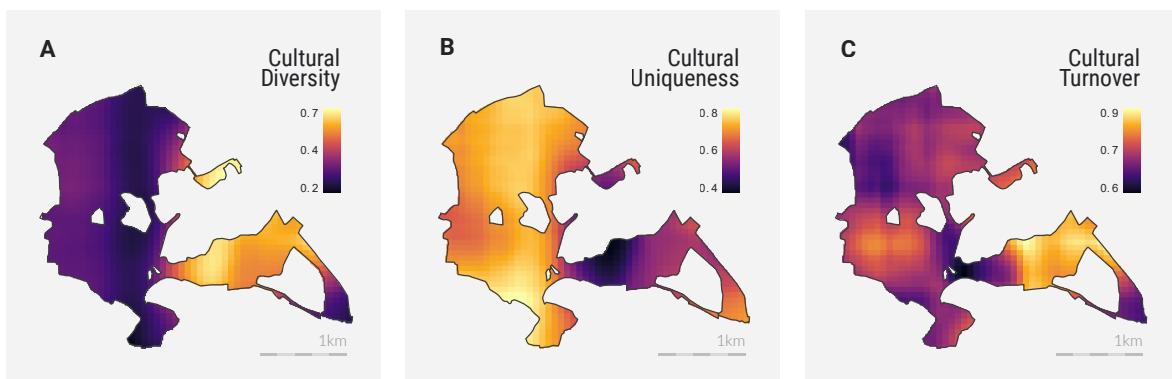
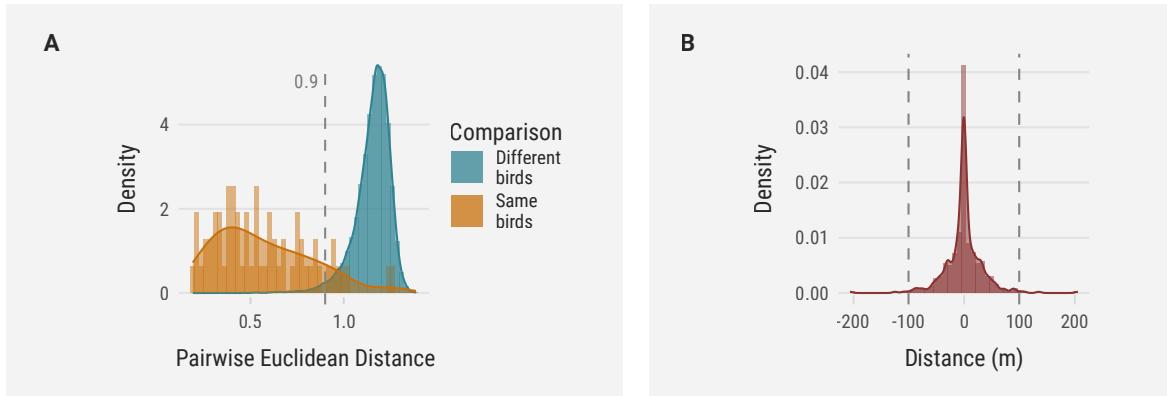


Figure S6. Spatial distribution of the neighbourhood-level cultural variables in the study.

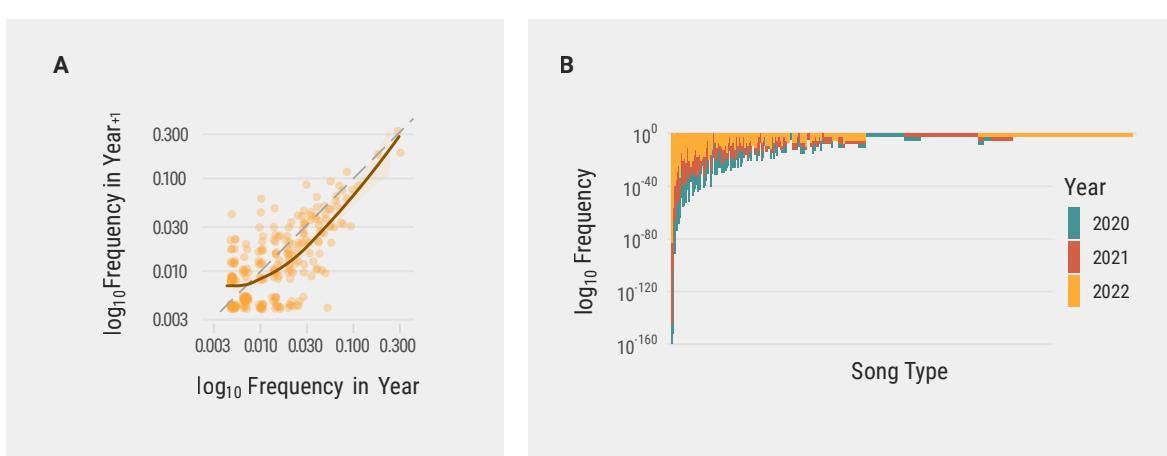
(A) Relative cultural diversity ('diversity'): the ratio of distinct song types recorded in a neighbourhood to the total number of songs recorded in that neighbourhood. Higher values indicate that there are more distinct song types in the neighbourhood relative to its total song output. (B) Uniqueness index: the complement of the logarithm of the mean population-wide frequency of the song types present in a neighbourhood. Higher values indicate that the songs in the neighbourhood are on average less common in the population. (C) Cultural turnover: the proportion of distinct song types recorded in a neighbourhood that were not present in the previous year. Higher values indicate that the neighbourhood's song repertoire has changed more from one year to the next. As described in Figure S5, (A) and (B) are anti-correlated due to the effect of sampling, but once this is adjusted for, neighbourhoods with more cultural diversity also tend to have more distinct songs, as expected.

**Figure S7. Thresholds for re-identifying individual birds based on their songs.**

We used conservative criteria to infer when two repertoires belong to the same bird. Acoustic similarity: A minimum of two matching songs must be more similar than the 0.025 quantile of the distance distribution (an acoustic distance of 0.9). Spatial proximity: The bird must be no more than 100 meters apart from the reference bird. Accuracy of the method: Using only acoustic distance: 0.3% error rate (34 out of 11,359 unique comparisons). Using acoustic distance and spatial constraint: 0.04% error rate (4 out of 11,359 comparisons). These error rates were calculated using only ground truth data from physically re-identified birds across years.

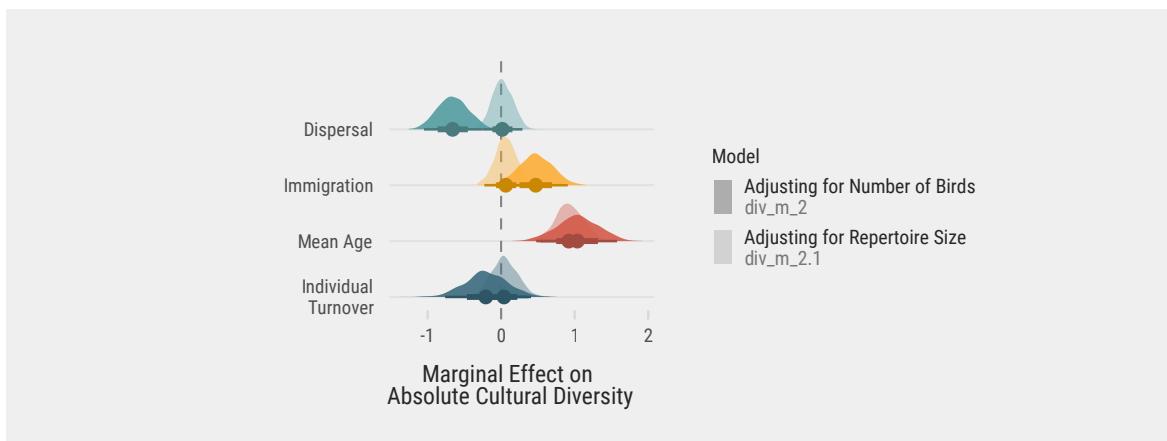
(A) Distribution of acoustic distances. Orange: Same song type sung by the same known bird in different years. Blue: Minimum pairwise distance between different birds and years. Vertical dashed line: x-intercept at 0.9, representing the acoustic distance threshold

(B) Distribution of distance changes between breeding sites for birds that bred more than once. Demonstrates high nest site fidelity in adult birds, which we use as an additional constraint for re-identification. Vertical dashed lines: 100 m threshold.

**Figure S8. Song frequencies and their relationship with abundance in the following year.**

(A) The abundance of a song type in a year predicts its abundance in the following year, with higher stochasticity around rare songs.

(B) Histogram showing the frequency of individual song types in the study.

**Figure S9. Effect of demographic variation on absolute cultural diversity within neighbourhoods.**

To explore how the number of individuals and their repertoire sizes within a neighbourhood affect the total number of distinct song types recorded within a neighbourhood (as opposed to the relative diversity reported in Figure 2), we fit two models: one adjusting for the nonlinear effect of the number of individuals (higher opacity fill, corresponding to model *div_m_2*), and a second adjusting for the nonlinear effect of the number of song types, including repeated variants (lower opacity fill, *div_m_2.1*). See Table S2 for full model specifications.

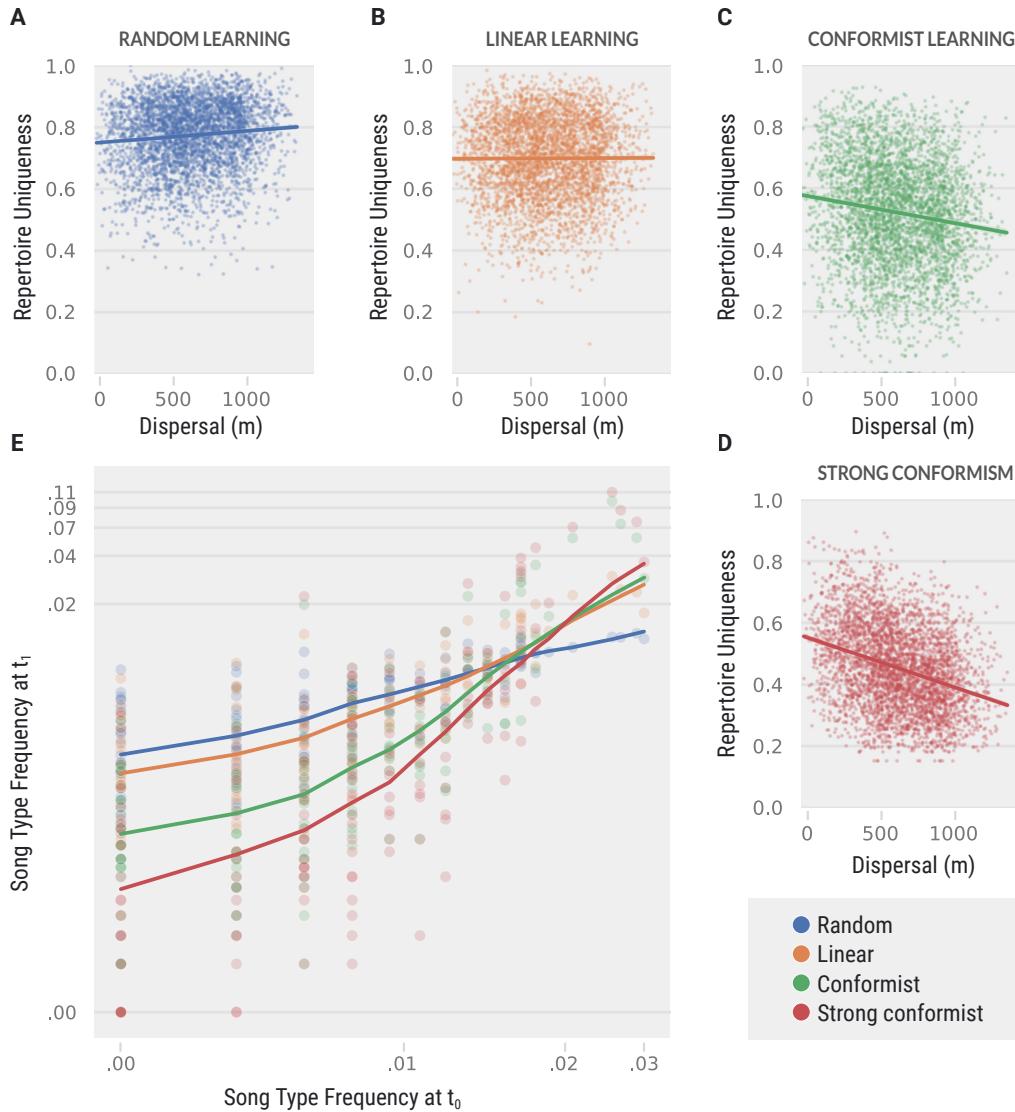
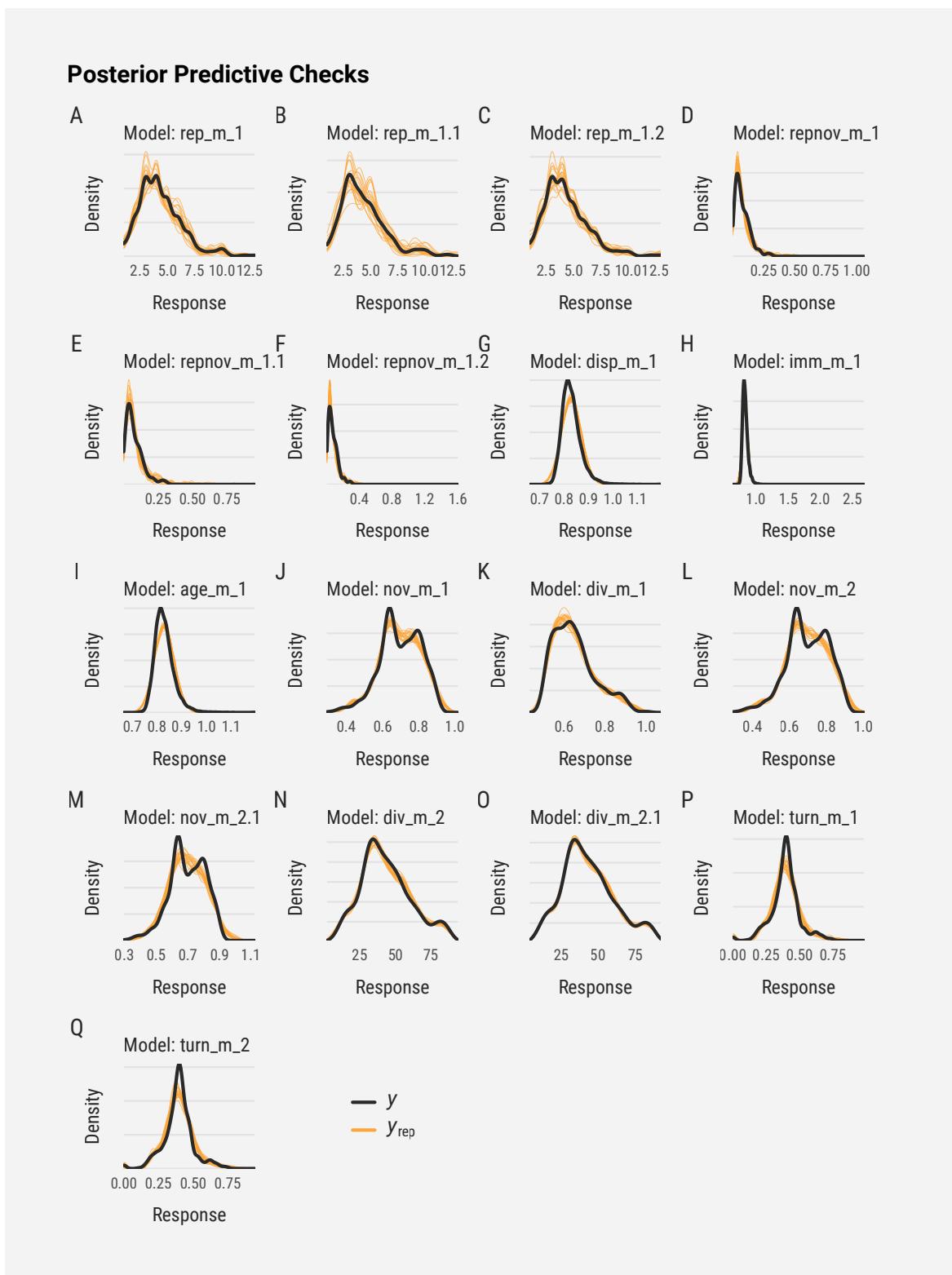


Figure S10. Simulation of the effect of natal dispersal on repertoire uniqueness.

We simulate the relationship between pre-breeding bird movement and the uniqueness of songs in their repertoires (relative to the population). We initialize 200 birds in a 1500×1500 square, each capable of singing 4 songs selected from a pool of 200 song types. Birds do not initially move. New birds hatch and move based on a log-normal distribution parametrized to represent realistic dispersal behaviour in our population. Each bird can learn the songs it hears within a 200 m radius as it moves. At the end of their movement, a bird's crystallized repertoire is determined by its learning mechanism: (A) random learning of songs, (B) linearly frequency-dependent learning, (C) positively frequency-dependent learning, or (D) learn the most popular songs (strong conformism). The simulation is repeated n times per learning strategy, and we record the average uniqueness of songs in each bird's repertoire, which is a transformation of the average frequency of the bird's songs, as well as the distance that each bird has moved. The results show that the relationship between dispersal and repertoire uniqueness depends on the learning mechanism, and that the effect of dispersal detected in our study might be expected to arise if being exposed to a larger number of songs influences learning in a nonlinear frequency-dependent manner.

**Figure S11. Posterior predictive checks for the main models in the study.**

Comparing simulations from the posterior predictive distribution y^{rep} (thin orange lines) with the outcome y (black lines) using Kernel density estimates. The posterior predictive distribution is a distribution of possible outcomes of the model given the data and the model parameters, here used to check the fit of the model to the data.