

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 dataset 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.

30

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

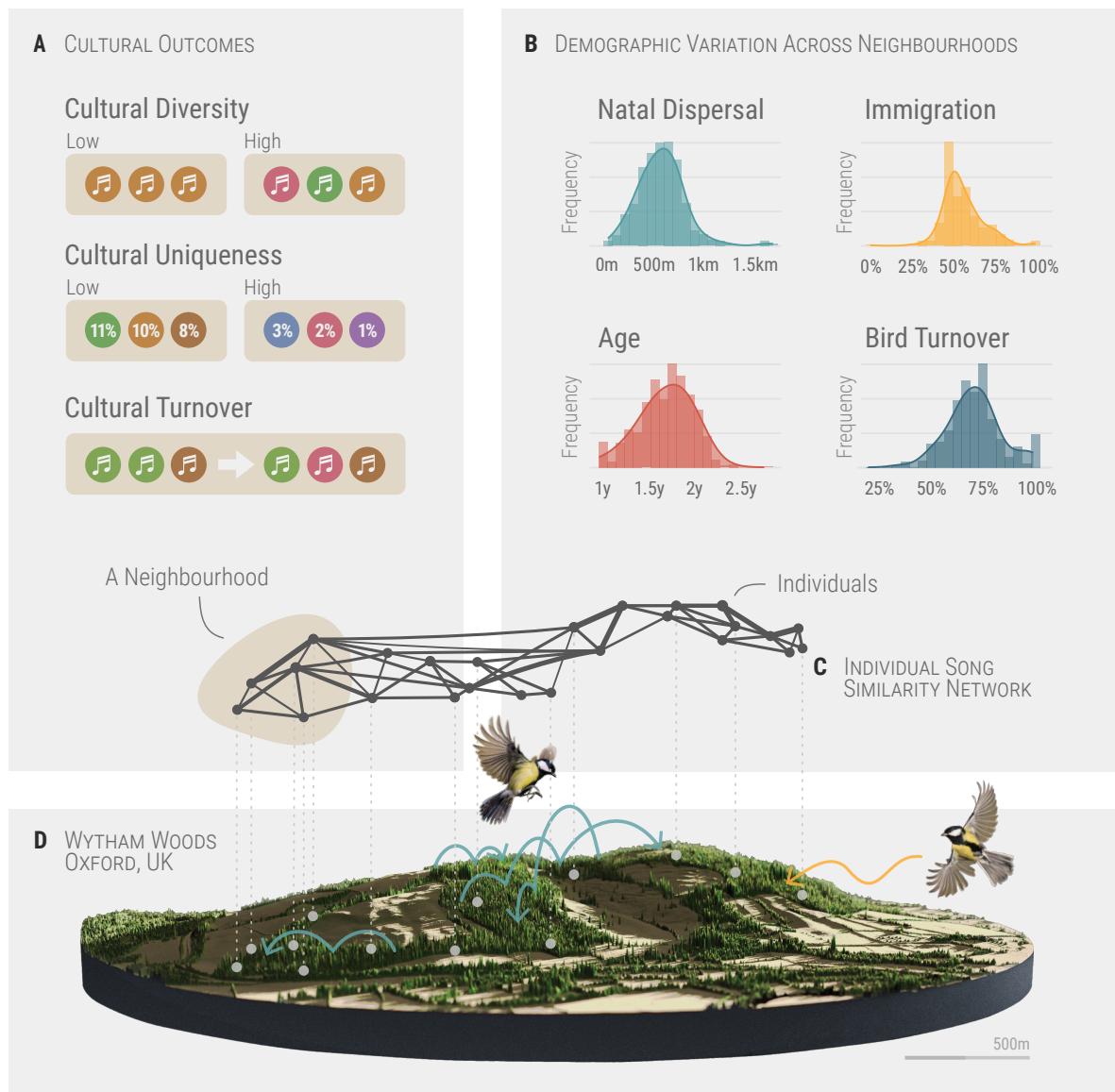


Figure 1. Study system and main variables in our analysis.

(A) Cultural variables measured at the neighbourhood level. Higher values of cultural diversity indicate that there are more different 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.

To contribute to this goal, we built a comprehensive dataset that spans three years and documents the dawn songs produced by male great tit birds during 454 breeding attempts in a single population located in Wytham Woods, UK. The population’s marked variation in individual turnover, postnatal dispersal distances, age structure, and immigration across space—known through ongoing long-term monitoring³⁸—allowed us to estimate their effects on song cultural repertoires at both individual and group levels. First, we assigned more than 109,000 songs in 330 song repertoires to 242 individual birds through a combination of direct physical capture, radio frequency identification microchips, and a novel song-based re-identification method using a deep metric learning model. Then, we quantified individual and group-level traits and analysed variation in song cultural 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.

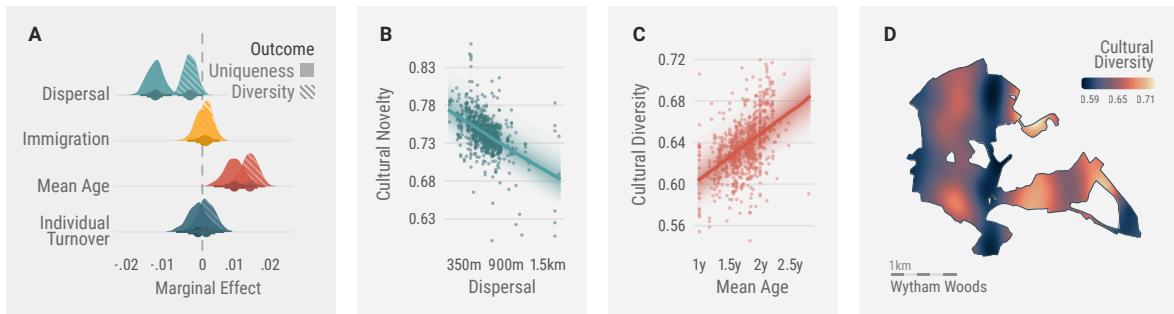


Figure 2. Influence of demographic variables on cultural diversity and uniqueness within neighbourhoods.

(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

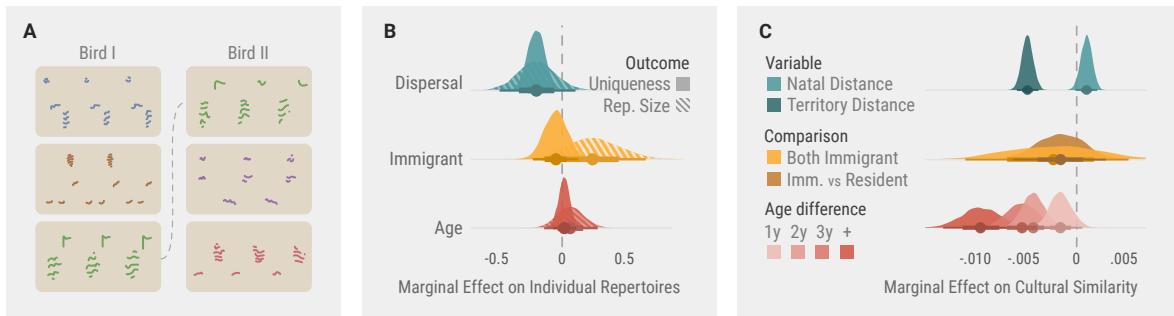


Figure 3. Individual and dyadic analysis of cultural diversity and similarity.

(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, those songs are in the entire 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 ex-
101 ample, may bring cultural novelty with them. But this is not the case for great tits, whose young disperse in late
102 summer and autumn, shortly after achieving independence, learn their songs until the end of their first winter,⁴⁷
103 and become chiefly sedentary as adults.^{49–51} In this species, then, we anticipate that immigrant birds will learn
104 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 popu-
106 lation significantly differ acoustically from those of resident birds ($mem = -0.002, CI_{95\%} [-0.006, 0.002]$; Figure
107 3C). This, in conjunction with the observation that song repertoire similarity between individuals is predicted
108 by the distance between breeding territories ($mem = -0.005, CI_{95\%} [-0.006, -0.004]$; Figure 3C; Table S3), sup-
109 ports the hypothesis that great tits are critical period learners that learn primarily from territorial neighbours
110 after dispersal.^{46,47}

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

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

135 We now shift our focus from static measures of cultural diversity to cultural turnover, examining how quickly
136 song types disappear from neighbourhoods and the consequences this has for their cultural makeup. The pri-
137 mary driver of cultural turnover within neighbourhoods is individual turnover (total effect $mem = 0.072 CI_{95\%}$

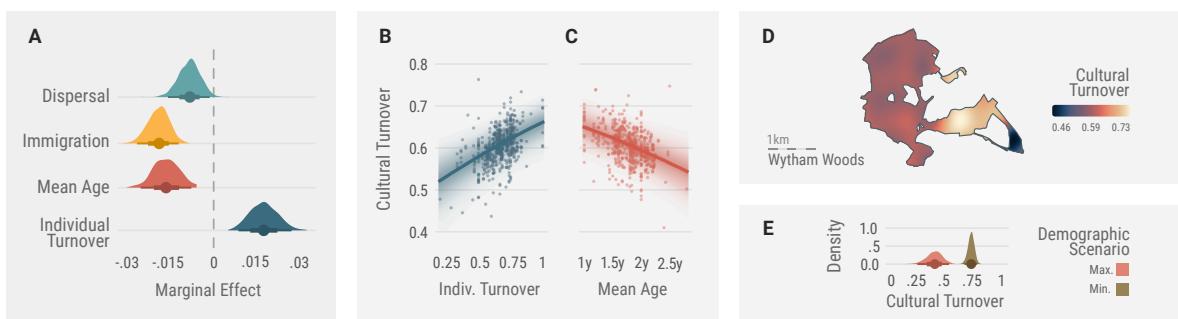


Figure 4. Influence of demographic variables on cultural turnover within neighbourhoods.

(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.

[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 ($P(\beta_{\text{age}} < 0 | D) = 1$, $\text{mem} = -0.044$, $\text{CI}_{95\%} [-0.063, -0.026]$; 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.

170 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 dataset of song repertoires. These outcomes are most likely driven by differences in individual learning and exposure to cultural variants. In particular, we

177 find that dispersal within the population reduces cultural diversity and uniqueness. Birds that hatched outside
 178 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 examines how demographic processes affect cultural diversity and the rate of cultural change on
 186 small spatial and temporal scales. We demonstrate that these factors can significantly influence cultural dynamics,
 187 but their impact on longer-term cultural diversification and persistence remains an open question. Both
 188 empirical studies and modeling efforts on cultural change take account for the population's demographic charac-
 189 teristics and their inherent heterogeneity across time and space, as these factors shape individuals' exposure to
 190 cultural variants and learning opportunities, thereby influencing emergent group-level cultural dynamics.

191 METHODS

192 Resource availability

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

196 Data collection

197 Study system and fieldwork

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

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

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

227 Nest box occupancy and breeding density vary across the study area, with some areas having a higher density
 228 of nest boxes and a higher proportion of occupied boxes, which we account for in some of our analyses as
 229 described in the sections below. In the years of our study, 261, 289 and 278 nest boxes were occupied by pairs
 230 of great tits, with 173, 184 and 184 that led to successful breeding attempts where at least one chick fledged. See
 231 [Figure S1](#) for a map of the study site and sampling locations.

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

This approach is supported by previous studies on great tit dawn song,^{52,74–77} as well as our observations that: (a) recordings from consecutive days contain renditions of the same song types clearly sung by a single individual cycling through its repertoire, (b) renditions of the same song types across different days can be assigned to a single individual by our deep metric learning model (see [deep metric learning model training](#)), and (c) when we recapture the same bird in a different field season (often in the same location due to adult site fidelity), we can easily match its songs to those previously recorded. To further ensure that we were recording the correct birds, we discarded rare recordings with more than one vocalizing bird unless one was distinctly louder than the others during the segmentation process. Additionally, we excluded all songs with a maximum amplitude below -16 dB, calculated as $20 \log_{10} \left(\frac{A}{A_0} \right)$, with $A = 5000$ and $A_0 = 32767$ (the maximum value for 16-bit digital audio). This threshold was established based on observations showing that an amplitude cutoff greater than 4000 unambiguously differentiated the focal bird from its closest neighbours when simultaneous recordings from nearby spatial locations captured multiple birds. It is important to note that these values are not calibrated and are relative to our recording equipment and settings, as well as other factors like sound directionality and vegetation cover.

Our recording efforts captured birds belonging to around half of all breeding attempts [Figure S2](#) (including both successful and unsuccessful attempts, with or without linked individual data), which may result in some rare song types being underrepresented or undetected if they are sung by less successful or late-breeding individuals. We do not currently have evidence suggesting this skews our results, but it remains a plausible consideration. Importantly, the birds that we did record are representative of the neighbourhood's breeding density, dispersal distances, contribution of immigration, and age distribution (see [Figure S2](#)). In a related way, those birds that sing more frequently are more likely to be recorded, but as these are also likely to be the primary contributors to the local song pool, we believe our sample adequately reflects the overall song repertoire of the breeding population in each area.

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

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

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

Recording equipment and schedule

We used 60 (30 in 2020) AudioMoth recorders,⁸⁰ which were housed in custom-built waterproof enclosures. Recording began approximately one hour before sunrise (05:36 – 04:00 UTC during the recording period) and consisted of seven consecutive 60-minute-long recordings with a sample rate of 48 kHz and a depth of 16-bit. To sample as many birds as possible, we left each recorder at the same location for at least three consecutive

289 days before moving it to a different nest box. We relocated 20 recorders (10 in 2020) every day throughout the
290 recording period.

291 Data processing and annotation

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

297 Characterizing repertoire similarity

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

305 Continuous similarity (individual-level analyses)

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

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

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

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

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

332 where we compare each song feature vector a in set A with all song feature vectors b in set B and compute
333 their Euclidean distance $|a - b|_2$. We then retain the minimum distance for each element in set A and obtain the
334 AMED by averaging these minimum distances over all elements in set A . The main advantage of this approach
335 is that it allows us to avoid imposing discrete population-wide song categories. On the other hand, if song
336 learning is categorical and not very precise in terms of fine song structure, this method could underestimate it
337 or fail to detect it. We used this approach for all individual-level analyses in this paper.

338 Automated clustering (first step for neighbourhood analyses)

339 Instead of calculating a continuous measure of repertoire similarity, we can build a pairwise distance matrix for
340 all songs, assign them to discrete clusters using a clustering algorithm, and then calculate the intersection be-

341 between repertoires by using the Jaccard coefficient or modelling it as a binomial process, with n = the combined
 342 repertoire size and s = the number of songs in the same cluster. Here we used UPGMA hierarchical clustering
 343 and dynamic tree-cut techniques to classify the syllables into distinct types (since songs consist of repeated syllables,
 344 syllable and song types are synonymous in this species). We allowed a minimum cluster size of 1 to ensure
 345 the representation of rare song types. The usefulness of this method relies on the global properties of the embedding
 346 space derived from the continuous similarity process. In a low-dimensional space where linear distances
 347 effectively capture meaningful variation, creating clusters by cutting the hierarchical tree at different heights
 348 yields varying cluster counts while maintaining meaningful groupings. However, in a high-dimensional space
 349 where global distances are not meaningful, only relatively small clusters of nearby points remain interpretable.
 350 This is the case with our dataset and embedding space: we find that the method reliably groups song renditions
 351 by the same bird across different years, alone or together with other birds with highly similar songs, yet
 352 consistently splits songs that are similar by human (and perhaps great tit⁹⁰) standards, ultimately leading to a
 353 very large number of clusters (the most stable clustering solutions were close to the total number of different
 354 individual song types, >1000). Due to these issues, we did not directly use song types defined in this way, and
 355 performed an additional manual categorization step.

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

357 Our neighbourhood-level analyses require that we define discrete cultural units (namely, population-wide song
 358 types). With over 100,000 songs, our dataset is much larger than is common in the field and would have been
 359 impossible to label entirely manually. Instead, we used the output of the automated clustering process described
 360 above, consisting of labelled song repertoires (birdID x song type). This made the problem 57 times smaller: 1920
 361 song types that were already assigned to small clusters of highly similar songs, which we reviewed manually
 362 using the criteria followed by McGregor and Krebs^{46,91,92} and subsequent work.^{30,90,93,94} This process is both
 363 inevitable and partly subjective. However, despite its clear problems, human perceptual judgments might be our
 364 best available substitute for those of the birds for some tasks (but see recent work by Morfi et al.⁹⁵ and Zandberg
 365 et al.⁹⁶). Indeed, across fields, advanced classification algorithms are routinely evaluated against ground truth
 366 created by humans, and this is also the case in bird song research.

367 Following common practice in the field, we statistically validated our resulting 335 manually assigned labels
 368 to evaluate whether if they represent quantitatively robust clusters. To do this, we retrained the ResNet50-based
 369 classifier described in Merino Recalde⁸² on a random subset of labelled song spectrograms data and obtained an
 370 accuracy of 0.87 on the validation set (see other metrics in the repository). For comparison, an equivalent process
 371 by Fayet et al.³⁰ was able to reach 0.71 accuracy for 374 songs. We further explored the result by building a
 372 dendrogram based on the confusion matrix during test time and reviewing classes that were not well supported,
 373 which, following,³⁰ led us to collapse seven classes into two. With the caveats already mentioned, this means
 374 that our classification following McGregor and Krebs⁴⁶ is indeed successful at finding song type clusters that
 375 reduce intraclass variation.

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

386 See Figure S4 for examples of song types defined in this study. The exact code used to perform this song type
 387 validation process, along with the figures generated during it, can be found in the main narrative notebook and
 388 a dedicated repository.

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

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

396 Briefly, we calculated pairwise song distances using the feature vectors obtained from a vision transformer

397 on a metric learning task. This model achieved a mean average precision at 5 (mAP5) of 0.98 and a cumulative
 398 matching characteristic at 1 (CMC1) of 0.98, which roughly means that in 98% of the queries made to the similar-
 399 ity space on a held-out test dataset of known songs the returned candidate song type by a bird is the correct one.
 400 Given that the model was trained on almost 2000 classes, this means that there is enough individual information
 401 contained in each song type to distinguish between birds with very high confidence: even when birds sing very
 402 similar songs, this model can still tell them apart.

403 We then use these distances between song embeddings to infer when two repertoires belong to the same bird,
 404 even if had not been physically identified more than once. To do this, we set very conservative criteria: that a
 405 minimum of two songs are more similar than the 0.025 quantile of the distribution of distances for all song types
 406 sung by birds already known to be different, or 0.9, and that the bird is no more than 100 metres apart from the
 407 reference bird. If we query the metric learning model across the songs of the entire population, which increases
 408 the chances of a false positive, we find that the percentage of wrongly assigned birds in our ground truth data
 409 (birds that we have physically re-identified across years) is 0.3%, or 34 out of 11,359 unique comparisons if we
 410 only use acoustic distance—further reduced to 0.04%, or 4 out of 11359, if we also add the spatial constraint (see
 411 Figure S7 for a graphic explanation).

412 Quantification and statistical analysis

413 Modelling pairwise similarity and individual repertoires

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

420 **Individual repertoires** We first modelled individual repertoire size using Poisson and negative binomial models,
 421 but this led to poor performance as assessed through posterior predictive checks (both underestimation of mean
 422 values and either under or over-estimation of very low repertoire sizes). Instead, we built continuation ratio
 423 models, a type of sequential ordinal model where reaching a particular level (number of song types in the reper-
 424toire) 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-
 425 grant status, distance dispersed, age, and repertoire size. Three further log-normal models, $repnov_{m_1}$, $repnov_{m_{1,1}}$,
 426 $repnov_{m_{1,2}}$, do the same for the average cultural uniqueness of individual repertoires, defined as one minus the
 427 mean of the relative frequencies of each song type present in the repertoire.

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

440 Modelling group-level outcomes

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

452 the spatial locations based on their distance.^{101–103} We confirmed that this eliminated the residual spatial auto-
 453 correlation via Moran's I tests. Note that we fit a separate GP for each year, as treating the spatial dependence
 454 as fixed across the study duration, as is often done, risks further underestimating uncertainty.
 455 We define our predictor variables in the following way:

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

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

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

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

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

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

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

501 **Model estimates and reporting**

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

506 returns a posterior distribution of possible values instead of point estimates. By convention, we report posterior
 507 central estimates (means or medians) and their 95% credible intervals, but also include plots with full posteriors.
 508 Note that categorical predictors are dummy-coded and continuous predictions z-score transformed.

509 For each parameter of interest, we calculated predictions or marginal effects at the means or other relevant val-
 510 ues. Regression plots show predicted values of the mean and their credible intervals, as well as partial residuals
 511 adjusted to the means or other relevant values of the explanatory terms included in the model.^{107,108} We have
 512 tried to build reasonable models, but even then our estimates should not be interpreted causally. Figure S11
 513 shows posterior predictive checks for all models in the study. See the software section at the end for a complete
 514 list of libraries used in the various analyses and the code repository for full model 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 Cura-
 531 tion, 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,
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870 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

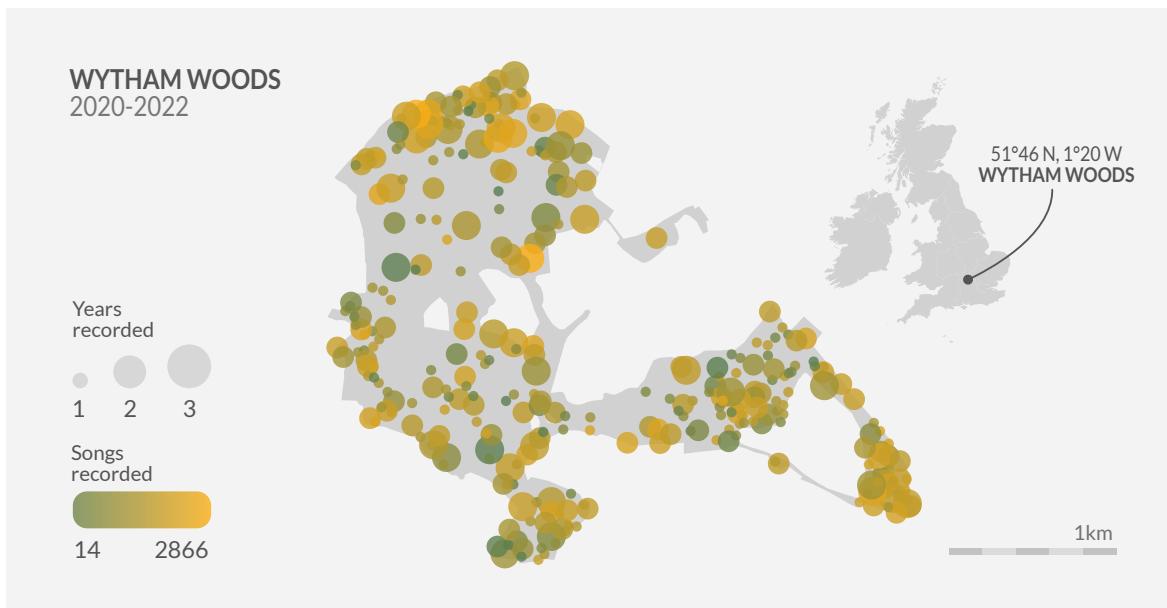
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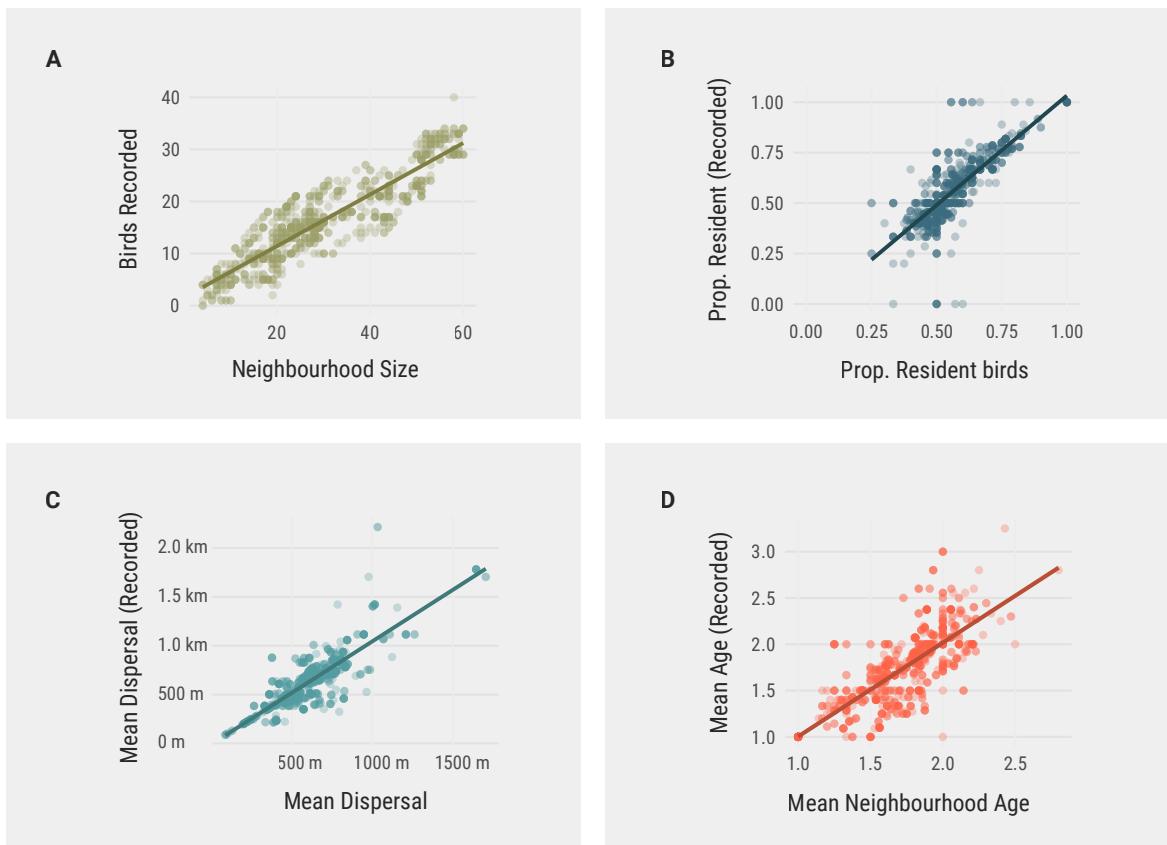
Table S3. Model estimates (Continued)

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

877 ^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.

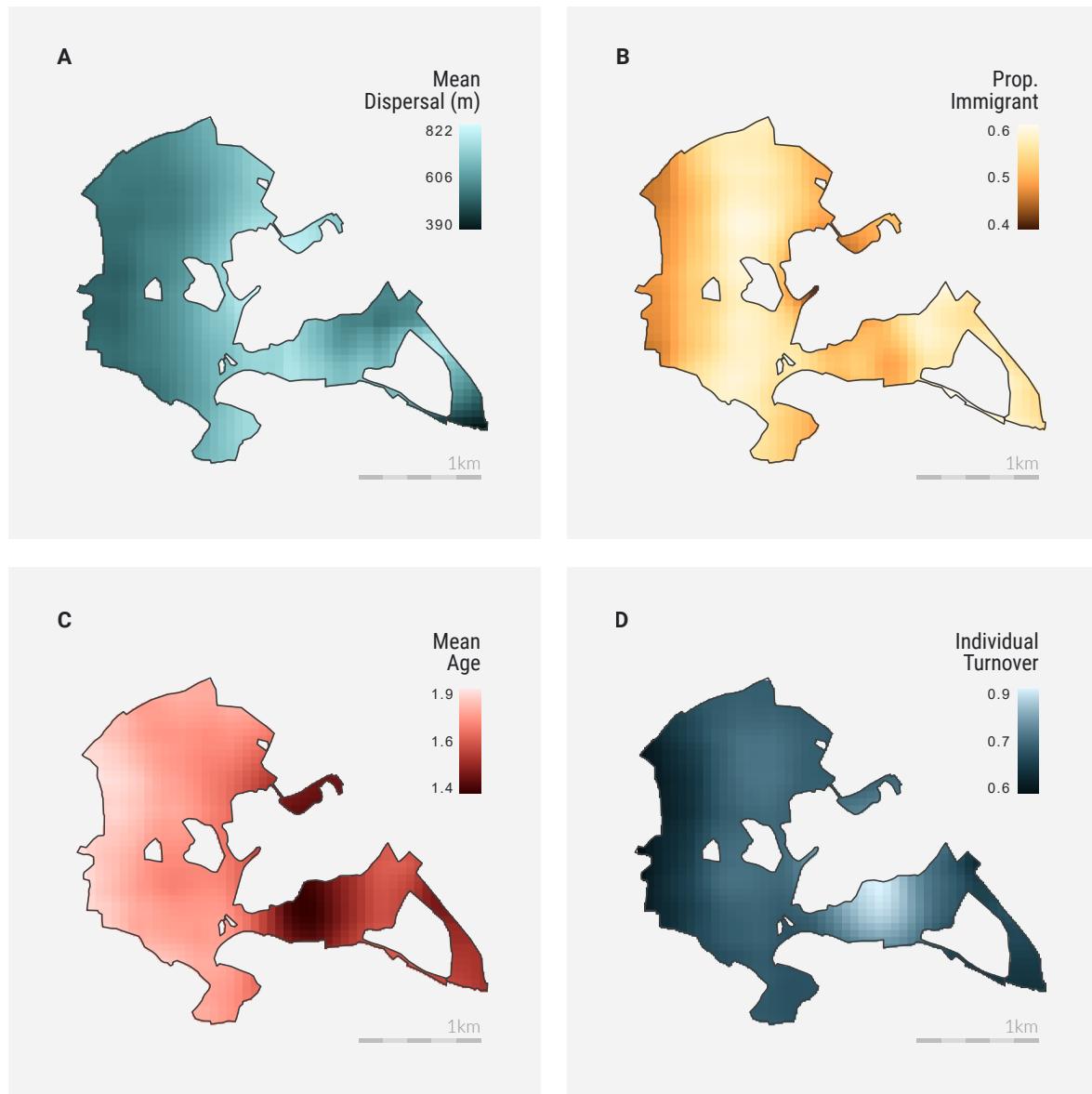
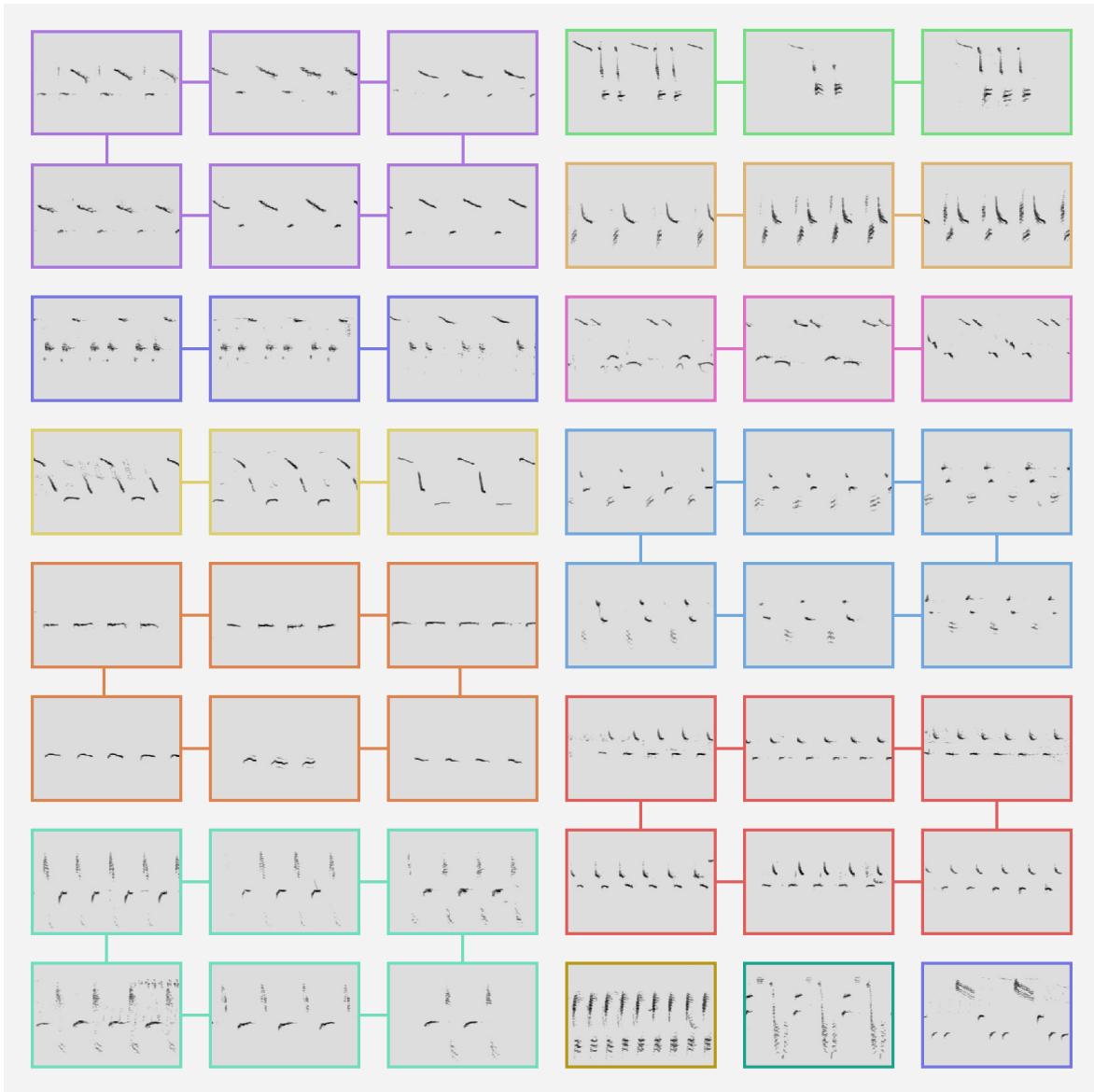


Figure S3. Spatial distribution of the neighbourhood-level predictor variables in the study.

(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

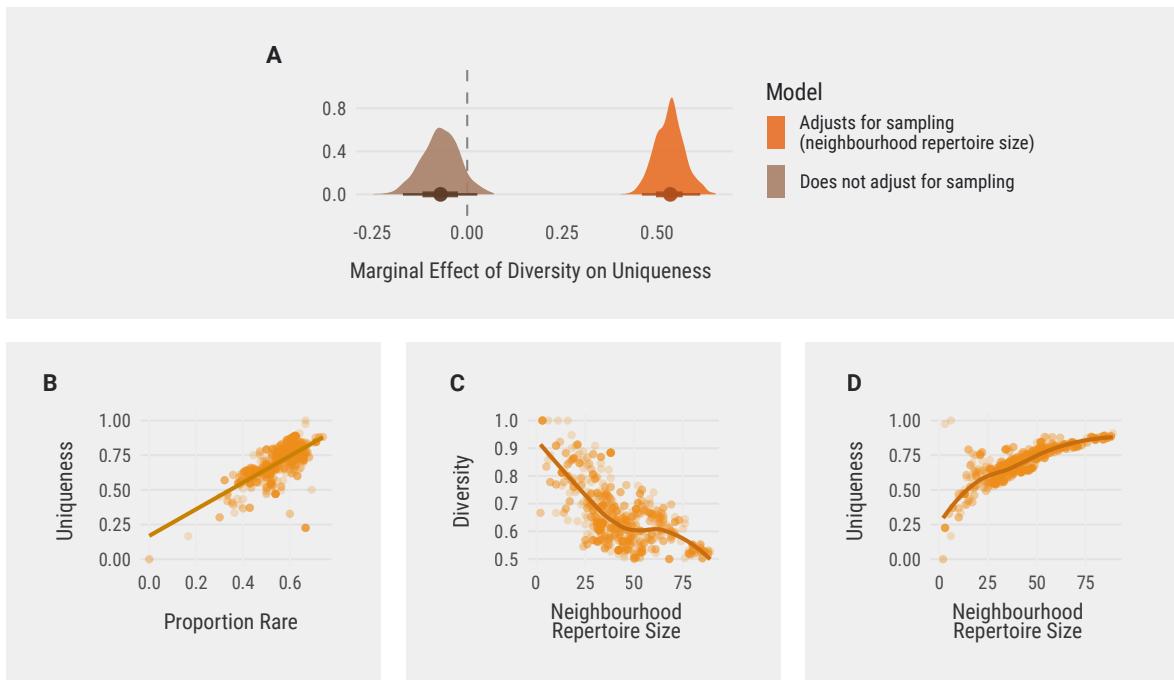


Figure S5. Estimates of cultural outcomes depend on the size of the neighbourhood repertoire.

(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 (C) and higher average estimates of uniqueness (D), 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. (B) 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.

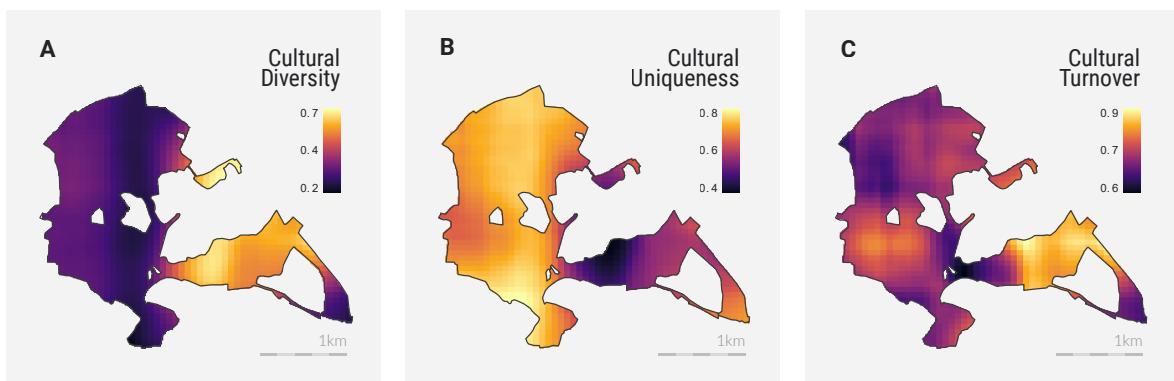
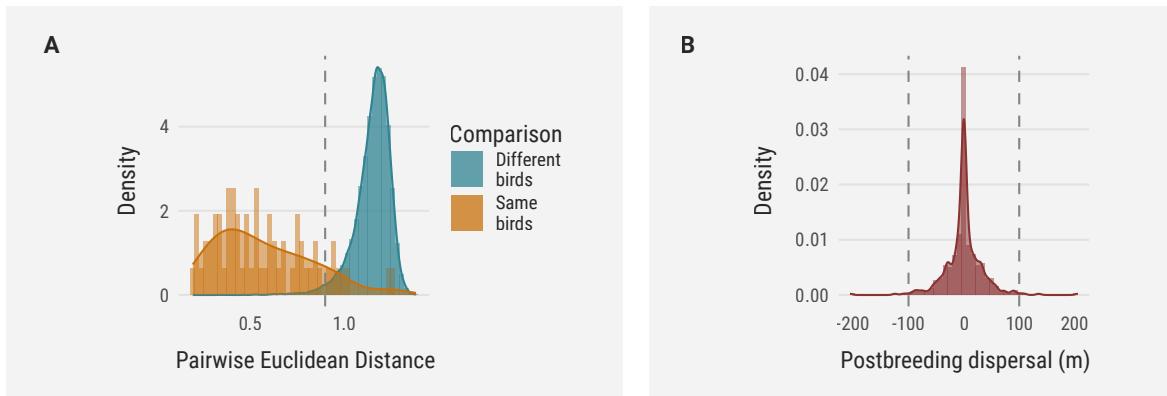


Figure S6. Spatial distribution of the neighbourhood-level cultural variables in the study.

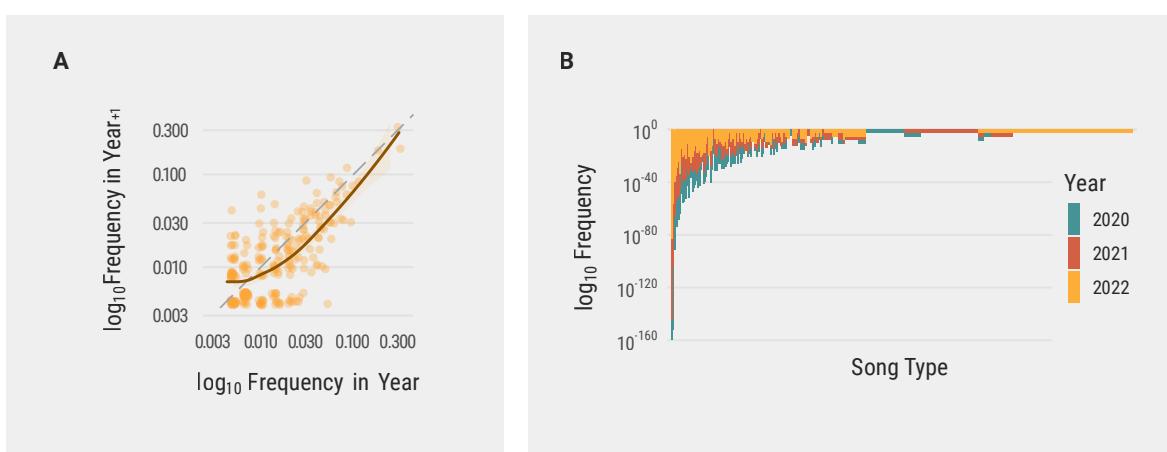
(A) Relative cultural diversity ('diversity'): the ratio of distinct song types recorded in a neighbourhood to the total number of songs recorded in that neighbourhood. Higher values indicate that there are more distinct song types in the neighbourhood relative to its total song output. (B) Uniqueness 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.

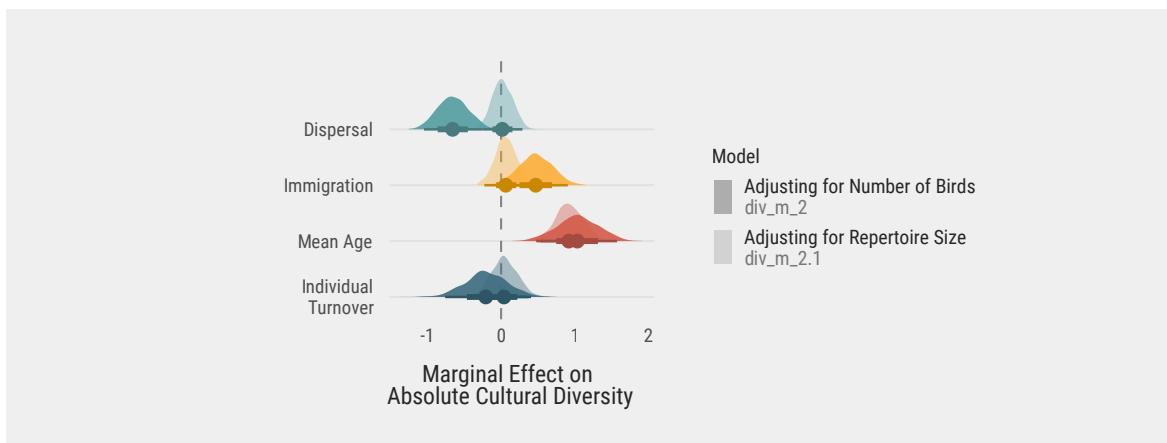
(A) Distribution of acoustic distances. Orange: Same song type sung by the same known bird in different years. Blue: Minimum pairwise distance between different birds and years. Vertical dashed line: x-intercept at 0.9, representing the acoustic distance threshold

(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.

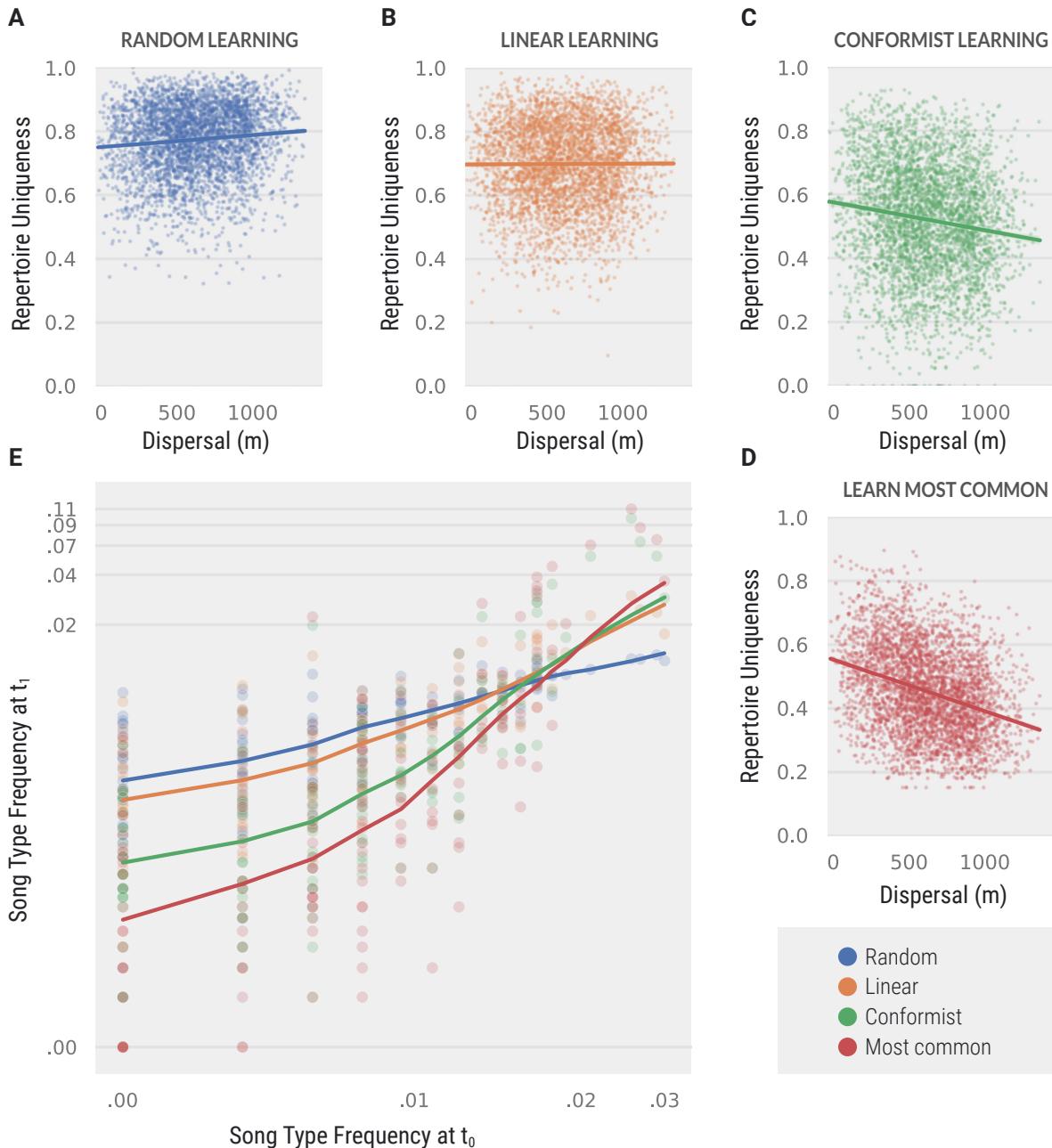
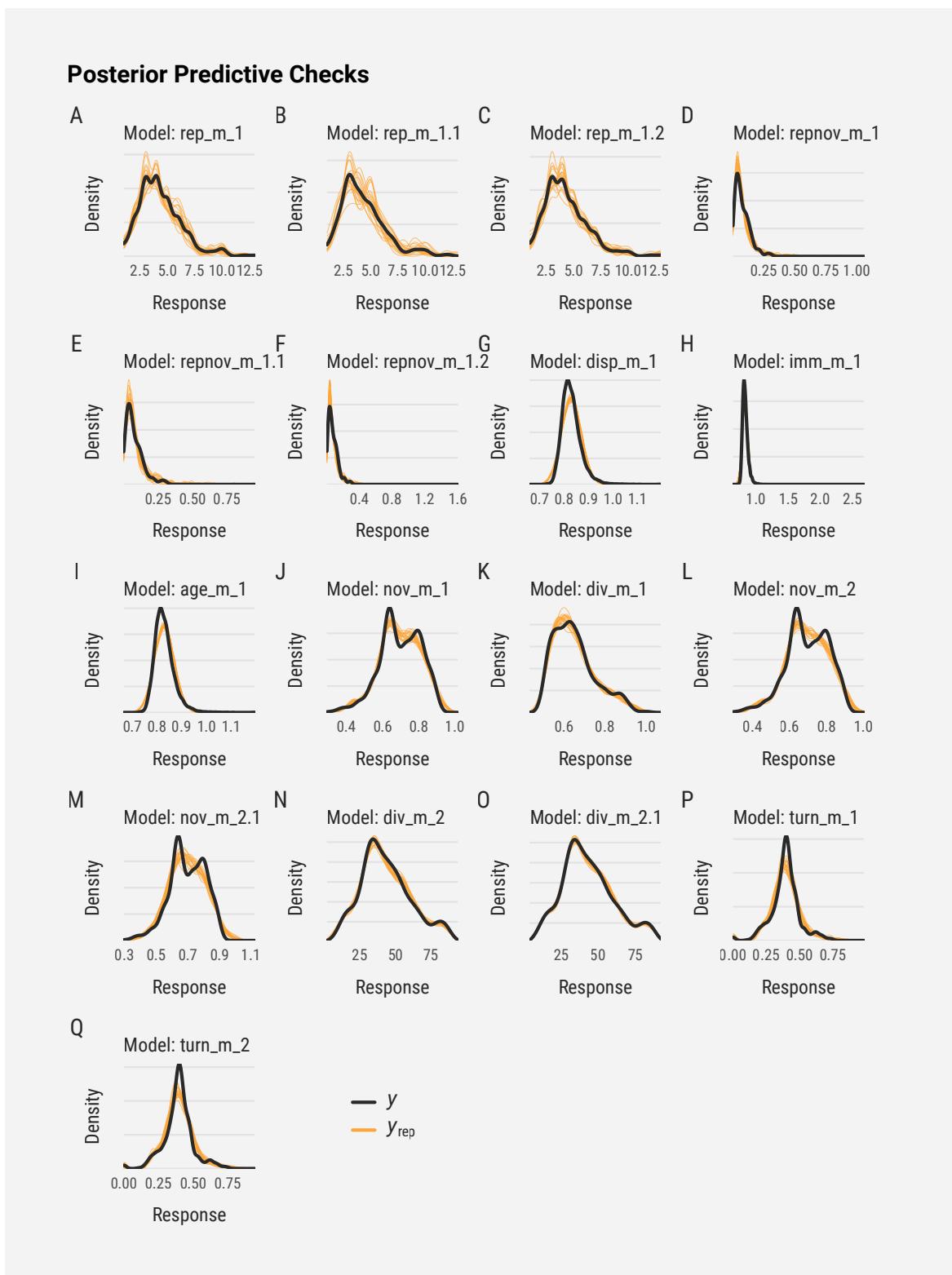


Figure S10. Simulation of the effect of natal dispersal on repertoire uniqueness.

We simulate the relationship between pre-breeding bird movement and the uniqueness of songs in their repertoire (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.