

The demographic drivers of cultural evolution in bird song: a multilevel study

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Summary

Social learning within communities sometimes leads to shared behavioural patterns that persist over time, which we know as culture. Examples of culture include learned bird and whale songs, cetacean feeding techniques, and avian and mammalian migratory routes. Shaped by neutral and selective forces, animal cultures evolve dynamically and lead to cultural traditions that differ 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 other 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 built a multi-generational dataset containing over 109,000 songs from >400 individuals from a population of Great Tits (*Parus major*), which we study using a deep metric learning model to re-identify individuals and quantify song similarity. We show that demographic variation at the small spatial scales at which learning takes place has the potential to strongly impact the pace and outcome of animal cultural evolution. For example, age distributions skewed towards older individuals are associated with slower cultural change and increased diversity, while higher local population turnover leads to elevated rates of cultural change. Our analyses support theoretical expectations for a key role of demographic processes resulting from individual behaviour in determining cultural evolution, and emphasize that these processes interact with species-specific factors such as the timing of song acquisition. Implications extend to large-scale cultural dynamics and the formation of dialects or traditions.

Keywords: animal culture; bird song; demography, cultural evolution

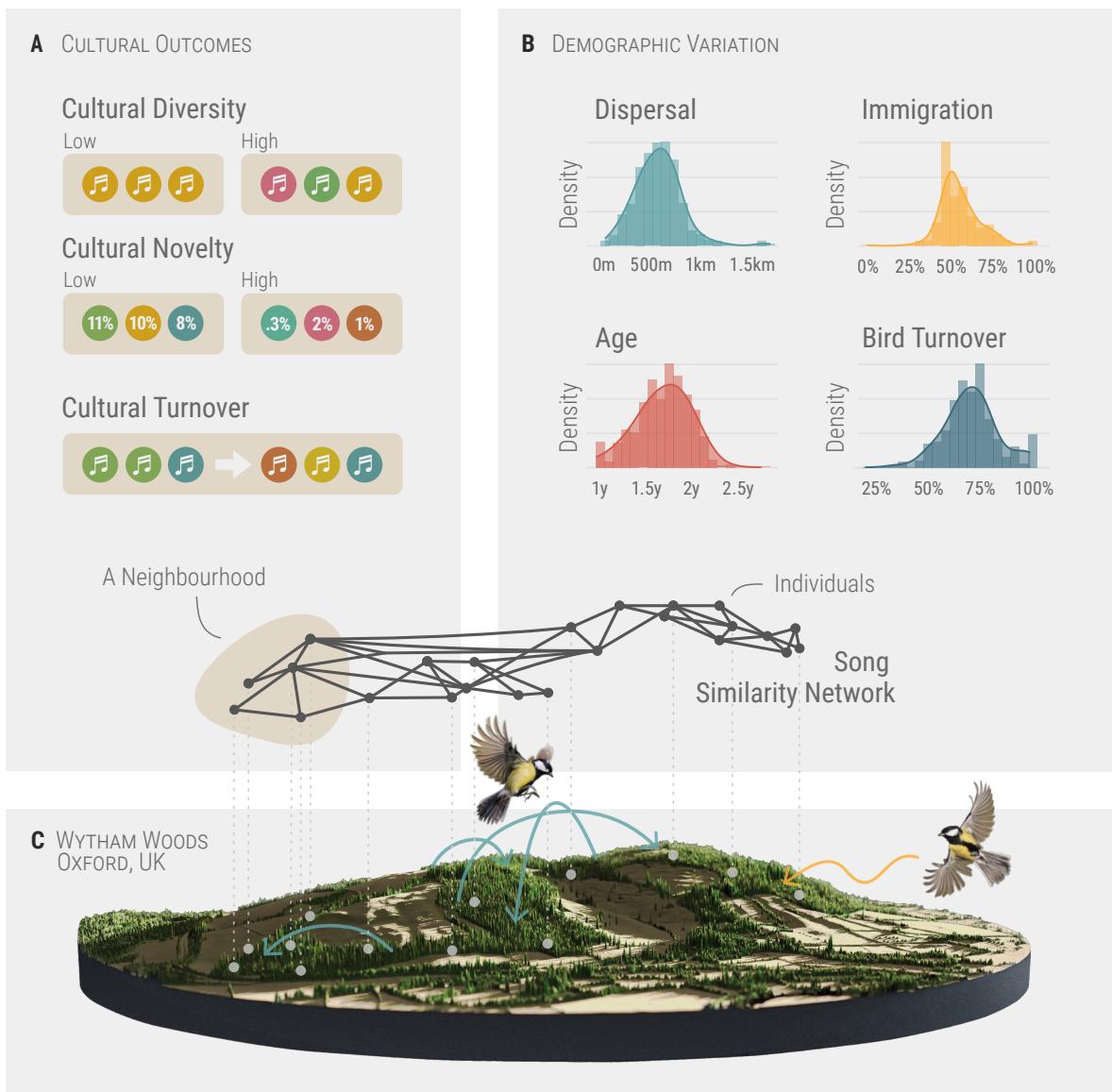
RESULTS AND DISCUSSION

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, migration routes,^{3–5} and the feeding techniques of some cetaceans.^{6,7} Animal cultures are not static: neutral and selective mechanisms influence the frequency of cultural traits,^{8,9} leading to a process of cultural evolution. The resulting cultural traditions differ considerably in their diversity and stability,¹⁰ determined by both learning biases and mechanisms and the demographic structure of populations.^{11,12}

While the role of social learning strategies and biases—frequency dependence, tutor biases, etc.—has been extensively studied,^{13–17} 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 and 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 emphasised by theoretical work.^{11,18–25} However, translating theoretical expectations into empirical evidence remains a challenge (see Chimento et al.²⁶ or Fayet et al.²⁷ for exceptions).

Culture is increasingly recognised as both a fundamental aspect of many animals' lives and a valuable tool in monitoring and conservation efforts.^{30,31} 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,³⁰ and can be lost when habitat fragmentation and population decline lead to reduced learning opportunities.^{32,33} 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 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

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

(A) Cultural variables measured at the neighbourhood level. See methods for definitions. (B) Variation in the properties and composition of neighbourhoods across the population. See methods for definitions. (C) 3D render of our study site, Wytham Woods, based on first return LiDAR data²⁸ and made with rayshader.²⁹ Elevation is exaggerated. The network represents pairwise repertoire similarity between individuals with known spatial locations, used in the models reported in Fig. 2. 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 Woods, UK. The population's marked variation in individual turnover, postnatal dispersal distances, age structure,
 53 and immigration across space (Figure 1) known through ongoing long-term monitoring³⁴ allowed us to
 54 estimate their effects on song cultural repertoires at both individual and group levels. First, we assign more
 55 than 109,000 songs in 330 song repertoires to 242 individual birds through a combination of direct physical cap-
 56 ture, radio frequency identification microchips, and a novel song-based reidentification method using a deep
 57 metric learning model. Then we quantified individual and group-level traits and analysed variation in song
 58 cultural similarity, diversity, and turnover using network and spatially explicit Bayesian multilevel regression
 59 models.

60 Our results reveal an interplay of demographics and song cultural dynamics that, albeit complex, largely
 61 matches theoretical expectations, as discussed below. This work also demonstrates that bird song, which already
 62 provides what is perhaps the largest body of evidence for cultural change in animals,³⁵ also has the potential to
 63 help us shed light on the impact of other population processes on animal cultures, owing to the fact that we can
 64 sample song cultural repertoires with relative ease.

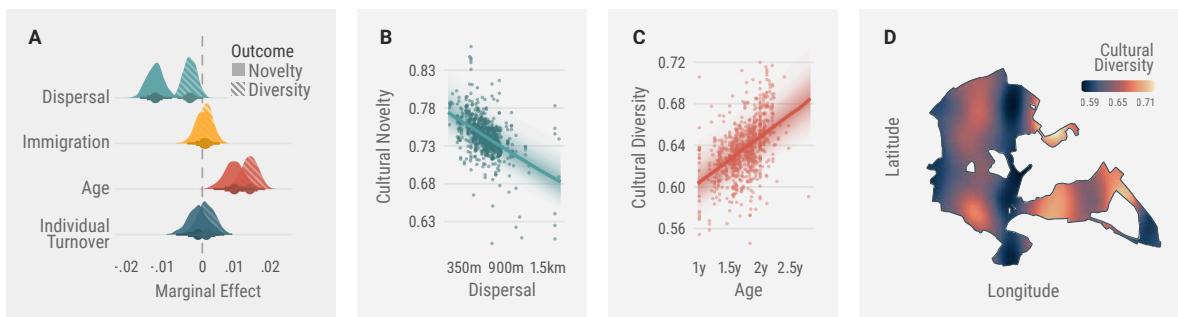


Figure 2. Influence of demographic variables on cultural diversity and novelty.

(A) Marginal effects at the mean of neighbourhood characteristics including mean dispersal distance, proportion of immigrant birds, average age, and individual turnover. (B) Adjusted predictions and partial residuals of the effect of mean neighbourhood dispersal distance on cultural novelty. Low-dispersal neighbourhoods are those in which birds were born 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.

65 Reduced dispersal, increased immigration and an aged population are associated with higher cultural diversity

66 Population genetics provides robust evidence supporting the notion that high dispersal rates facilitate gene 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 divergence.^{36–38} Were we to adhere to an analogy from genetics to culture, we would anticipate that reduced dispersal rates will decelerate the diffusion of cultural traits.²⁴ This, in turn, should result in the maintenance of distinct behavioural patterns within populations,^{39,40} leading to a greater number of cultural variants unique to a neighbourhood or region. Our analysis indeed indicates that neighbourhoods where more birds have remained in proximity to their natal areas harbour greater relative cultural diversity and novelty (*diversity*: $P(\beta_{disp(\bar{m})} < 0|D) = 1$, $mem = -0.018$, $CI_{95\%} [-0.023, -0.012]$; *novelty*: $P(\beta_{disp(\bar{m})} < 0|D) = 0.96$, $mem = -0.005$, $CI_{95\%} [-0.01, 0]$; Figure 2A&B, Table S2), in line with prior research at a much coarser grain.²⁷

67 The analogy breaks down as soon as we consider the underlying individual-level mechanisms, however, due to complex interactions between the timing of dispersal and learning mechanisms that are specific to the cultural domain. Some species only learn songs early in life from their parents, in a manner reminiscent of genetic inheritance, while others learn continuously from their neighbours, or only after dispersal (see⁴¹ for an overview of different strategies). In the case of our study species, the great tit, these learning mechanisms are thought to involve selective retention or modification of songs encountered early in life, while they disperse, and up until before they begin breeding for the first time—a process that results in crystallized repertoires of 1 to \approx 10 different song types.^{42–44} In our individual-level analysis, we see that birds that dispersed over longer distances tend to have learned repertoires composed of songs that are more common within the population (*novelty*: $P(\beta_{disp(m)} < 0|D) = 1$, $mem = -0.2$, $CI_{95\%} [-0.3, -0.09]$; Figure 3B, Table S2), and possibly smaller 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 S2). We hypothesize that birds with more extensive movements are more likely to sample and acquire a larger proportion of common cultural variants, simply because they are exposed to more songs across their learning period. This finds support in a spatially explicit simulation of song learning with dispersal, which shows this pattern emerging under positively frequency-dependent learning or a more complex process leading to similar acquisition curves (see Figure ??, note that we do not currently know which learning strategies are employed by great tits).

68 Building on our understanding of cultural dynamics in relation to dispersal we expect that, when song learning is relatively precise and dispersal is limited, cultural differences between populations will accumulate, and immigration will introduce cultural novelty to the recipient population. However, the extent to which immigration introduces new cultural variants also hinges on an interplay between the species' learning programme, the 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,⁴³ and become chiefly sedentary as adults.^{45–47} 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.^{48,49}

69 Indeed, in our population, we find no evidence that the repertoires of birds originating from outside the population significantly differ from those of resident birds ($mem = -0.002$, $CI_{95\%} [-0.006, 0.002]$; Figure 3C). This,

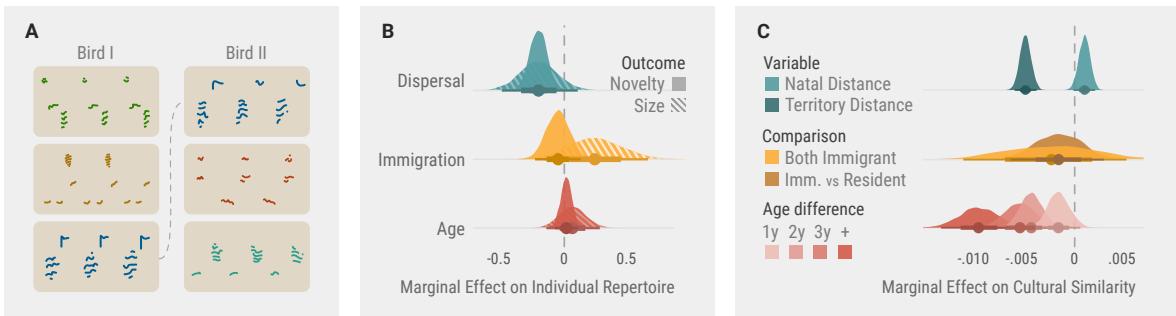


Figure 3. Individual and dyadic analysis of cultural diversity and similarity.

(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 stylised 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 variants sang by that bird) and their relative novelty (how frequent, 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 were born, whereas natal distance may have a weak positive effect on cultural similarity. Immigration: There is no strong evidence that birds born outside the population are dissimilar from resident birds. Age difference: Birds are less culturally similar the greater the difference in their birth years.

in conjunction with the observation that cultural similarity between individuals is predicted by the distance between breeding territories ($mem = -0.005, CI_{95\%} [-0.006, -0.004]$; Figure 3C; Table S2), supports the hypothesis that great tits are predominantly closed-end learners that learn primarily from territorial neighbours after dispersal.^{42,43}

This leads to a somewhat contradictory scenario, however: immigrant birds, while not acoustically distinct, tend to exhibit larger repertoires compared to their resident counterparts (Figure 3B; $P(\beta_{imm.} > 0|D) = 0.87, mem = 0.24, CI_{95\%} [-0.098, 0.593]$; Table S2). At the group level, this small and uncertain effect amplifies, such that neighbourhoods with a higher proportion of immigrant birds do not have increased cultural diversity relative to the total number of songs ($mem = 0.002 CI_{95\%} [-0.004, 0.007]$; Figure 2A); but they do have a higher absolute cultural diversity—above what would be 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 S5, Table S2).

Previous research⁵⁰ has revealed that most birds arriving from outside the population disperse over two kilometres, significantly farther than the typical distances observed within the population (median for males = 558 metres⁴⁵). This extended dispersal may have qualitative consequences for cultural diversity, through a combination of factors: first, an initial exposure to songs from the source population; then, a heightened pressure to adopt vocalisations similar to those of territorial neighbours to avoid any social or reproductive costs associated with non-local signals, as seen in other species.⁵¹⁻⁵⁵

Finally, we find that individual turnover does not significantly affect cultural diversity or novelty, and we uncover an association between age structure and cultural diversity and novelty (Figure 2B). Individuals of the same generation share the most similar song repertoires and, while age itself does not directly relate to changes in the repertoires of individual birds (Figure 3B), the acoustic similarity between pairs of individuals decreases as the age gap between them widens (Figure 3C; Table S2). This is expected in birds that cease to learn new songs as they age, and has detectable consequences for neighbourhoods: those with a higher proportion of older individuals have heightened levels of cultural diversity and novelty. Conversely, in areas where the majority of the population comprises active learners surrounded by their peers, birds tend to produce fewer unique songs that are also more common within the population (Figure 2A; Figure S5; diversity: $P(\beta_{age} < 0|D) = 1, mem = 0.021, CI_{95\%} [0.014, 0.027]$; novelty: $P(\beta_{age} < 0|D) = 0.99, mem = 0.012, CI_{95\%} [0.005, 0.019]$).

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

We now shift our focus from static measures of cultural diversity to cultural turnover, examining how quickly song variants disappear from neighbourhoods and the consequences this has for their cultural makeup. The primary driver of cultural turnover within neighbourhoods is individual turnover (total effect $mem = 0.072 CI_{95\%} [0.051, 0.093]$): as birds leave or die, many song variants disappear with them. Across the three-year study period, now considering the entire population, cultural turnover between consecutive years hovers around 45% (0.47% and 0.44%; the specific values are contingent on the granularity of the definition of song types, see Manual categorization). If all variants faced an equal chance of disappearing, this high turnover rate would lead to complete cultural replacement within a short time span. However, with a two-year gap, turnover only slightly increases to 0.59%. We anticipate this rate to taper further over longer periods, as rare variants encounter

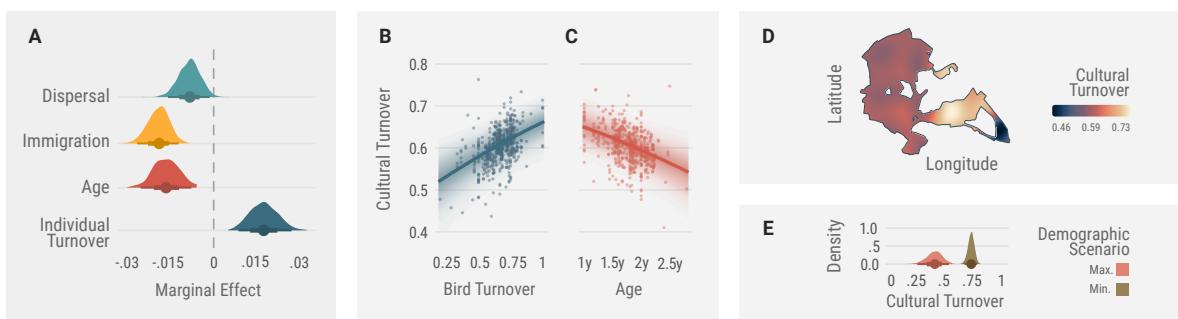


Figure 4. Influence of demographic variables on the rate of local cultural change.

(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. (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 (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, adjusting for individual turnover. Cultural turnover is expected to be over two times higher when neighbourhood dispersal, immigration and age are low.

142 greater stochasticity while common songs endure (Figure S4A). Indeed, some common song types documented
143 over four decades ago persist within the population.^{42,48} This persistence may result from accurate, frequency-
144 dependent learning and/or strong convergent biases.^{16,17,56,57}

145 After factoring in individual turnover, we examine how mean natal dispersal distance, the proportion of
146 immigrant birds, and mean neighbourhood age affect cultural change within a neighbourhood. We find that
147 higher levels of these factors correlate with slower cultural change (Figure 4A; Table S2). Specifically, when
148 there is substantial dispersal, a high influx of immigrants, and an age distribution skewed towards older indi-
149 viduals, the model predicts slower cultural change, at less than half the rate compared to the converse scenario
150 (0.28 CI_{95%} [0.23, 0.34] vs. 0.61 CI_{95%} [0.49, 0.76], as illustrated in Figure 4E). This twofold difference in cul-
151 tural turnover, based on realistic parameter values, is likely to significantly influence the cultural composition
152 of neighbourhoods over time if it persists, highlighting the importance of the demographic structure of popula-
153 tions in also moderating the pace of cultural change.

154 The observed slowdown in cultural change due to dispersal and immigration aligns with our findings that
155 dispersal homogenizes song repertoires, and immigrants tend to adopt the existing population's variants rather
156 than introducing new ones (see Figure 2A and Figure 3A). At the same time, our estimate for the effect of neigh-
157 bourhood age ($P(\beta_{age} < 0 | D) = 1$, $mem = -0.044$, $CI_{95\%} [-0.063, -0.026]$; Figure 4C) aligns with modelling
158 work suggesting that learning from older individuals should also slow down cultural change.²³ Age may serve
159 as a brake on change, potentially increasing the relative cultural diversity and novelty within neighbourhoods
160 by preserving song types now less frequent in the population, as supported by the individual-level analysis
161 where birds become more dissimilar as they are further in time (Figure 3C).

162 Consequences for cultural structure, stability and diversity

163 Cultural traits, learnt bird song in this case, are shaped by many factors: some external, such as those discussed
164 here, others intrinsic to learning and culture, and yet others that arise from selective processes driven by prefer-
165 ence and function. Even within the confines of a relatively small population—Wytham Wood spans a mere four
166 kilometres—we have recovered associations between heterogeneity in the demographic composition of neigh-
167 bourhoods and cultural outcomes. This emphasises the need for both empirical studies and modelling efforts
168 on cultural change to account for the population's demographic characteristics and their inherent heterogeneity
169 across time and space, which shape individuals' exposure to cultural variants and opportunities for learning
170 and, therefore, emergent group-level cultural dynamics.

171 METHODS

172 Resource availability

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

176 Data collection

177 Study system and fieldwork

178 Great tits are small, short-lived birds—average lifespan: 1.9 years—that sing acoustically simple yet highly
179 diverse songs. Each male great tit has a repertoire of one to over 10 song variants, referred to as 'song types,'

which are repeated multiple times in short bursts separated by longer periods of silence. During the breeding season, from March to June, great tit pairs are socially monogamous and defend territories around their nests.⁵⁸ In Wytham Woods, Oxfordshire, UK ($51^{\circ}46'N, 1^{\circ}20'W$), a population of these birds has been the focus of a long-term study since 1947.³⁴ Wytham Woods is a semi-natural, predominantly deciduous and partly discontinuous woodland that spans an area of approximately 385 hectares and is surrounded by farmland. Most great tits in this population breed in nest boxes with known locations, and the majority of individuals are marked with a unique British Trust for Ornithology (BTO) metal leg ring as either nestlings or adults.

We collected data from late March to mid-May during the 2020, 2021, and 2022 breeding seasons. Every year, fieldworkers checked each of the 1018 nest boxes at least once a week before and during the egg-laying period, which typically lasts from one to 14 days,⁵⁹ and recorded the identities of breeding males and females, the dates of clutch initiation and egg hatching, clutch size, and fledgling number and condition under standardised protocols. We found the first egg date by assuming that one egg is laid every day and counting back from the day of observation. In cases where we did not observe the chicks on their day of hatching, the actual hatching date was determined by assessing the weight of the heaviest chicks and extrapolating their age from established growth curves.^{60,61}

Nest box occupancy and breeding density vary across the study area, with some areas having a higher density of nest boxes and a higher proportion of occupied boxes. In the years of our study, XXX, XXX and XXX were occupied, with XXX, XXX and XXX successful breeding attempts where at least one chick fledged.

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.⁶² 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.^{63,64} 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. Our goal was to maintain a consistent position and orientation for the recorder. 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, and 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 was 10 metres.⁶⁵ The birds also changed perches and moved around during our recording. Although variation in sound amplitude due to changes in distance and direction could affect song selection, we did not observe systematic bias, ruling out potential issues like consistently low signal-to-noise ratios causing exclusion of entire song types.

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).

215 Recording equipment and schedule

We used 60 (30 in 2020) AudioMoth recorders,⁶⁶ 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 days before moving it to a different nest box. We relocated 20 recorders (10 in 2020) every day throughout the recording period.

222 Data processing and annotation

We processed and annotated the song recordings, 109,963 in total, using custom software and scripts written in Python³⁶⁷ and the open source package `pykanto`.⁶⁸ These are available from github.com/nilomr/great-tit-hits-setup.⁶⁹ Our annotated dataset and a detailed description of the process can be found in Merino Recalde et al.⁴⁴

227 Identifying individuals and their traits

We were able to identify an additional 31 song repertoires and assign them to a subset of birds that we failed to capture or identify using PIT (Passive Integrated Transponder) tags by training a deep metric learning model (see⁴⁴ for details) to recognise individual songs, which we then used to assign unknown repertoires to existing individual IDs. This increased the number of identified repertoires from 299 to 330, belonging to 242 unique birds. Briefly, we calculated pairwise song distances using the feature vectors obtained from the trained model. Then we assigned unknown song repertoires to known birds if they met two conservative criteria: that at least

234 two songs had a Euclidean distance below 0.9, and that the unknown singer was recorded less than 100 me-
 235 tres apart from the known individual (see Figure S3 for a graphic explanation). Natal dispersal distance was
 236 calculated as the straight line distance from the natal site to the breeding site. The dispersal distances of birds
 237 classed as immigrants (not ringed as chicks in the population) are not known, but most are thought to come
 238 from other populations at least 1 km, and likely more than 2.5 km, away.^{50,70} We determined age based on the
 239 year of hatching for birds born in the population; and plumage characteristics for immigrants, which are most
 240 often caught as yearlings (76%)—allowing us to age them accurately.⁷¹

241 Characterising repertoire similarity

242 Our analyses require i) a measure of the acoustic similarity between any two birds, and ii) a way to identify
 243 song cultural variants. The underlying assumption is that song repertoires will be more similar if one bird has
 244 learned it at least in part from a second, or if they have both learnt from other individuals who are themselves
 245 similar due to intergenerational cultural descent. There is no single optimal solution for this problem, both due
 246 to technical challenges and because we do not know enough about song perception and learning mechanisms
 247 in this species. There are three main possible approaches, each with its own advantages and disadvantages.

248 Continuous similarity

249 Traditional methods used to compare bird vocalisations include visual inspection of spectrograms and measure-
 250 ment of hand-picked acoustic features. However, these approaches have limitations in dealing with noise and
 251 variations in performance and can be extremely time-consuming. So, instead, we adopted a data-driven ap-
 252 proach by training a Vision Transformer (ViT) model for feature extraction in a metric learning task. Our goal
 253 was to create a similarity space based on inherent variation in the data, using categorical labels of song types
 254 sung by individual birds, which we know to be perceptually and behaviourally significant.⁷² Further details
 255 and code are available at⁶⁸ and⁴⁴. We used the resulting model to calculate feature vectors for each song in
 256 the dataset (109,963 samples x 384 dimensions), which serve as compressed representations that can be used to
 257 compare them.

258 Great tits have variable repertoire sizes and there is no evidence that they ever learn them en bloc.^{42,73} There-
 259 fore, the simplest continuous measure (an average pairwise Euclidean distance between all songs) would mask
 260 any signatures of learning if the average repertoire similarity is similar across the population, and does not take
 261 into account the asymmetry in total repertoire size. To improve on this, we define repertoire similarity as the
 262 average minimum Euclidean distance (AMED), given by

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

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

269 Automated clustering

270 Instead of calculating a continuous measure of repertoire similarity, we can build a pairwise distance matrix for
 271 all songs, assign them to discrete clusters using a clustering algorithm, and then calculate the intersection be-
 272 tween repertoires by using the Jaccard coefficient or modelling it as a binomial process, with n = the combined
 273 repertoire size and s = the number of songs in the same cluster. Here we used UPGMA hierarchical cluster-
 274 ing and dynamic tree-cut techniques to classify the syllables into distinct types (since songs consist of repeated
 275 syllables, syllable and song types are synonymous in this species). We allowed a minimum cluster size of 1 to
 276 ensure the representation of rare song types. The usefulness of this method relies on the global properties of the
 277 embedding space derived the *Continuous similarity* process. In a low-dimensional space where linear distances
 278 effectively capture meaningful variation, creating clusters by cutting the hierarchical tree at different heights
 279 yields varying cluster counts while maintaining meaningful groupings. However, in a high-dimensional space
 280 where global distances are not meaningful, only relatively small clusters of nearby points remain interpretable.
 281 This is the case with our dataset and embedding space: we find that the method reliably groups song rendi-
 282 tions by the same bird across different years, alone or together with other birds with highly similar songs, yet
 283 consistently splits songs that are similar by human (and perhaps great tit⁷⁴) standards, ultimately leading to a
 284 very large number of clusters (the most stable clustering solutions were close to the total number of different
 285 individual song types, >1000). Due to these issues, we did not use song types defined in this way.

286 **Manual categorization**

287 All great tit song research has, to date, visually classified songs into population-level types.^{27,42,74–78} This process
 288 is both inevitable and very subjective. However, despite its clear problems, human perceptual judgments might
 289 be our best available substitute for those of the birds (but see recent work by Morfi et al.⁷⁹ and Zandberg et al.⁸⁰)
 290 for some tasks. Indeed, across fields, advanced classification algorithms are often evaluated against ground
 291 truth created by humans, and this is also the case in bird song research.

292 Our neighbourhood-level analyses require that we define discrete cultural units, so, given the difficulties
 293 with the alternatives described above, we adopted a variant of this approach and used the criteria followed by
 294 McGregor and Krebs⁴² and most subsequent work. With over 100,000 songs, our dataset is much larger than is
 295 common in the field and would have been impossible to label entirely manually. Instead, we used the output of
 296 the automated clustering process described above, consisting of labelled song repertoires (birdID x song type).
 297 This made the problem 57 times smaller: 1920 song variants that were already assigned to small clusters of
 298 highly similar songs, which we reviewed manually.

299 Following common practice in the field, we validated our manually assigned labels statistically, although
 300 we note that i) the ability of a statistical method to differentiate between manually defined clusters does not
 301 mean that these are perceptually meaningful, only that they can be distinguished in a manner that aligns with
 302 human classification, and ii) a large range of clustering solutions will be compatible with the data. To do this,
 303 we retrained the ResNet50-based classifier described in Merino Recalde⁶⁸ using a random subset of the data and
 304 obtained an accuracy of 0.87 on the validation set (see other metrics in the repository). With the caveats already
 305 mentioned, this means that our manual classification following McGregor and Krebs⁴² is successful at finding
 306 a stable solution that reduces intraclass variation. A comparable process by Fayet et al.²⁷ was able to reach 0.71
 307 accuracy for 374 songs. We further explored the result by building a dendrogram based on the confusion matrix
 308 during test time and reviewing the classes that were not well-supported, which led us to combine seven classes
 309 into two. There is an inverse relationship between how densely occupied a region of the song space is and
 310 the ease with which we can find categorical divisions: the more examples the more graded the variation and,
 311 in consequence, what may have seemed like clear-cut categories if we had fewer data blend into one another
 312 without an obvious transition.

313 In practical terms, because most of the great tits in our population sing some variation of the well-known 'tea-
 314 cher, tea-cher' song, these are much harder to categorize than the many rare songs with complex structures only
 315 sung by one or a few birds. This was our impression when manually labelling the songs, and it was also the case
 316 when applying the supervised classification algorithm. As mentioned in the main text, the direct consequence
 317 of this for our analysis is that the absolute estimates of cultural turnover depend on the granularity of this
 318 process: when we lump all similar 'tea-cher' songs, as McGregor and Krebs⁴² do, the estimates of turnover are
 319 necessarily lower—but, crucially, any relative differences remain the same. The code used to perform the song
 320 type validation process, along with the figures generated during it, can be found in [the main narrative notebook](#)
 321 and a [dedicated repository](#).

322 **Quantification and statistical analysis**323 **Pairwise similarity and individual repertoire models**

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

330 **Individual repertoires** We first modelled individual repertoire size using Poisson and negative binomial models,
 331 but this led to poor performance as assessed through posterior predictive checks (both underestimation of mean
 332 values and either under or over-estimation of very low repertoire sizes). Instead, we built continuation ratio
 333 models, a type of sequential ordinal model where reaching a particular level (number of song types in the reper-
 334toire) requires first reaching all lower levels.^{81,82} rep_{m_1} , $rep_{m_{1,1}}$, and $rep_{m_{1,2}}$ estimate the association between immi-
 335 grant status, distance dispersed, age, and repertoire size. Three further log-normal models, $repnov_{m_1}$, $repnov_{m_{1,1}}$,
 336 $repnov_{m_{1,2}}$, do the same for the average cultural diversity of individual repertoires

337 **Pairwise similarity** Our first model ($disp_{m_1}$) explores the interaction between natal distance, that is, the distance
 338 between the nests where two resident birds were born, and the distance between the centre of their breeding
 339 territories, adjusting for year and absolute age difference. We do not have direct information on how long birds
 340 have spent around one another, so instead we estimate the effect of the interaction of the distance at which

they were born and the distance at which they subsequently breed: If both are small, they will have had more opportunities for interaction and learning. We extract predictions for the interaction and calculate marginal effects at minimum distances, to answer the questions 'How does cultural similarity change with distance for birds that were born nearby' and 'Does how close a bird was born matter for birds that hold territories nearby'. We use a similar model structure (age_{m_1}) to estimate the marginal effects of the absolute age difference, this time adjusting for the natal and territorial distance between birds. Then, to study the effect of immigration, we fit a model (imm_{m_1}) with the possible combinations of immigration status (both immigrant, both residents, one of each) and adjust for age difference and territorial distance.

349 **Group-level properties**

350 **Defining neighbourhoods and their demographic properties** Song turnover, diversity, and novelty are group-level properties. However, our study lacks naturally occurring distinct subpopulations that we can use as units for analysis. Rather than partitioning the population using a discrete polygonal grid or non-overlapping areas, we opted to model neighbourhoods continuously across space, with a radius of 200 m around each nest box occupied at least once during the study²⁷ which we sampled across the duration of the study. This radius is necessarily arbitrary but strikes a good compromise between describing the relevant spatial scale at which vocal interactions occur, which extends up to around 180 metres,^{83,84} and maintaining an adequate sample size in areas of low density. Neighbourhoods defined in this way are highly non-independent, so we model both this methodological spatial dependence and other sources of spatial autocorrelation intrinsic to the study site by including a 2D Gaussian process (GP), which estimates a length-scale parameter defining a variance-covariance matrix for the spatial locations based on their distance.^{85–87} We confirmed that this eliminated the residual spatial autocorrelation via Moran's I tests. Note that we fit a separate GP for each year, as treating the spatial dependence as fixed across the study duration, as is often done, risks further underestimating uncertainty.

363 We define our predictor variables in the following way: Individual turnover is the proportion of birds that
 364 were not already in a neighbourhood in the preceding year ($Ind. Turn. = 1 - \frac{|N_{current} \cap N_{previous}|}{|N_{current}|}$). Dispersal is
 365 the mean of the distances that birds in the neighbourhood travelled to get from their natal territories to their
 366 breeding territories if they were hatched within the Wytham population. Immigration is the proportion of birds
 367 that were not ringed as nestlings in the population, and neighbourhood age is the mean age of the birds within
 368 it. Figure S1 illustrates that our sampling process did not introduce bias into any of these predictor variables:
 369 the birds from which we recorded song repertoires were, on average, representative of the true neighbourhood
 370 composition.

371 **Operational definitions of cultural diversity, novelty, and turnover** We calculated a simple diversity index by dividing
 372 the number of different song types by the total number of songs in a neighbourhood. To calculate the novelty
 373 index, we computed the relative frequency of each song type in the current year in the entire population. We
 374 then took the mean of these relative frequencies for each song type in the neighbourhood, took the logarithm of
 375 the inverse of this proportion and scaled it between 0 and 1. In this way, 'diversity' describes the proportion of
 376 unique songs in a neighbourhood, and 'novelty' refers to how uncommon, on average, the songs of the birds in
 377 a neighbourhood are. These two ways of characterising cultural diversity are (as expected) anti-correlated in our
 378 study site due to the effect of sampling: more frequent songs are sampled more readily, causing larger sample
 379 sizes (neighbourhoods with more density and therefore songs) to yield lower average estimates of diversity and
 380 higher average estimates of novelty, in a nonlinear manner. Once this is adjusted for, diversity and novelty are
 381 positively correlated, as expected (see Figure S2; models nov_{m_2} and $nov_{m_2,1}$). All of our models adjust for this
 382 sampling effect.

383 **Models** To study the effect of dispersal and immigration on local cultural diversity and novelty, we built log-
 384 normal models (div_{m_1} , nov_{m_1}) and estimated the marginal effects of the proportion of immigrants, mean dis-
 385 persal distance, and mean neighbourhood age, while also adjusting for individual turnover, year, and spatial
 386 dependence. Lastly, to examine whether the effects of immigration and dispersal on cultural diversity were
 387 related to individual differences in repertoire size and novelty, we fit two further models predicting the abso-
 388 lute number of unique songs in a neighbourhood while also adjusting for the number of birds (div_{m_2}) and the
 389 number of songs ($div_{m_2,1}$).

390 We calculated the rate of song cultural turnover as the proportion of unique song types in a given year that
 391 were not already present in the same neighbourhood the preceding year, and this was the response variable in
 392 two models: one ($turn_{m_1}$) trying to estimate the total effect of turnover and a second ($turn_{m_2}$) estimating the
 393 marginal effects of the proportion of immigrants, mean dispersal distance, and mean age while also adjusting
 394 for individual turnover, year, and spatial dependence. In both cases, we modelled the response distribution as
 395 a truncated log-normal with a hurdle (logistic) part to account for the zeroes.

396 **Model estimates and reporting**

397 We built the models and approximated the posterior distributions of the parameters of interest using brms,⁸⁸
 398 an interface to the Hamiltonian Monte Carlo engine Stan.⁸⁹ We then processed the posterior distributions with
 399 the help of the marginal effects package. We checked model convergence via the effective number of samples,
 400 visual inspection of the chain trace plots, and the Gelman-Rubin diagnostic. Estimation in a Bayesian framework
 401 returns a posterior distribution of possible values instead of point estimates. By convention, we report posterior
 402 central estimates (means or medians) and their 95% credible intervals, but also include plots with full posteriors.
 403 Note that categorical predictors are dummy-coded and continuous predictions z-score transformed.

404 For each parameter of interest, we calculated predictions or marginal effects at the means or other relevant
 405 values. Regression plots show predicted values of the mean and their credible intervals, as well as partial
 406 residuals adjusted to the means or other relevant values of the explanatory terms included in the model.^{90,91} We
 407 have tried to build reasonable models, but even then our estimates should not be interpreted causally. See the
 408 software section at the end for a complete list of libraries used in the various analyses and the code repository
 409 for full model specifications.

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415 **AUTHOR CONTRIBUTIONS**

416 **Nilo Merino Recalde:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation,
 417 Writing - Original Draft, Writing - Review & Editing, Visualization. **Andrea Estandía:** Investigation, Data
 418 Curation, Writing - Review & Editing. **Sara C. Keen:** Writing – Review & Editing. **Ella F. Cole:** Supervision,
 419 Project Administration. **Ben C. Sheldon:** Supervision, Project Administration, Writing – Review & Editing,
 420 Funding Acquisition.

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626 SUPPLEMENTARY INFORMATION

Table S1. 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
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	novelty ~ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(n_current_songs) + year + gp(x, y, by = year, k = 25, c = 5/4, scale = F)	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, k = 25, c = 5/4, scale = F)	lognormal	791	GP
nov_m_2	novelty ~ 0 + diversity + s(n_current_songs) + year + gp(x, y, by = year, k = 25, c = 5/4, scale = F)	lognormal	791	GP
nov_m_2.1	novelty ~ 0 + diversity + year + gp(x, y, by = year, k = 25, c = 5/4, scale = F)	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, k = 25, c = 5/4, scale = F)	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, k = 25, c = 5/4, scale = F)	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

Table S2. 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
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

629 ^a Estimates are Medians and 95% Credible Intervals

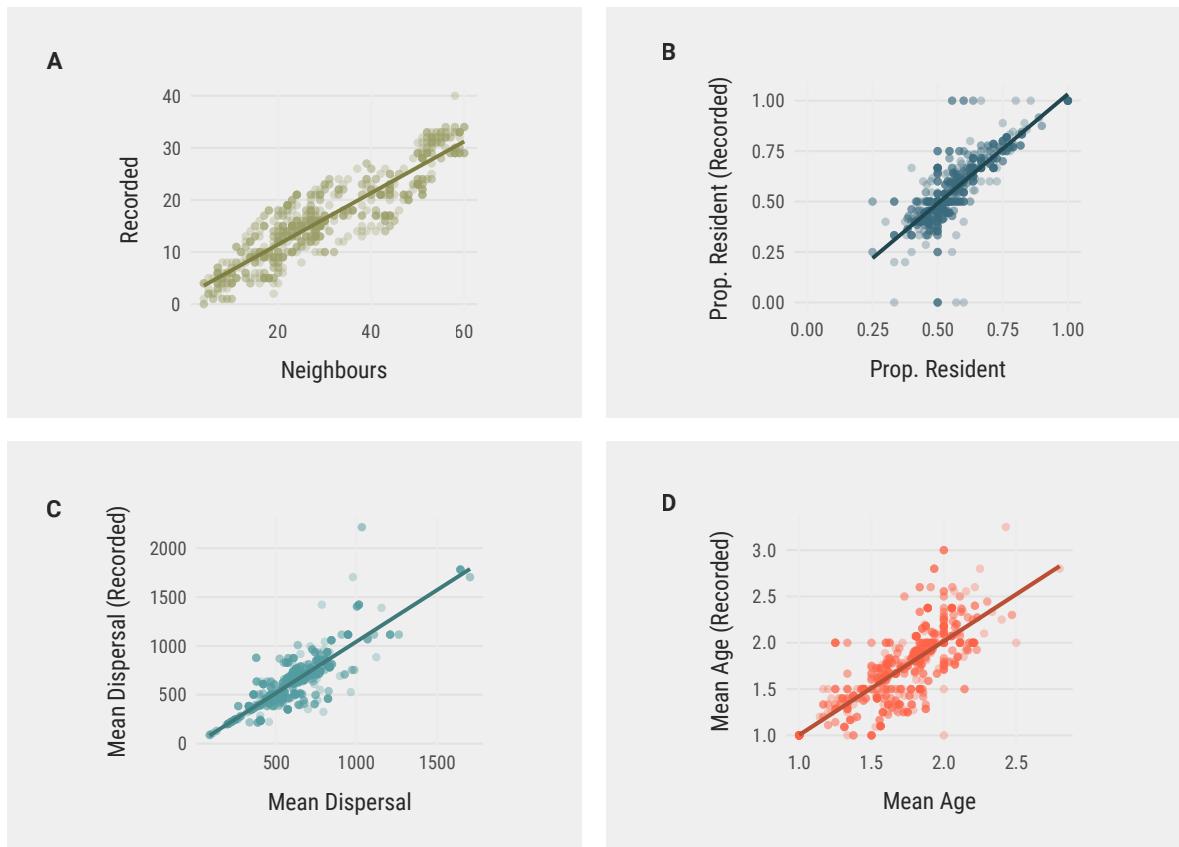


Figure S1. Absence of bias in the sampling of neighbourhood properties.

Correlation 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 with song recordings. (B) Proportion of resident birds from monitoring data and only those birds with song recordings. (C) Mean dispersal distance calculated from birds born in the study site and only those birds born in the study site with song recordings. (D) Mean age of birds in the study site and only those birds with song recordings.

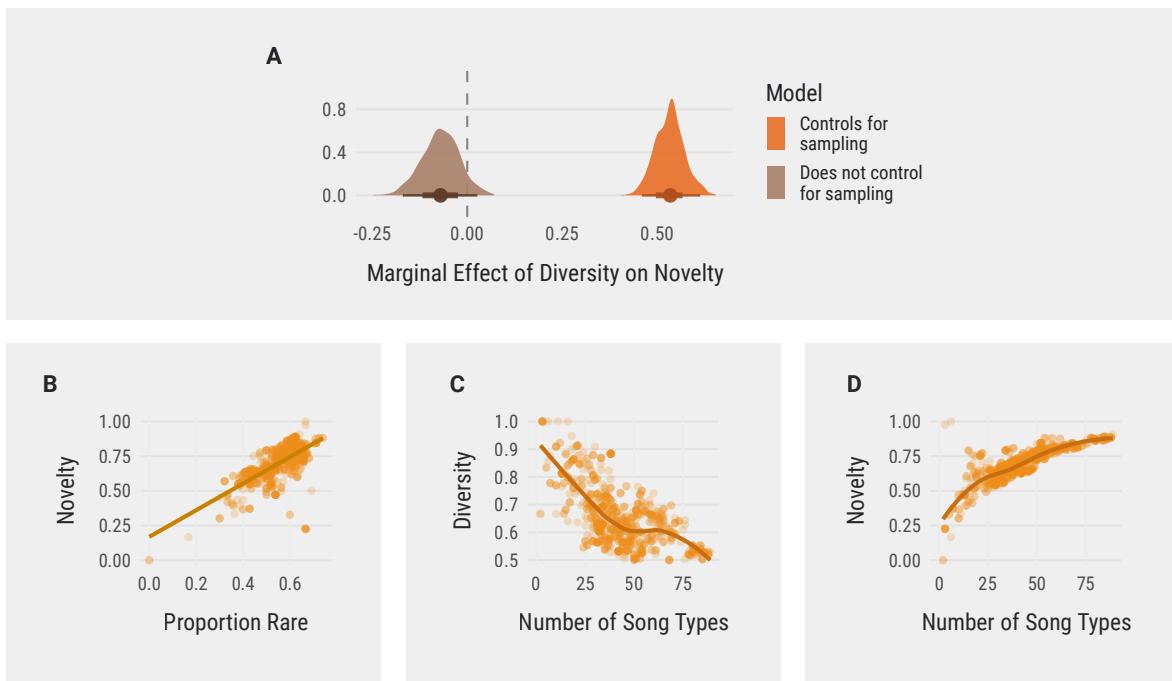


Figure S2. Relationships among outcome variables and sampling effects.

(A) Marginal effect of diversity—which describes the proportion of unique songs in a neighbourhood—on novelty, that is, how uncommon, on average, the songs of the birds in a neighbourhood are. These two ways of characterising cultural diversity are (as expected) 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 novelty (D), in a nonlinear manner. Once this is adjusted for, diversity and novelty are positively correlated, as expected. (B) Our measure of cultural novelty (y-axis) has the advantages of being continuous and not using an arbitrary cutoff, but is nonetheless correlated with definitions traditionally used in the literature, such as ‘songs shared by fewer than 4 birds’⁴².

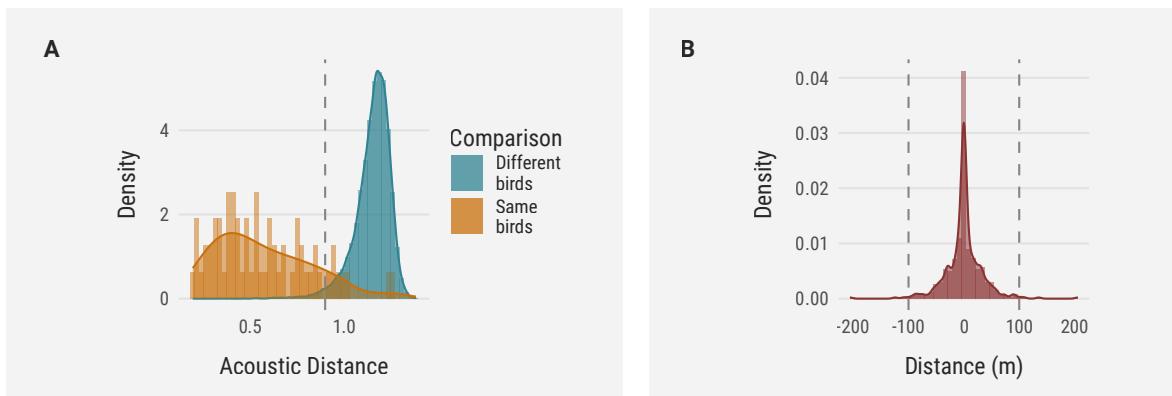


Figure S3. Thresholds used during the process of reidentifying individual birds based on their songs.

(A) Shows the distribution of the acoustic distances between the same song type sung by the same known bird in different years, in orange, and the minimum pairwise distance between different birds and years. The x-intercept of the vertical line = 0.9. (B) Shows the distribution of the change in distance from the natal nest box to the breeding site in different years for birds that bred more than once. Adult birds have high nest site fidelity, which we used as a further constraint when reidentifying them from their songs.

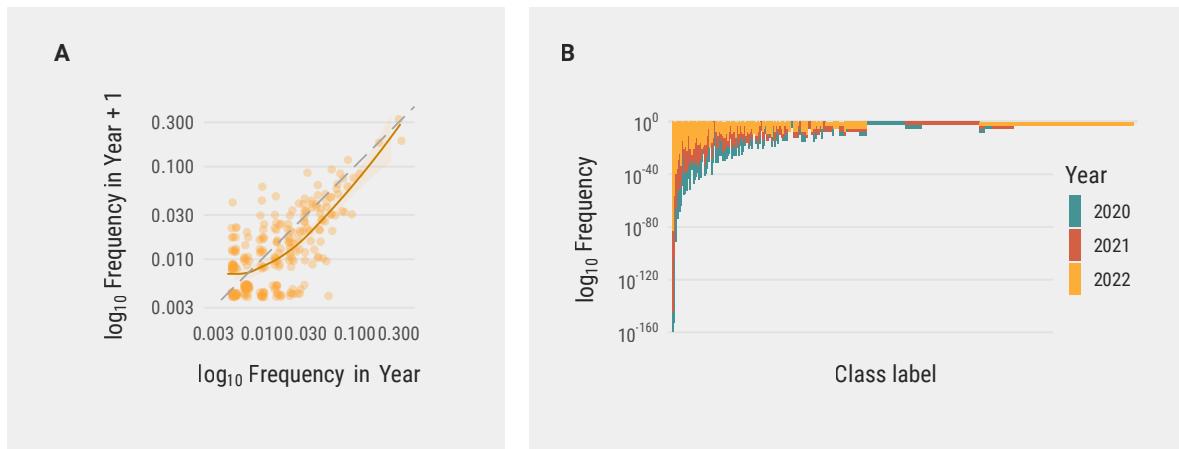


Figure S4. Song frequencies and their relationship with abundance in the following year.

(A) The abundance of a song type in a given year predicts its abundance in the following year, with higher variance around rare songs.
 (B) Histogram showing the frequency of individual song types in the study.

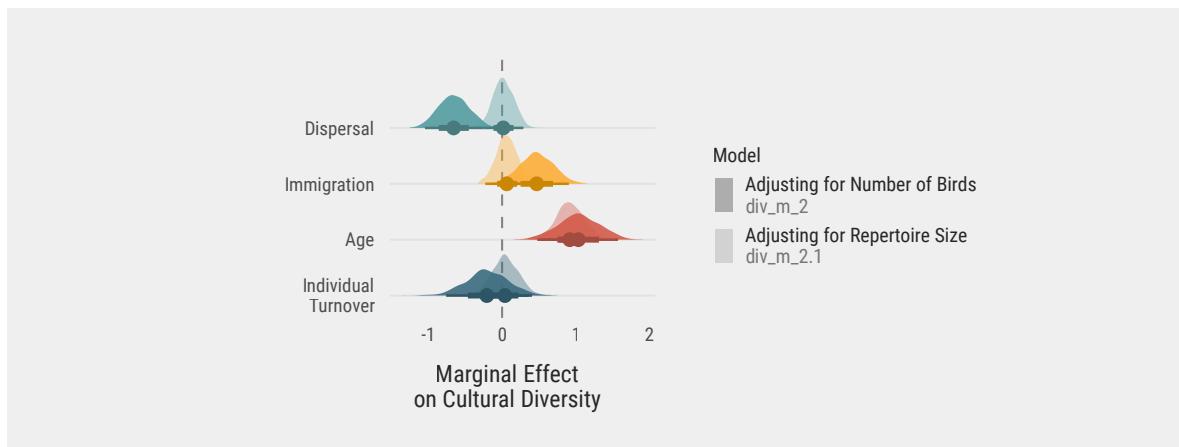


Figure S5. Marginal effects of demographic variables on absolute cultural diversity.

Marginal effects of our predictor variables on absolute cultural diversity (the number of different song types sampled in a neighbourhood), while adjusting for the effect of either number of individuals (higher opacity fill, corresponding to model div_m_2) or number of song variants, including repeated variants (lower opacity fill, $div_m_2.1$).

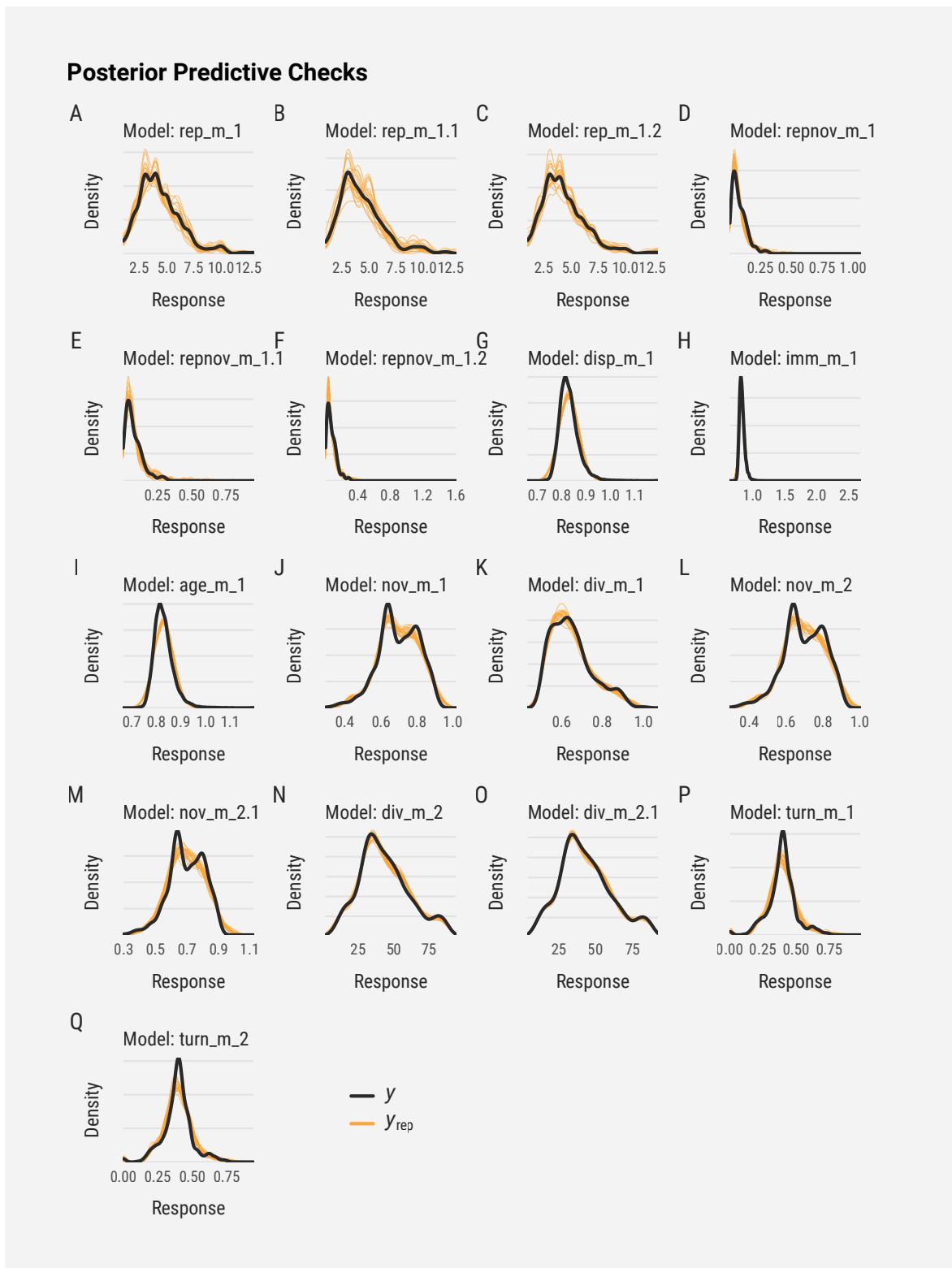


Figure S6. Posterior predictive checks for the main models in the study.

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.