

# 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 adopt existing 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. The main driver of cultural turnover is individual turnover; at the same time, dispersal, a higher proportion of immigrant birds, and an older population slow change down. Our analyses support theoretical expectations regarding a key role of demographic processes in cultural evolution, while highlighting their interaction with species-specific factors such as the timing of song acquisition.

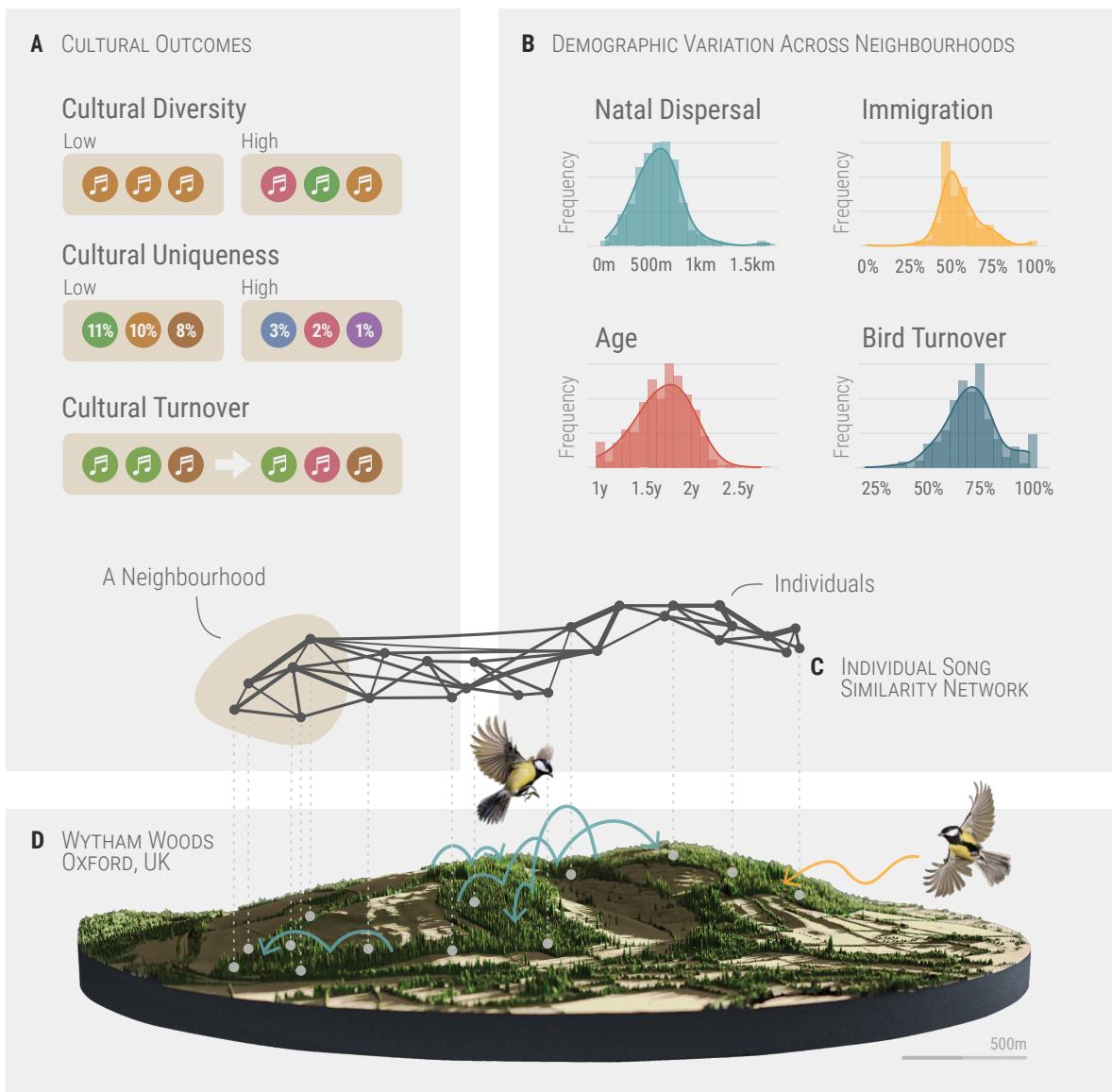
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## RESULTS AND DISCUSSION

Some behavioural traits are shared and persist within communities due to social learning.<sup>1</sup> We refer to these behaviours as 'animal culture', exemplified by tool use in capuchin monkeys,<sup>2</sup> the learned songs of oscine birds, migration routes,<sup>3–5</sup> and the feeding techniques of some cetaceans.<sup>6,7</sup> Animal cultures are not static: neutral and selective mechanisms influence the frequency of cultural traits,<sup>8,9</sup> leading to a process of cultural evolution. The resulting cultural traditions differ considerably in their diversity and stability,<sup>10</sup> determined by both learning biases and mechanisms and the demographic structure of populations.<sup>11,12</sup>

While the role of social learning strategies and biases—frequency dependence, tutor biases, etc.—has been extensively studied,<sup>13–17</sup> 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 emphasized by theoretical work.<sup>11,18–27</sup> However, translating theoretical expectations into empirical evidence remains a challenge (see<sup>28–30</sup> for exceptions).

Culture is increasingly recognized as both a fundamental aspect of many animals' lives and a valuable tool in monitoring and conservation efforts.<sup>33,34</sup> 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,<sup>33</sup> and can be lost when habitat fragmentation and population decline lead to reduced learning opportunities.<sup>35,36</sup> 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: Diversity is the relative number of unique song types in a neighbourhood; uniqueness is the complement of the average frequency of those song types in the entire population, and turnover is the proportion of unique song types in a given year not present in the same neighbourhood the preceding year. See [methods](#) for full definitions.

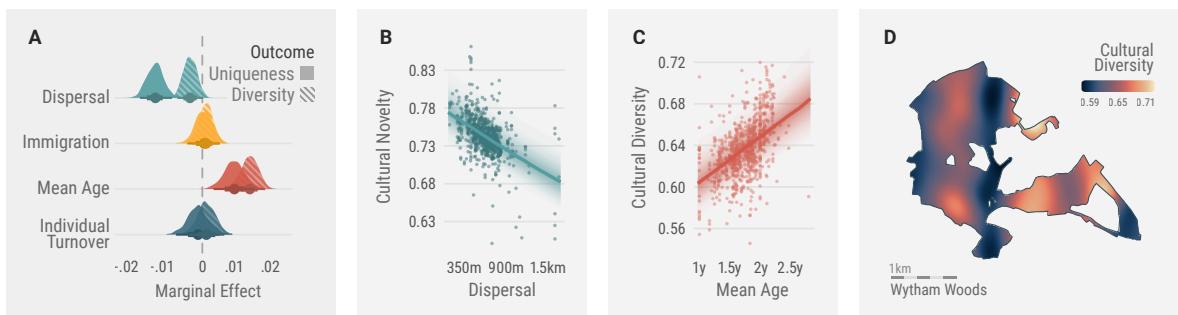
(B) Variation in the demographic properties and composition of neighbourhoods across the population. See [demographic variables](#) for full definitions.

(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 data<sup>31</sup> and made with rayshader.<sup>32</sup> Elevation is exaggerated. Aquamarine (darker) arrows represent natal dispersal within the population, and the yellow (lighter) arrow represents immigration into the population, two of the variables used in this work. Age and bird (individual) turnover are not depicted.

52 populations, as well as their relative importance.

53 To contribute to this goal, we built a comprehensive dataset that spans three years and documents the dawn  
 54 songs produced by male great tit birds during 454 breeding attempts in a single population located in Wytham  
 55 Woods, UK. The population's marked variation in individual turnover, postnatal dispersal distances, age struc-  
 56 ture, and immigration across space—known through ongoing long-term monitoring<sup>37</sup>—allowed us to estimate  
 57 their effects on song cultural repertoires at both individual and group levels. First, we assign more than 109,000  
 58 songs in 330 song repertoires to 242 individual birds through a combination of direct physical capture, radio fre-  
 59 quency identification microchips, and a novel song-based reidentification method using a deep metric learning  
 60 model. Then, we quantified individual and group-level traits and analysed variation in song cultural simi-  
 61 larity, diversity, and turnover (see [definitions](#)) using network and spatially explicit Bayesian multilevel regression  
 62 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. (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 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.

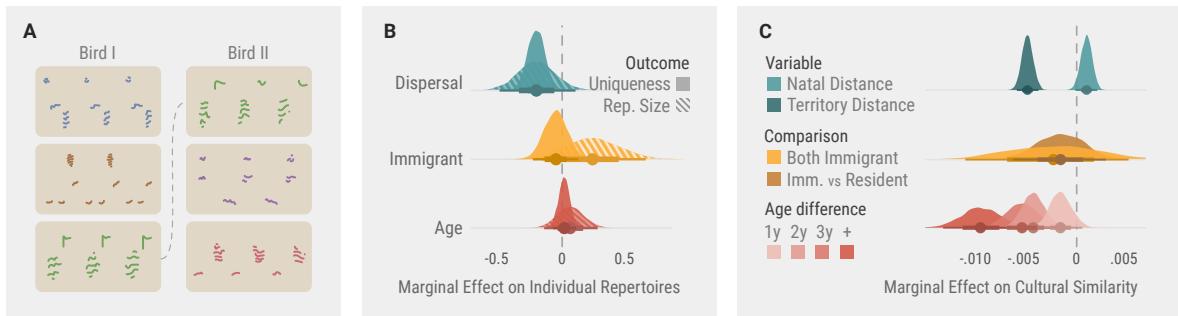
Our results reveal an interplay of demographics and song cultural dynamics that, albeit complex, largely matches theoretical expectations, as discussed below. This work also demonstrates that bird song, which already provides what is perhaps the largest body of evidence for cultural change in animals,<sup>38</sup> also has the potential to help us shed light on the impact of other population processes on animal cultures, owing to the fact that we can sample song cultural repertoires with relative ease.

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

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.<sup>39–41</sup> 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.<sup>24</sup> This, in turn, should result in the maintenance of distinct behavioural patterns within populations if learning is somewhat accurate, leading to a greater number of cultural variants unique to a neighbourhood or region.<sup>42,43</sup> Our analysis indeed indicates that neighbourhoods where more birds have remained in proximity to their natal areas harbour greater and more unique cultural diversity (*diversity*:  $P(\beta_{disp}(\bar{m}) < 0|D) = 1$ , *mem* =  $-0.018$ ,  $CI_{95\%} [-0.023, -0.012]$ ; *uniqueness*:  $P(\beta_{disp}(\bar{m}) < 0|D) = 0.96$ , *mem* =  $-0.005$ ,  $CI_{95\%} [-0.01, 0]$ ; Figure 2A&B, Table S3), in line with prior research at a much coarser grain.<sup>29</sup>

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 (see<sup>44</sup> 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  $\simeq 10$  different song types.<sup>45–47</sup> 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 (*uniqueness*:  $P(\beta_{disp(m)} < 0|D) = 1$ , *mem* =  $-0.2$ ,  $CI_{95\%} [-0.3, -0.09]$ ; Figure 3B, Table S3), 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 S3). 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 would emerge under positively frequency-dependent learning or a process leading to similar acquisition curves (see Figure S10; note that we do not currently know which learning strategies are employed by great tits).

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,<sup>46</sup>



**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 stylized 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 sang by that bird) and their relative 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 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.

and become chiefly sedentary as adults.<sup>48–50</sup> 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.<sup>51,52</sup>

Indeed, in our population, we find no evidence that the repertoires of birds originating from outside the population significantly differ acoustically from those of resident birds ( $mem = -0.002$ ,  $CI_{95\%} [-0.006, 0.002]$ ; Figure 3C). This, in conjunction with the observation that song repertoire similarity between individuals is predicted by the distance between breeding territories ( $mem = -0.005$ ,  $CI_{95\%} [-0.006, -0.004]$ ; Figure 3C; Table S3), supports the hypothesis that great tits are predominantly closed-end learners that learn primarily from territorial neighbours after dispersal.<sup>45,46</sup>

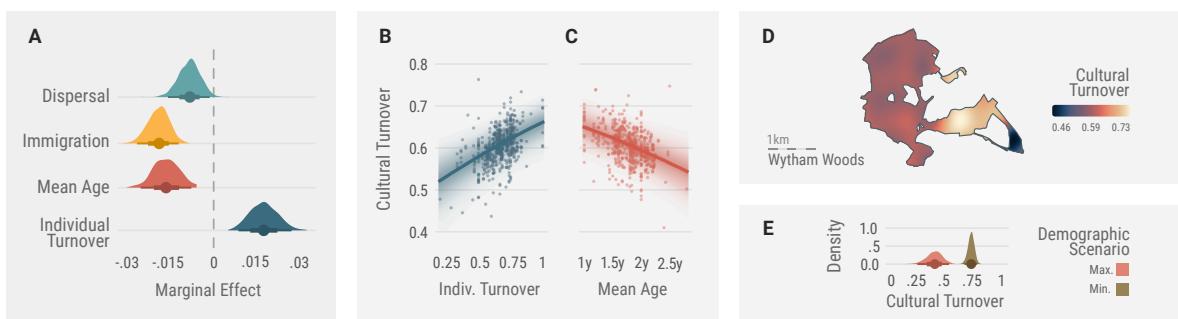
This leads to a somewhat contradictory scenario, however: immigrant birds, while not acoustically distinct, tend to have larger repertoires compared to their resident counterparts (Figure 3B;  $P(\beta_{imm.} > 0 | D) = 0.87$ ,  $mem = 0.24$ ,  $CI_{95\%} [-0.098, 0.593]$ ; Table S3). At the group level, 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 S9, Table S3).

Previous research<sup>53</sup> 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 metres<sup>48</sup>). 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.<sup>54–58</sup>

Finally, we find that individual turnover does not significantly affect cultural diversity or uniqueness, and we uncover an association between age structure and cultural diversity and uniqueness. 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 S3). 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 uniqueness (Figure 2A&C, Figure S9). Conversely, in areas where the majority of the population comprises younger birds surrounded by similar-aged peers, birds tend to produce fewer unique songs that are also more common within the population (diversity:  $P(\beta_{age} < 0 | D) = 1$ ,  $mem = 0.021$ ,  $CI_{95\%} [0.014, 0.027]$ ; uniqueness:  $P(\beta_{age} < 0 | D) = 0.99$ ,  $mem = 0.012$ ,  $CI_{95\%} [0.005, 0.019]$ ; Figure 2A&C, Table S3).

#### Demographic processes 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 types 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 types disappear with them, and the young birds that replace them might speed up the adoption of new song types.<sup>26</sup> Across the three-year study period, now considering



**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.

140 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 141 faced an equal chance of disappearing, this would quickly lead to complete cultural replacement. However, after 142 a two-year gap, turnover only slightly increases to 0.59%. We anticipate this rate to taper further over longer 143 periods, as rare variants encounter greater stochasticity while common songs endure ([Figure S8A](#)). Indeed, 144 some common song types documented over four decades ago persist within the population.<sup>45,51</sup> This persistence 145 might be due to different factors, like accurate learning based on song frequency, or strong tendencies to 146 converge on certain song types.<sup>16,17,59,60</sup>

147 After factoring in individual turnover, we examine how mean natal dispersal distance, the proportion of 148 immigrant birds, and mean neighbourhood age affect cultural change within a neighbourhood. We find that 149 higher levels of these factors correlate with slower cultural change ([Figure 4A](#); [Table S3](#)). Specifically, when 150 individuals have dispersed over greater distances to get to their breeding neighbourhood, there is a high influx 151 of immigrants, and the distribution of age is skewed towards older individuals, the model predicts slower 152 cultural change, at less than half the rate compared to the converse scenario ([0.66, 0.77] 0.39 CI<sub>95%</sub> [0.24, 0.51] 153 vs. 0.72 CI<sub>95%</sub>, as illustrated in [Figure 4E](#)). This twofold difference in cultural turnover, based on realistic 154 parameter values, is likely to significantly influence the cultural composition of neighbourhoods over time if it 155 persists, highlighting the importance of the demographic structure of populations in also moderating the pace 156 of cultural change.

157 The observed slowdown in cultural change due to dispersal and immigration aligns with our findings that 158 dispersal homogenizes song repertoires and that immigrants tend to adopt the existing population's variants 159 rather than introducing new ones (see [Figure 2A](#) and [Figure 3A](#)). At the same time, our estimate for the effect 160 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 161 modelling work suggesting that learning from older individuals should slow down cultural change.<sup>23</sup> Indeed, 162 age may serve as a brake on change, as older birds continue to sing song types that are becoming less frequent 163 in the population, an idea supported by the observation that individual birds' repertoires are least similar when 164 there is a large age difference ([Figure 3C](#)). The differences between the older and younger birds' repertoires also 165 increases cultural diversity and uniqueness within neighbourhoods that include many older birds, as discussed 166 above, suggesting an important role of age structure in shaping both cultural diversity and turnover.

## 168 Consequences for cultural structure, stability and diversity

169 Cultural traits, learnt bird song in this case, are shaped by many factors: some external, such as those discussed 170 here, others intrinsic to learning and culture, and yet others that arise from selective processes driven by preference 171 and function. Even within the confines of a relatively small population—Wytham Woods spans a mere 172 four kilometres—we have been able to recover associations between heterogeneity in the demographic composition 173 of neighbourhoods and cultural outcomes using a large dataset of song repertoires, and show that these 174 are most likely underlined by differences in individual learning and exposure to cultural variants. In particular, 175 dispersal within the population reduces cultural diversity and uniqueness. Birds that were born outside the 176 population seem to adopt existing 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 share similar song 177 types, while neighborhoods comprising both older and younger birds are more likely to exhibit a broader array 178 types, while neighborhoods comprising both older and younger birds are more likely to exhibit a broader array

of song types. Additionally, such neighborhoods are more likely to host a greater number of birds singing rare song types, perhaps because, as we also find, aged neighbourhoods have slower cultural turnover. The main driver of cultural turnover is individual turnover, and, at the same time, longer postnatal dispersal distances, a higher proportion of immigrant birds, and an older population slow it down. This emphasizes the need for both empirical studies and modelling efforts on cultural change to account for the population's demographic characteristics and their inherent heterogeneity across time and space, as these shape individuals' exposure to cultural variants and opportunities for learning and, therefore, emergent group-level cultural dynamics.

## 186 METHODS

### 187 Resource availability

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

### 191 Data collection

#### 192 Study system and fieldwork

193 Great tits are small, short-lived birds—average lifespan: 1.9 years—that sing acoustically simple yet highly di-  
194 verse songs. Each male great tit has a repertoire of one to over 10 song types, also referred to as song types,  
195 which are repeated multiple times in short bursts separated by longer periods of silence. Although detailed  
196 studies on how individual great tits learn their songs are limited, existing evidence suggests several key points.  
197 First, it appears that great tits do not learn their song repertoires from their fathers.<sup>45</sup> Instead, their song devel-  
198 opment is influenced by the songs they encounter during their early life until they establish a territory and breed  
199 for the first time. We do not currently know how precisely great tits learn songs, or how social interactions affect  
200 the process. This period of vocal learning results in a final crystallized repertoire that remains relatively stable  
201 afterward—a process known as close-ended learning.<sup>46</sup> Additionally, while there is evidence that birds can con-  
202 tinue to learn to recognize new songs later in life (that is, learning for discrimination, as opposed to learning  
203 for production), this ability seems to be limited compared to their early learning experiences.<sup>61</sup> Furthermore,  
204 females are able to individually recognize males based on their songs,<sup>62</sup> and even across a large population,  
205 individual song renditions can accurately indicate the identity of the bird producing them.<sup>47</sup>

206 During the breeding season, from March to June, great tit pairs are socially monogamous and defend terri-  
207 tories around their nests.<sup>63</sup> In Wytham Woods, Oxfordshire, UK (51°46 N, 1°20 W), a population of these birds  
208 has been the focus of a long-term study since 1947.<sup>37</sup> Wytham Woods is a semi-natural, predominantly decid-  
209 uous and partly discontinuous woodland that spans an area of approximately 385 hectares and is surrounded  
210 by farmland. Most great tits in this population breed in nest boxes with known locations, and the majority of  
211 individuals are marked with a unique British Trust for Ornithology (BTO) metal leg ring as either nestlings or  
212 adults.

213 We collected data from late March to mid-May during the 2020, 2021, and 2022 breeding seasons. Every year,  
214 fieldworkers checked each of the 1018 nest boxes at least once a week before and during the egg-laying period,  
215 which typically lasts from one to 14 days,<sup>64</sup> and recorded the identities of breeding males and females, the  
216 dates of clutch initiation and egg hatching, clutch size, and fledgling number and condition under standardized  
217 protocols. We found the first egg date by assuming that one egg is laid every day and counting back from the  
218 day of observation. In cases where we did not observe the chicks on their day of hatching, the actual hatching  
219 date was determined by assessing the weight of the heaviest chicks and extrapolating their age from established  
220 growth curves.<sup>65,66</sup>

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

226 To record the vocalisations of male great tits we took advantage of their behaviour during the reproductive  
227 period, when they engage in continuous singing near their nests at dawn before and during egg laying.<sup>67</sup> Col-  
228 lectively, this vocal display is referred to as the dawn chorus, and has been demonstrated to yield a reliable  
229 estimation of the song repertoire of individuals when recorded in full.<sup>68,69</sup> As soon as we suspected that a pair  
230 of great tits were using a nest box—based on nest lining materials, egg size if present, or other signs of activity—  
231 we deployed an autonomous sound recorder nearby. The microphone faced upwards and slightly away from  
232 the nest box, aligning with the nest box entrance hole's direction. The birds sang near the recorder: although  
233 we did not gather data on this aspect, our anecdotal observations were in line with a different population where

234 the average distance to the nest box while singing was 10 metres.<sup>70</sup> The birds also changed perches and moved  
 235 around during our recording. Although variation in sound amplitude due to changes in distance and direction  
 236 could affect song selection, we did not observe systematic bias, ruling out potential issues like consistently low  
 237 signal-to-noise ratios causing exclusion of entire song types.

238 For this study, we calculated postnatal dispersal distance was as the straight line distance from the natal site to  
 239 the breeding site. The dispersal distances of birds classed as immigrants (not ringed as chicks in the population)  
 240 are not known, but most are thought to come from other populations at least 1 km, and likely more than 2.5  
 241 km, away.<sup>53,71</sup> We determined age based on the year of hatching for birds born in the population and using  
 242 plumage characteristics for immigrants, which are most often caught as yearlings (76%)—allowing us to age  
 243 them accurately.<sup>72</sup>

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

#### 248 **Recording equipment and schedule**

249 We used 60 (30 in 2020) AudioMoth recorders,<sup>73</sup> which were housed in custom-built waterproof enclosures.  
 250 Recording began approximately one hour before sunrise (05:36 – 04:00 UTC during the recording period) and  
 251 consisted of seven consecutive 60-minute-long recordings with a sample rate of 48 kHz and a depth of 16-bit.  
 252 To sample as many birds as possible, we left each recorder at the same location for at least three consecutive  
 253 days before moving it to a different nest box. We relocated 20 recorders (10 in 2020) every day throughout the  
 254 recording period.

#### 255 **Data processing and annotation**

256 We processed and annotated the song recordings, 109,963 in total, using custom software and scripts written  
 257 in Python 3<sup>74</sup> and the open source package `pykanto`.<sup>75</sup> These are available from [github.com/nilomr/great-tit-hits-setup](https://github.com/nilomr/great-tit-hits-setup).<sup>76</sup> Our annotated dataset and a detailed description of the process can be found in Merino Recalde et  
 258 al.<sup>47</sup>

#### 260 **Re-identifying individuals from their songs**

261 In some cases, we failed to capture or identify birds using PIT (Passive Integrated Transponder) tags, as tags  
 262 sometimes malfunction, birds can be difficult to catch, or disappear before their chicks are old enough to attempt  
 263 this. We were able to match an additional 31 song repertoires belonging to this subset of birds with existing  
 264 individual IDs by training a deep metric learning model to recognize individual songs. This increased the  
 265 number of identified repertoires from 299 to 330, belonging to 242 unique birds. We summarise the process here,  
 266 but see<sup>47</sup> for details on model design and training.

267 Briefly, we calculated pairwise song distances using the feature vectors obtained from a vision transformer  
 268 on a metric learning task. This model achieved a mean average precision at 5 (mAP5) of 0.98 and a cumulative  
 269 matching characteristic at 1 (CMC1) of 0.98, which roughly means that in 98% of the queries made to the simi-  
 270 larity space on a held out test dataset the returned candidate song type by a bird is the correct one. Given that  
 271 the model was trained on almost 2000 classes, this means that there is enough individual information contained  
 272 in each song type to distinguish between birds with high confidence, even if we don't know just how precisely  
 273 they are able to learn songs from a tutor.

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

#### 283 **Characterizing repertoire similarity**

284 Our analyses require i) a measure of the acoustic similarity between any two birds for the individual-level  
 285 analyses, and ii) a way to identify categorical song types for the neighbourhood analyses. The underlying  
 286 assumption is that song repertoires will be more similar if one bird has learned it at least in part from a second,  
 287 or if they have both learnt from other individuals who are themselves similar due to intergenerational cultural

288 descent. There is no single optimal solution for this problem, both due to technical challenges and because we  
 289 do not know enough about song perception and learning mechanisms in this species. There are three main  
 290 possible approaches, each with its own advantages and disadvantages, which we describe below.

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

292 Traditional methods used to compare bird vocalisations include visual inspection of spectrograms and mea-  
 293 surement of hand-picked acoustic features. However, these approaches have limitations in dealing with noise  
 294 and variations in performance and can be extremely time-consuming. So, instead, we adopted a data-driven  
 295 approach by training a Vision Transformer (ViT) model for feature extraction in a metric learning task on spec-  
 296 trogram representations of great tit songs. Our goal was to create a similarity space based on inherent variation  
 297 in the data, using categorical labels of song types sung by individual birds, which we know to be perceptu-  
 298 ally and behaviourally significant.<sup>62</sup> Further details, data, and code to reproduce this process are available at<sup>75</sup>  
 299 and,<sup>47</sup> we include a summary here.

300 We optimized model performance using Triplet loss, a loss function that ensures the projection of a positive  
 301 sample (belonging to the same class as the anchor point) is closer to the anchor's projection than that of a  
 302 negative sample (belonging to a different class) by a specified margin.<sup>77,78</sup> During training, we mined hard  
 303 triplets—where the negative sample is closer to the anchor than the positive—and used the Adam optimizer  
 304 with a fixed learning rate of  $1 \times 10^{-5}$ .

305 To prevent the model from overfitting to irrelevant features within localized portions of the training data or  
 306 background noise, we applied various train-time data augmentation techniques.<sup>79–81</sup> These included random  
 307 cropping in the time domain, dropping out parts of the spectrogram, adding Gaussian and multiplicative noise,  
 308 equalization, sharpening, changes to brightness and contrast, blurring, and slight shifting in both time and  
 309 frequency domains. This leads to a more robust model that can generalize better.

310 Finally, we used the resulting model to calculate feature vectors for each song in the dataset (109,963 samples  
 311  $\times$  384 dimensions), which serve as compressed representations that can be used to compare them. Great tits have  
 312 variable repertoire sizes and there is no evidence that they ever learn them en bloc.<sup>45,82</sup> Therefore, the simplest  
 313 continuous measure (an average pairwise Euclidean distance between all songs) would mask any signatures of  
 314 learning if the average repertoire similarity is similar across the population, and does not take into account the  
 315 asymmetry in total repertoire size. To improve on this, we define repertoire similarity as the average minimum  
 316 Euclidean distance (AMED), given by

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

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

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

324 Instead of calculating a continuous measure of repertoire similarity, we can build a pairwise distance matrix for  
 325 all songs, assign them to discrete clusters using a clustering algorithm, and then calculate the intersection be-  
 326 tween repertoires by using the Jaccard coefficient or modelling it as a binomial process, with  $n$  = the combined  
 327 repertoire size and  $s$  = the number of songs in the same cluster. Here we used UPGMA hierarchical clustering  
 328 and dynamic tree-cut techniques to classify the syllables into distinct types (since songs consist of repeated syllas-  
 329 bles, syllable and song types are synonymous in this species). We allowed a minimum cluster size of 1 to ensure  
 330 the representation of rare song types. The usefulness of this method relies on the global properties of the embed-  
 331 ding space derived from the *continuous similarity* process. In a low-dimensional space where linear distances  
 332 effectively capture meaningful variation, creating clusters by cutting the hierarchical tree at different heights  
 333 yields varying cluster counts while maintaining meaningful groupings. However, in a high-dimensional space  
 334 where global distances are not meaningful, only relatively small clusters of nearby points remain interpretable.  
 335 This is the case with our dataset and embedding space: we find that the method reliably groups song renditions  
 336 by the same bird across different years, alone or together with other birds with highly similar songs, yet consis-  
 337 tently splits songs that are similar by human (and perhaps great tit<sup>83</sup>) standards, ultimately leading to a very  
 338 large number of clusters (the most stable clustering solutions were close to the total number of different individ-  
 339 ual song types,  $>1000$ ). Due to these issues, we did not use song types defined in this way, and performed an  
 340 additional manual categorization step.

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

342 All great tit song research has, to date, visually classified songs into population-level types.<sup>29,45,83–87</sup> This process  
 343 is both inevitable and very subjective. However, despite its clear problems, human perceptual judgments might  
 344 be our best available substitute for those of the birds for some tasks (but see recent work by Morfi et al.<sup>88</sup> and  
 345 Zandberg et al.<sup>89</sup>). Indeed, across fields, advanced classification algorithms are routinely evaluated against  
 346 ground truth created by humans, and this is also the case in bird song research.

347 Our neighbourhood-level analyses require that we define discrete cultural units, so, given the difficulties  
 348 with the alternatives described above, we adopted a variant of this approach and used the criteria followed by  
 349 McGregor and Krebs<sup>45</sup> and most subsequent work. With over 100,000 songs, our dataset is much larger than is  
 350 common in the field and would have been impossible to label entirely manually. Instead, we used the output of  
 351 the automated clustering process described above, consisting of labelled song repertoires (birdID x song type).  
 352 This made the problem 57 times smaller: 1920 song types that were already assigned to small clusters of highly  
 353 similar songs, which we reviewed manually.

354 Following common practice in the field, we validated our resulting 335 manually assigned labels statistically  
 355 (see [Figure S8](#)), although we note that i) the ability of a statistical method to differentiate between manually  
 356 defined clusters does not mean that these are perceptually meaningful, only that they can be distinguished in a  
 357 manner that aligns with human classification, and ii) a large range of clustering solutions will be compatible with  
 358 the data. To do this, we retrained the ResNet50-based classifier described in Merino Recalde<sup>75</sup> using a random  
 359 subset of the data and obtained an accuracy of 0.87 on the validation set (see other metrics in the repository).  
 360 With the caveats already mentioned, this means that our manual classification following McGregor and Krebs<sup>45</sup>  
 361 is successful at finding a stable solution that reduces intraclass variation. A comparable process by Fayet et al.<sup>29</sup>  
 362 was able to reach 0.71 accuracy for 374 songs. We further explored the result by building a dendrogram based  
 363 on the confusion matrix during test time and reviewing the classes that were not well supported, which led us  
 364 to combine seven classes into two. There is an inverse relationship between how densely occupied a region of  
 365 the song space is and the ease with which we can find categorical divisions: the more examples the more graded  
 366 the variation and, in consequence, what may have seemed like clear-cut categories if we had fewer data blend  
 367 into one another without an obvious transition.

368 In practical terms, because most of the great tits in our population sing some variation of the well-known ‘tea-  
 369 cher, tea-cher’ song, these are much harder to categorize than the many rare songs with complex structures only  
 370 sung by one or a few birds. This was our impression when manually labelling the songs, and it was also the case  
 371 when applying the supervised classification algorithm. As mentioned in the main text, the direct consequence  
 372 of this for our analysis is that the absolute estimates of cultural turnover depend on the granularity of this  
 373 process: when we lump all similar ‘tea-cher’ songs, as McGregor and Krebs<sup>45</sup> do, the estimates of turnover are  
 374 necessarily lower—but, crucially, any relative differences remain the same. Precisely quantifying turnover using  
 375 categorical metrics might be altogether impossible in some species, because song categories are not likely to be  
 376 natural kinds beyond the scale of interacting neighbours. See [Figure S4](#) for examples of song types defined in  
 377 this study.

378 The code used to perform this song type validation process, along with the figures generated during it, can  
 379 be found in the main narrative notebook and a dedicated repository.

380 **Quantification and statistical analysis**

381 **Modelling pairwise similarity and individual repertoires**

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

388 **Individual repertoires** We first modelled individual repertoire size using Poisson and negative binomial models,  
 389 but this led to poor performance as assessed through posterior predictive checks (both underestimation of mean  
 390 values and either under or over-estimation of very low repertoire sizes). Instead, we built continuation ratio  
 391 models, a type of sequential ordinal model where reaching a particular level (number of song types in the reper-  
 392 toire) requires first reaching all lower levels.<sup>90,91</sup>  $rep_{m_1}$ ,  $rep_{m_{1,1}}$ , and  $rep_{m_{1,2}}$  estimate the association between immi-  
 393 grant status, distance dispersed, age, and repertoire size. Three further log-normal models,  $repnov_{m_1}$ ,  $repnov_{m_{1,1}}$ ,  
 394  $repnov_{m_{1,2}}$ , do the same for the average cultural uniqueness of individual repertoires, defined as one minus the  
 395 mean of the relative frequencies of each song type present in the repertoire.

396 **Pairwise similarity** Our first model ( $disp_{m_1}$ ) explores the interaction between natal distance, that is, the distance  
 397 between the nests where two resident birds were born, and the distance between the centre of their breeding  
 398 territories, adjusting for year and absolute age difference. We do not have direct information on how long birds  
 399 have spent around one another, so instead we estimate the effect of the interaction of the distance at which  
 400 they were born and the distance at which they subsequently breed: If both are small, they will have had more  
 401 opportunities for interaction and learning. We extract predictions for the interaction and calculate marginal  
 402 effects at minimum distances, to answer the questions 'How does cultural similarity change with distance for  
 403 birds that were born nearby' and 'Does how close a bird was born matter for birds that hold territories nearby'.  
 404 We use a similar model structure ( $age_{m_1}$ ) to estimate the marginal effects of the absolute age difference, this time  
 405 adjusting for the natal and territorial distance between birds. Then, to study the effect of immigration, we fit  
 406 a model ( $imm_{m_1}$ ) with the possible combinations of immigration status (both immigrant, both residents, one of  
 407 each) and adjust for age difference and territorial distance.

#### 408 *Modelling group-level outcomes*

409 **Defining neighbourhoods and their demographic properties** Song turnover, diversity, and uniqueness are group-level  
 410 properties. However, our study lacks naturally occurring distinct subpopulations that we can use as units for  
 411 analysis. Rather than partitioning the population using a discrete polygonal grid or non-overlapping areas, we  
 412 opted to model neighbourhoods continuously across space, with a radius of 200 m around each of 549 nest boxes  
 413 occupied at least once during the study,<sup>29</sup> which we sampled across the duration of the study. This radius is  
 414 necessarily arbitrary but strikes a good compromise between describing the relevant spatial scale at which vocal  
 415 interactions occur, which extends up to around 180 metres,<sup>92,93</sup> and maintaining an adequate sample size in  
 416 areas of low density (neighbourhood sizes range from 7 to 60, mean  $30.3 \pm 14.9$ ). Importantly, neighbourhoods  
 417 defined in this way are highly non-independent, so we model both this methodological spatial dependence and  
 418 other sources of complex spatial autocorrelation intrinsic to the study site by including a 2D Gaussian process  
 419 (GP), which estimates a length-scale parameter defining a variance-covariance matrix for the spatial locations  
 420 based on their distance.<sup>94–96</sup> We confirmed that this eliminated the residual spatial autocorrelation via Moran's  
 421 I tests. Note that we fit a separate GP for each year, as treating the spatial dependence as fixed across the study  
 422 duration, as is often done, risks further underestimating uncertainty.

423 We define our predictor variables in the following way:

- 424 • Individual turnover is the proportion of birds that were not already in a neighbourhood in the preceding  
 425 year.
- 426 • Dispersal is the mean of the distances, in metres, that birds in the neighbourhood travelled to get from  
 427 their natal territories to their current territories if they were hatched within the Wytham population.
- 428 • Immigration is the proportion of birds that were not ringed as nestlings in the population, and
- 429 • Neighbourhood age is the mean age of the birds within it.

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

433 **Operational definitions of cultural diversity, uniqueness, and turnover** In this paper we use simple descriptions of cul-  
 434 tural diversity, uniqueness, and turnover, that intuitively capture relevant aspects of the collective song reper-  
 435 toires of neighbourhoods in relation to the rest of the population. We define our outcome variables in the  
 436 following way:

- 437 • We calculated a simple relative diversity index by dividing the number of unique song types by the total  
 438 number of songs in a neighbourhood.
- 439 • To calculate the uniqueness index, we computed the relative frequency of each song type in the current  
 440 year in the entire population. We then took the complement (1 - ) of the logarithm of the mean of the  
 441 relative frequencies of each song type present in the neighbourhood.
- 442 • We calculated the rate of song cultural turnover as the proportion of unique song types in a given year that  
 443 were not already present in the same neighbourhood the preceding year.

444 In this way, 'diversity' describes the relative proportion of unique songs in a neighbourhood, and 'uniqueness'  
 445 refers to how uncommon, on average, the songs of the birds in a neighbourhood are. These two ways of charac-  
 446 terizing cultural diversity are (as expected) anti-correlated in our study site due to the effect of sampling: more  
 447 frequent songs are sampled more readily, causing larger sample sizes—neighbourhoods with more density and  
 448 therefore songs—to yield lower average estimates of diversity and higher average estimates of uniqueness, in  
 449 a nonlinear manner. Once this is adjusted for, which we do by including a GAM term capturing the nonlinear  
 450 effect of the sample size, diversity and uniqueness are positively correlated, as expected (see **Figure S5**; models

451  $nov_{m_2}$  and  $nov_{m_{2,1}}$ ; spatial distribution of these variables in Figure S6). All the relevant models adjust for these  
452 effects of neighbourhood density and sampling.

453 **Models** To study the effect of dispersal and immigration on local cultural diversity and uniqueness, we built  
454 log-normal models ( $div_{m_1}$ ,  $nov_{m_1}$ ) and estimated the marginal effects of the proportion of immigrants, mean  
455 dispersal distance, and mean neighbourhood age, while also adjusting for individual turnover, year, and spatial  
456 dependence. Lastly, to examine whether the effects of immigration and dispersal on cultural diversity were  
457 related to individual differences in repertoire size and uniqueness, we fit two further models predicting the  
458 absolute number of unique songs in a neighbourhood while also adjusting for the number of birds ( $div_{m_2}$ ) and  
459 the number of songs ( $div_{m_{2,1}}$ ).

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

#### 465 **Model estimates and reporting**

466 We built the models and approximated the posterior distributions of the parameters of interest using brms,<sup>97</sup>  
467 an interface to the Hamiltonian Monte Carlo engine Stan.<sup>98</sup> We then processed the posterior distributions with  
468 the help of the marginal effects package. We checked model convergence via the effective number of samples,  
469 visual inspection of the chain trace plots, and the Gelman-Rubin diagnostic. Estimation in a Bayesian framework  
470 returns a posterior distribution of possible values instead of point estimates. By convention, we report posterior  
471 central estimates (means or medians) and their 95% credible intervals, but also include plots with full posteriors.  
472 Note that categorical predictors are dummy-coded and continuous predictions z-score transformed.

473 For each parameter of interest, we calculated predictions or marginal effects at the means or other relevant  
474 values. Regression plots show predicted values of the mean and their credible intervals, as well as partial  
475 residuals adjusted to the means or other relevant values of the explanatory terms included in the model.<sup>99,100</sup> We  
476 have tried to build reasonable models, but even then our estimates should not be interpreted causally. Figure S11  
477 shows posterior predictive checks for all models in the study. See the software section at the end for a complete  
478 list of libraries used in the various analyses and the code repository for full model specifications.

#### 479 **Software**

480 Song processing and analyses were carried out using pykanto<sup>75</sup> and rely on the following open-source scientific  
481 libraries or tools: numpy,<sup>101</sup> scipy,<sup>102</sup> pandas,<sup>103</sup> numba,<sup>104</sup> pytorch,<sup>105</sup> torchvision,<sup>106</sup> pytorch lightning,<sup>107</sup>  
482 tqdm,<sup>108</sup> ray,<sup>109</sup> soundfile,<sup>110</sup> umap,<sup>111</sup> joblib,<sup>112</sup> hdbscan,<sup>113</sup> seaborn,<sup>114</sup> scikit-image,<sup>115</sup> librosa,<sup>116</sup> bokeh,<sup>117</sup>  
483 ujson,<sup>118</sup> psutil,<sup>119</sup> attrs.<sup>120</sup> We also used R version 4.2.1<sup>121</sup> and the following R packages: bayesplot,<sup>122,123</sup>  
484 box,<sup>124</sup> brms,<sup>97,125</sup> ClustGeo,<sup>126</sup> colorspace,<sup>127</sup> config,<sup>128</sup> devtools,<sup>129</sup> DHARMa,<sup>130</sup> fs,<sup>131</sup> ggdist,<sup>132</sup> ggraph,<sup>133</sup>  
485 httpgd,<sup>134</sup> igraph,<sup>135,136</sup> insight,<sup>137</sup> kableExtra,<sup>138</sup> languageserver,<sup>139</sup> marginaleffects,<sup>140</sup> modelsummary,<sup>141</sup>  
486 patchwork,<sup>142</sup> progress,<sup>143</sup> renv,<sup>144</sup> rprojroot,<sup>145</sup> scales,<sup>146</sup> scico,<sup>147</sup> sf,<sup>148,149</sup> svglite,<sup>150</sup> terra,<sup>151</sup> tidygraph,<sup>152</sup>  
487 tidyverse,<sup>153</sup> viridis.<sup>154</sup> See the code repositories for specific versions of these libraries.

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#### 493 **AUTHOR CONTRIBUTIONS**

494 **Nilo Merino Recalde:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Cura-  
495 tion, Writing - Original Draft, Writing - Review & Editing, Visualization. **Andrea Estandía:** Investigation, Data  
496 Curation, Writing - Review & Editing. **Sara C. Keen:** Writing – Review & Editing. **Ella F. Cole:** Supervision,  
497 Project Administration. **Ben C. Sheldon:** Supervision, Project Administration, Writing – Review & Editing,  
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815 **SUPPLEMENTARY INFORMATION****Table S1.** Model information

Model	Formula	Family	N	Groups
<b>Individual Repertoires</b>				
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
<b>Cultural Similarity</b>				
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
<b>Cultural Novelty and Diversity</b>				
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
<b>Cultural Turnover</b>				
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 S2.** Model variable key

Variable	Description
repertoire_size	Number of distinct song types sung by an individual

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**Table S2.** Model variable key (Continued)

Variable	Description
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
n_current_songs	Absolute number of song types in a neighbourhood (not unique song types), which correlates with neighbourhood size but we use to further adjust for the fact that some birds sing more songs
gp(x, y)	2D Gaussian process to model spatial dependency in the data
n_unique_current_songs	Number of unique song types in a neighbourhood
uniqueness	The uniqueness of a bird's repertoire, quantified as 1 minus the logarithm of the mean frequency of the songs in its repertoire for 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 S3.** Model estimates

Model	Hypothesis	Estimate <sup>a</sup>	Evid. Ratio	Post. Prob
<b>Individual Repertoires</b>				
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
<b>Cultural Similarity</b>				
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

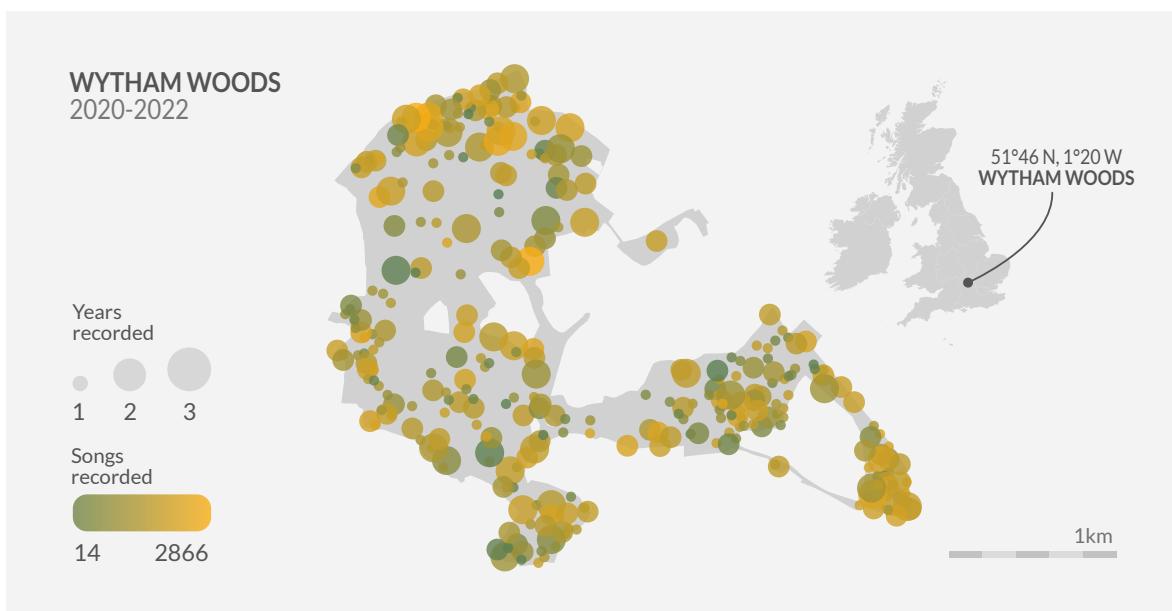
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**Table S3.** Model estimates (Continued)

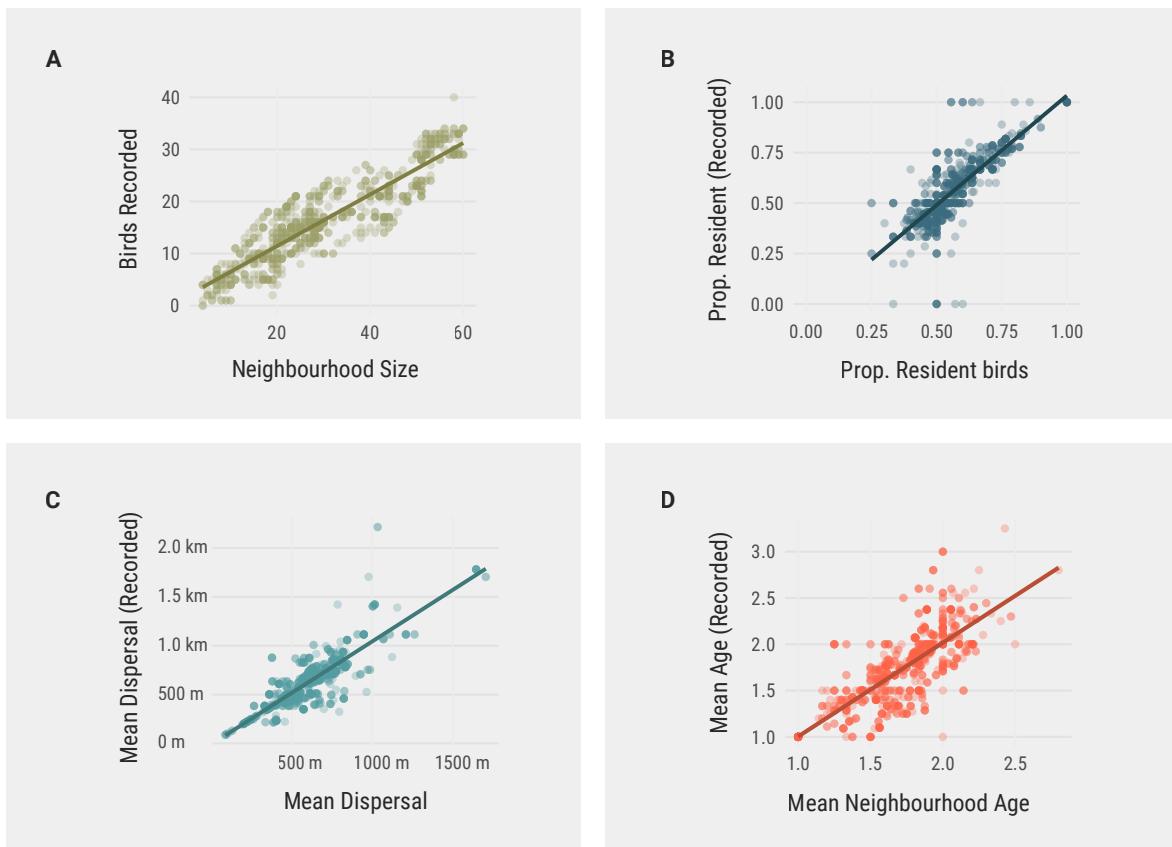
<b>Model</b>	<b>Hypothesis</b>	<b>Estimate<sup>a</sup></b>	<b>Evid. Ratio</b>	<b>Post. Prob</b>
imm_m_1	both resident-both immigrant < 0	0.002 [-0.005, 0.01]	0.438	0.304
imm_m_1	both resident-one immigrant < 0	0.002 [-0.002, 0.006]	0.331	0.248
age_m_1	age difference 0-1 > 0	0.002 [0, 0.003]	12.289	0.925
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
<b>Cultural Novelty and Diversity</b>				
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
<b>Cultural Turnover</b>				
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

822 <sup>a</sup> Estimates are Medians and 95% Credible Intervals



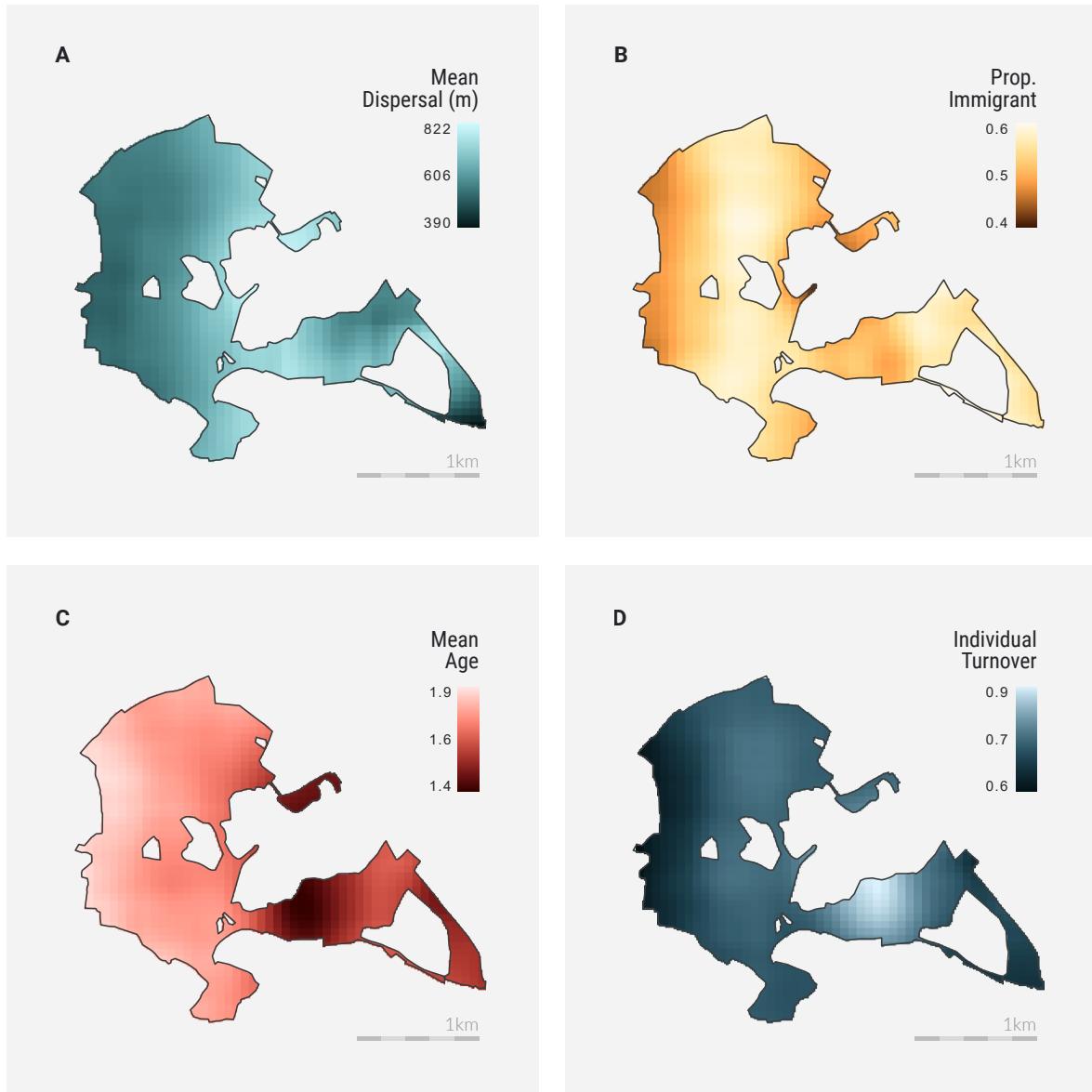
**Figure S1. Map of the study site and sampling locations.**

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 loggers. The map shows the location of the nest boxes where we recorded song repertoires.



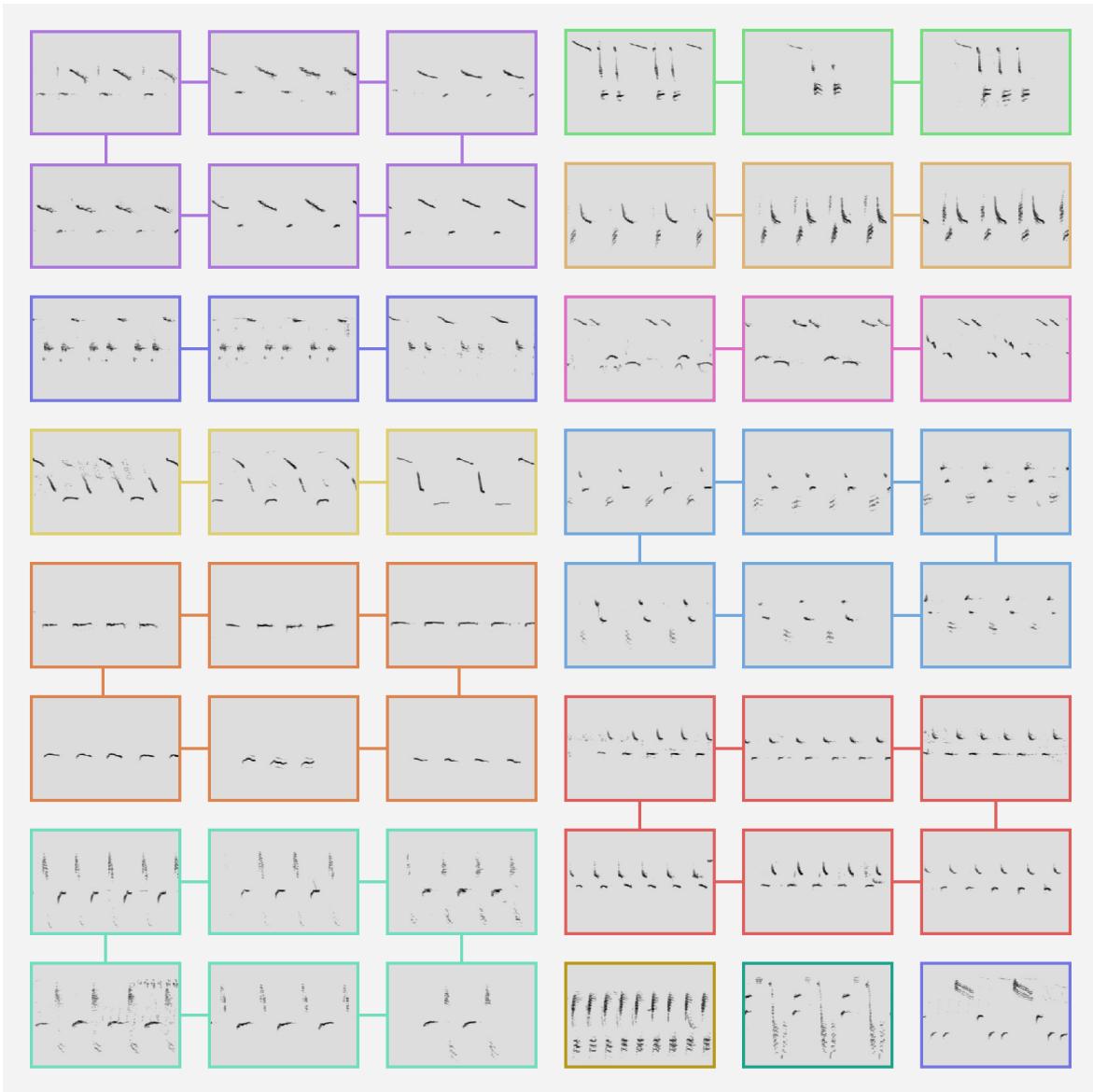
**Figure S2. Demographic characteristics of recorded birds compared to those of all birds in the neighbourhood.**

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.



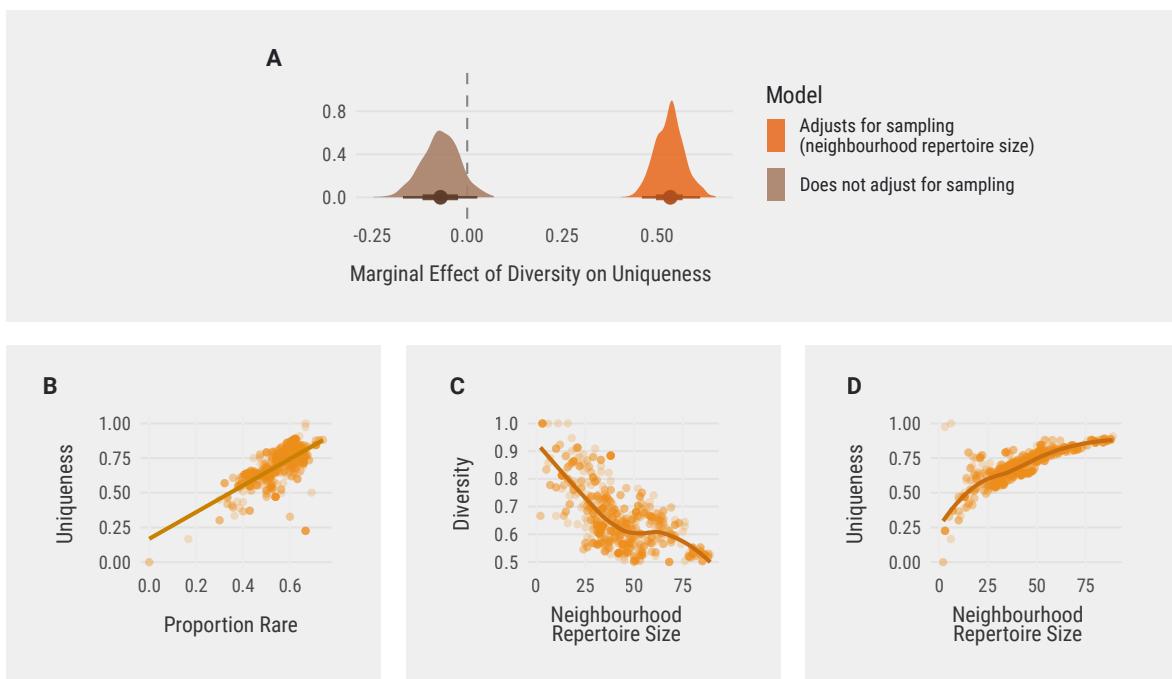
**Figure S3. Spatial distribution of the neighbourhood-level predictor variables in the study.**

(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.



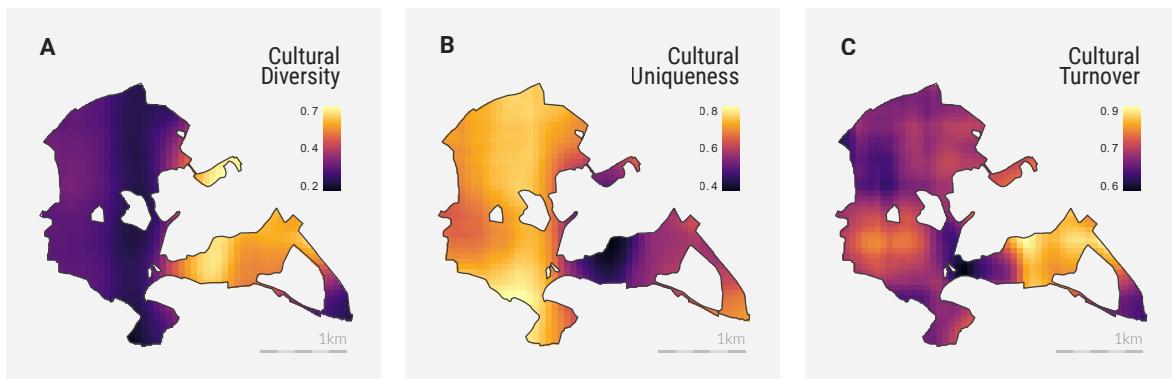
**Figure S4. Examples of song type clusters in the study population.**

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.<sup>45</sup>



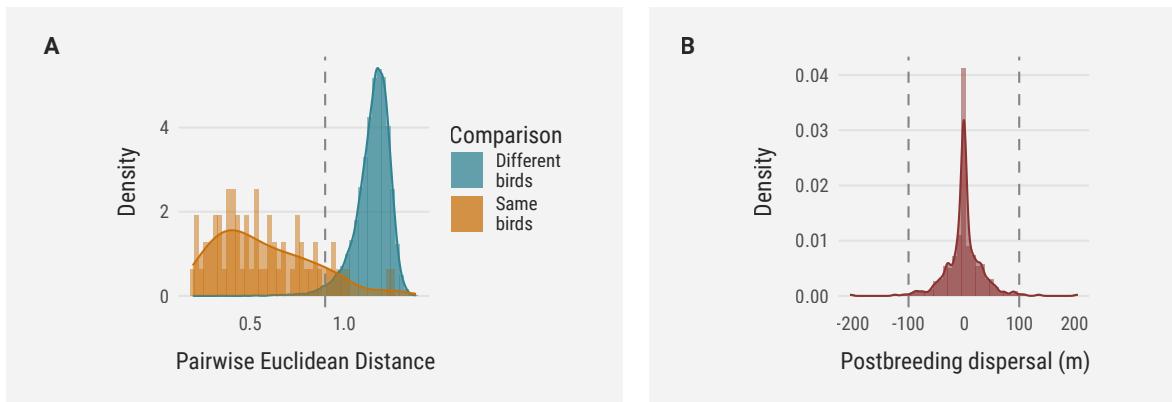
**Figure S5. Estimates of cultural outcomes depend on the size of the neighbourhood repertoire.**

(A) Marginal effect of diversity—which describes the proportion of unique songs in a neighbourhood—on uniqueness, that is, how uncommon, on average, the songs of the birds in a neighbourhood are. 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’,<sup>45</sup> here on the x-axis.



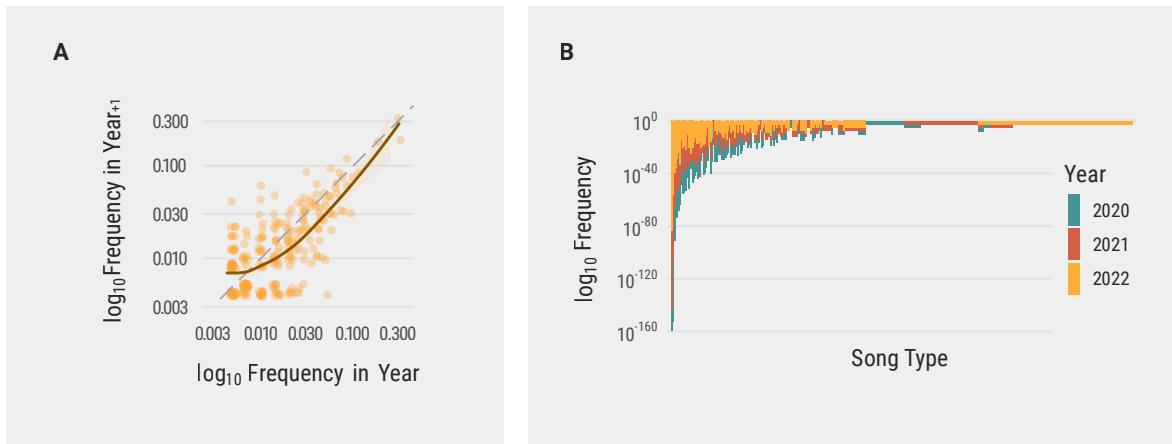
**Figure S6. Spatial distribution of the neighbourhood-level cultural variables in the study.**

(A) Relative diversity, or the proportion of unique songs in a neighbourhood. (B) Uniqueness, or how uncommon, on average, the songs of the birds in a neighbourhood are. (C) Rate of song cultural turnover, or the proportion of unique song types in a given year that were not already present in the same neighbourhood the preceding year. 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 unique songs, as expected.



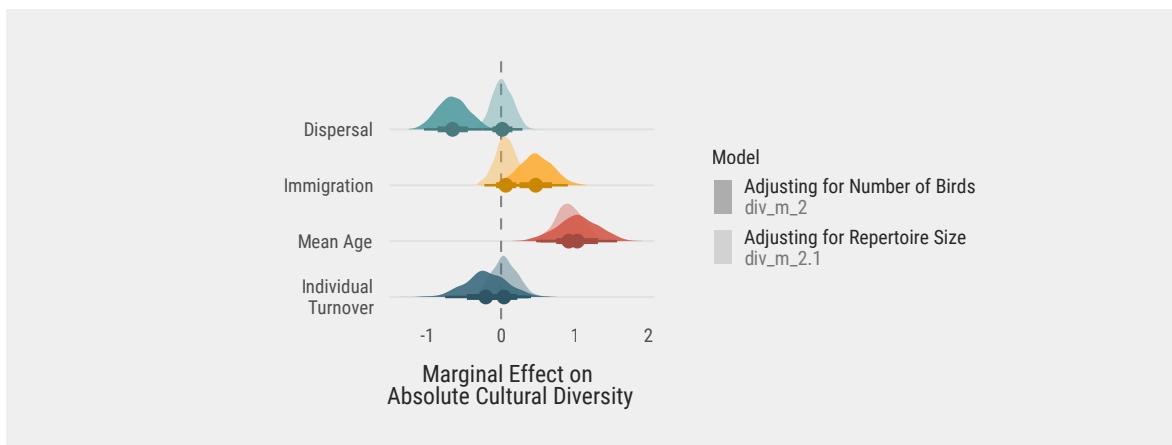
**Figure S7. Thresholds used during the process of reidentifying individual birds based on their songs.**

(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.



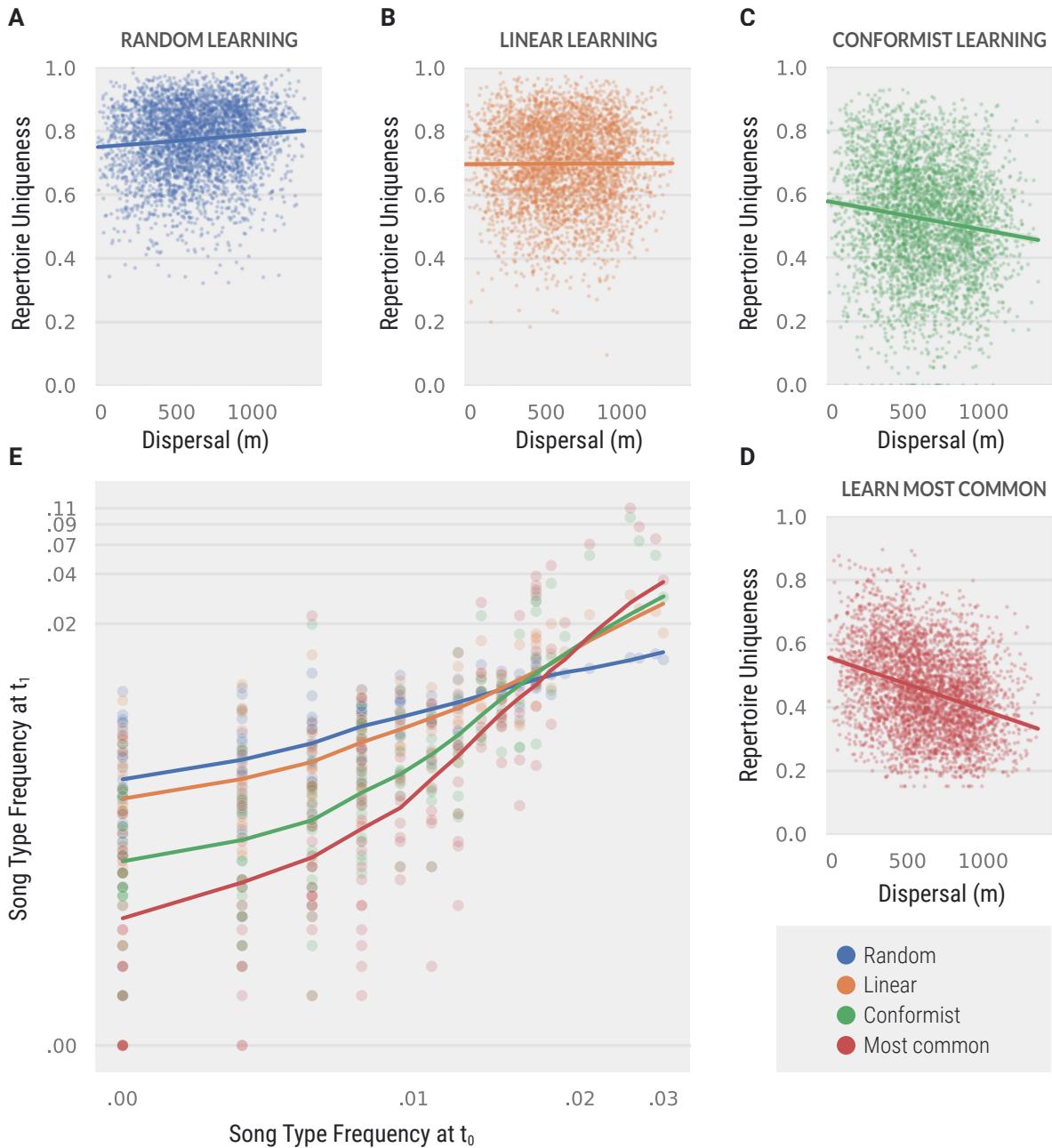
**Figure S8. Song frequencies and their relationship with abundance in the following year.**

(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.

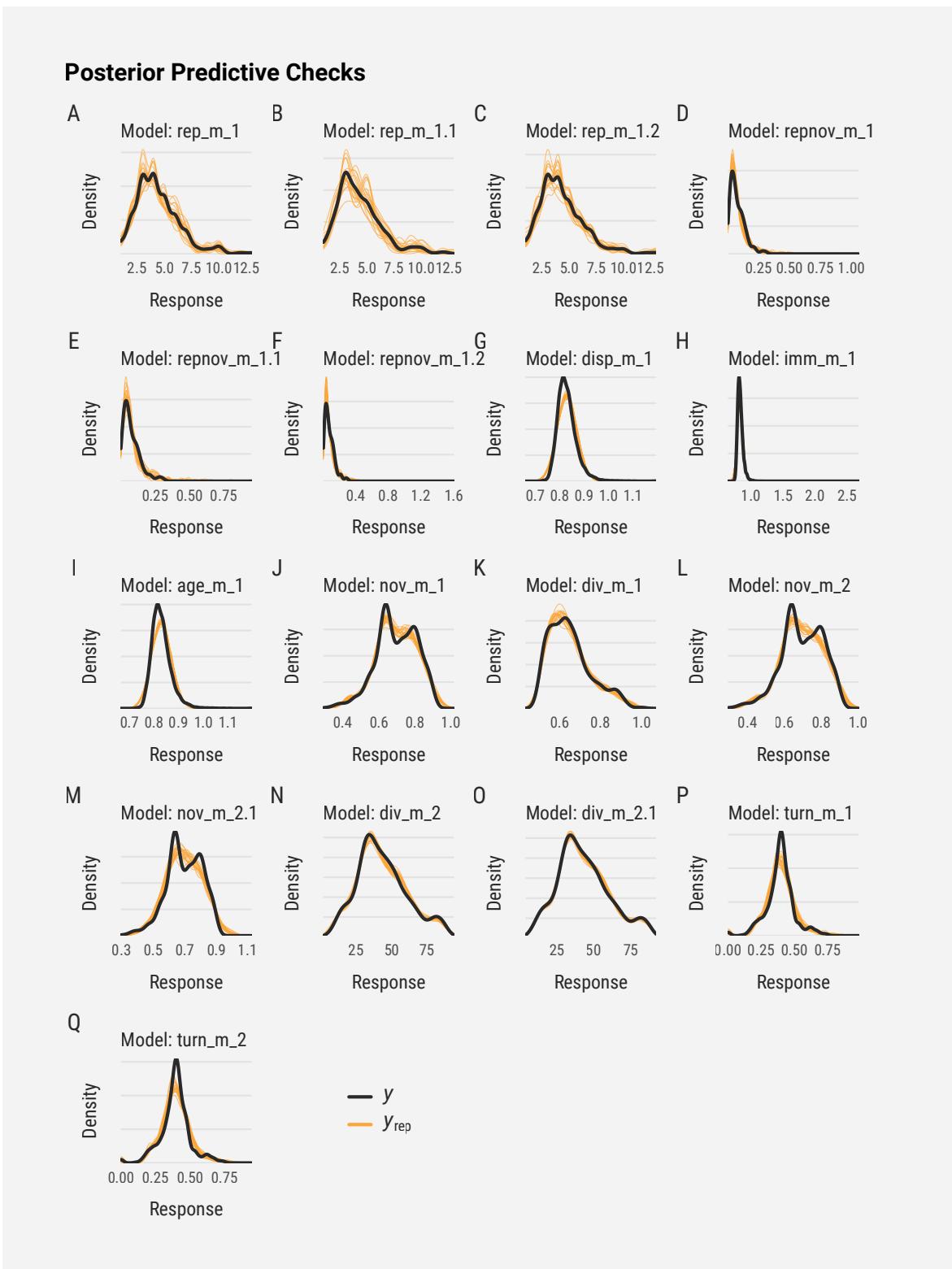


**Figure S9. Effect of demographic variation on absolute cultural diversity within neighbourhoods.**

To explore how the number of individuals and their repertoire sizes within a neighbourhood affect the absolute number of different song types (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 S1 for full model specifications.

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

We simulate the relationship between pre-breeding bird movement and the uniqueness of songs in their repertoires (relative to the population). We initialize 200 birds in a  $1500 \times 1500$  square, each capable of singing 4 songs selected from a pool of 200 song types. Birds do not initially move. New birds are born 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.