

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

Nilo Merino Recalde  ^{1,*}, Andrea Estandía  ¹, Sara C. Keen  ^{1,2},
Ella F. Cole  ¹, and Ben C. Sheldon  ¹

¹ Edward Grey Institute, Department of Biology, University of Oxford, Oxford, UK

² Earth Species Project, 1536 Oxford St. Berkeley CA 94709, US

*Corresponding author: nilo.recalde@biology.ox.ac.uk

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

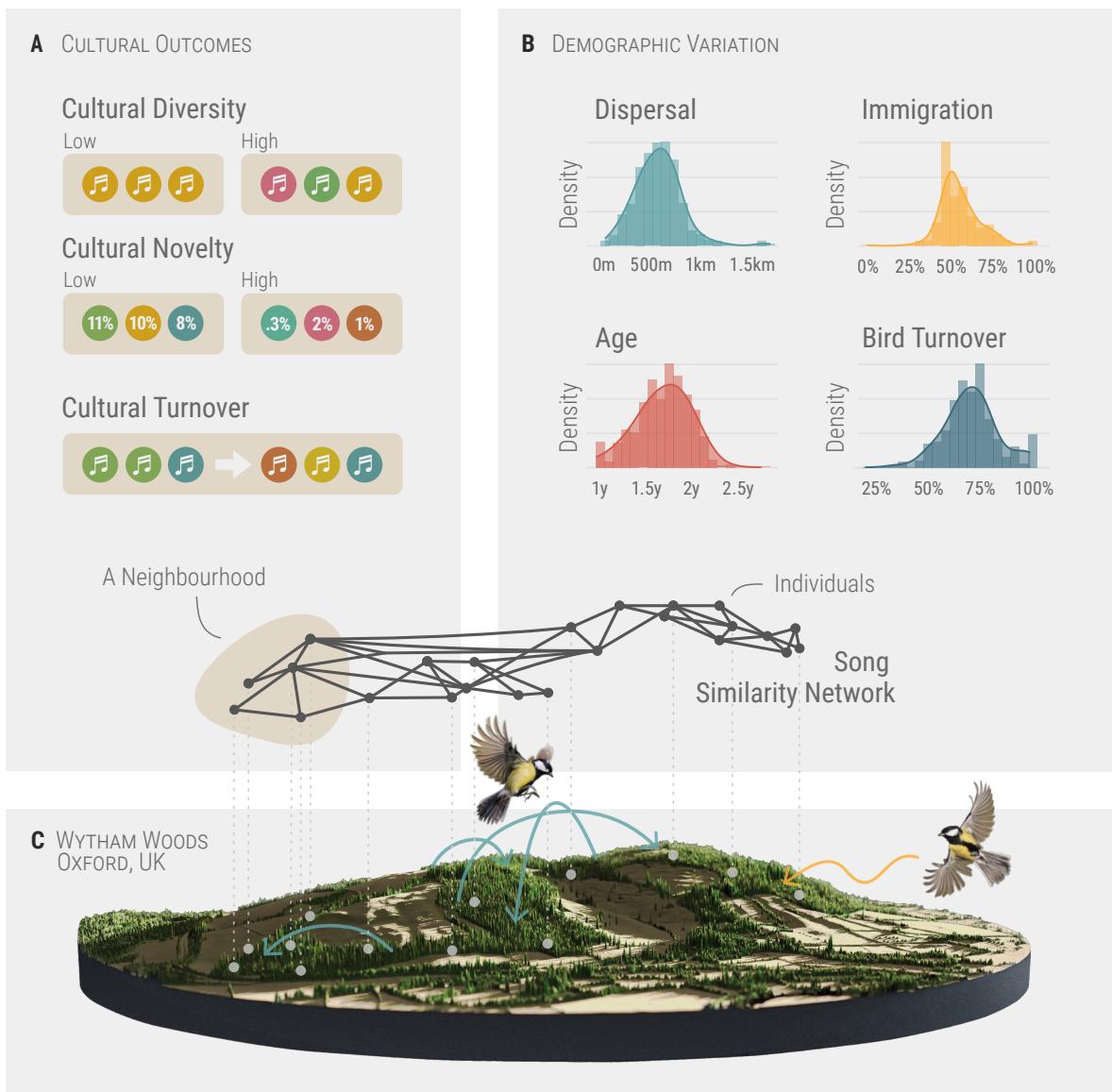
RESULTS AND DISCUSSION

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.

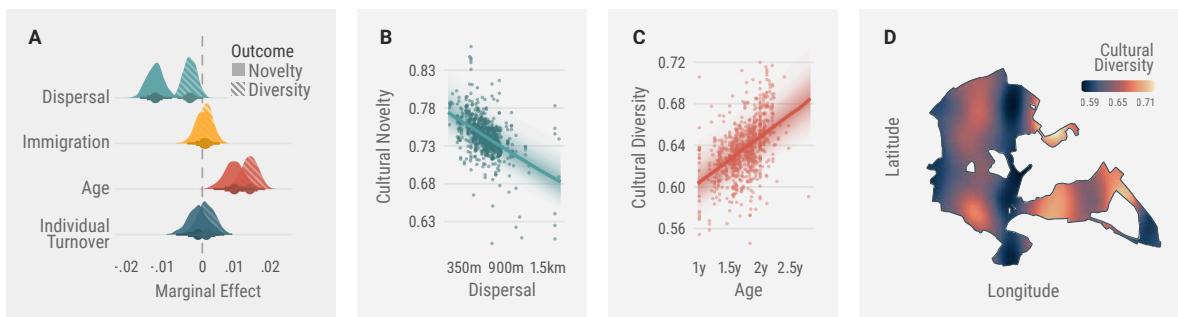


Figure 2. Influence of demographic variables on cultural diversity and novelty.

(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, 67 which, in turn, reduces the efficacy of selection and diversification. Conversely, low dispersal facilitates genetic 68 differentiation through mechanisms such as mutation and drift, leading to allopatric population divergence.^{36–38} 69 Were we to adhere to an analogy from genetics to culture, we would anticipate that reduced dispersal rates will 70 decelerate the diffusion of cultural traits.²⁴ This, in turn, should result in the maintenance of distinct behavioural 71 patterns within populations,^{39,40} leading to a greater number of cultural variants unique to a neighbourhood 72 or region. Our analysis indeed indicates that neighbourhoods where more birds have remained in proximity to 73 their natal areas harbour greater relative cultural diversity and novelty (*diversity*: $P(\beta_{disp(\bar{m})} < 0|D) = 1$, *mem* = 74 -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 75 2A&B, Table S3), in line with prior research at a much coarser grain.²⁷

76 The analogy breaks down as soon as we consider the underlying individual-level mechanisms, however, due 77 to complex interactions between the timing of dispersal and learning mechanisms that are specific to the cultural 78 domain. Some species only learn songs early in life from their parents, in a manner reminiscent of genetic in- 79 heritance, while others learn continuously from their neighbours, or only after dispersal (see⁴¹ for an overview 80 of different strategies). In the case of our study species, the great tit, these learning mechanisms are thought 81 to involve selective retention or modification of songs encountered early in life, while they disperse, and up 82 until before they begin breeding for the first time—a process that results in crystallized repertoires of 1 to \simeq 83 10 different song types.^{42–44} In our individual-level analysis, we see that birds that dispersed over longer dis- 84 tances tend to have learned repertoires composed of songs that are more common within the population (*novelty*: 85 $P(\beta_{disp(m)} < 0|D) = 1$, *mem* = -0.2 , $CI_{95\%} [-0.3, -0.09]$; Figure 3B, Table S3), and possibly smaller repertoires 86 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 hypoth- 87 esize that birds with more extensive movements are more likely to sample and acquire a larger proportion of 88 common cultural variants, simply because they are exposed to more songs across their learning period. This 89 finds support in a spatially explicit simulation of song learning with dispersal, which shows this pattern emerg- 90 ing under positively frequency-dependent learning or a more complex process leading to similar acquisition 91 curves (see Figure ??, note that we do not currently know which learning strategies are employed by great tits).

92 Building on our understanding of cultural dynamics in relation to dispersal we expect that, when song learn- 93 ing is relatively precise and dispersal is limited, cultural differences between populations will accumulate, and 94 immigration will introduce cultural novelty to the recipient population. However, the extent to which immigra- 95 tion introduces new cultural variants also hinges on an interplay between the species' learning programme, the 96 timing of dispersal, and the spatial movements of individuals. Animals that learn first and then disperse, for ex- 97 ample, may bring cultural novelty with them. But this is not the case for great tits, whose young disperse in late 98 summer and autumn, shortly after achieving independence, learn their songs until the end of their first winter,⁴³ 99 and become chiefly sedentary as adults.^{45–47} In this species, then, we anticipate that immigrant birds will learn 100 or retain songs they encounter upon arrival, either before or during the establishment of their territories.^{48,49}

101 Indeed, in our population, we find no evidence that the repertoires of birds originating from outside the pop- 102 ulation significantly differ from those of resident birds (*mem* = -0.002 , $CI_{95\%} [-0.006, 0.002]$; Figure 3C). This,

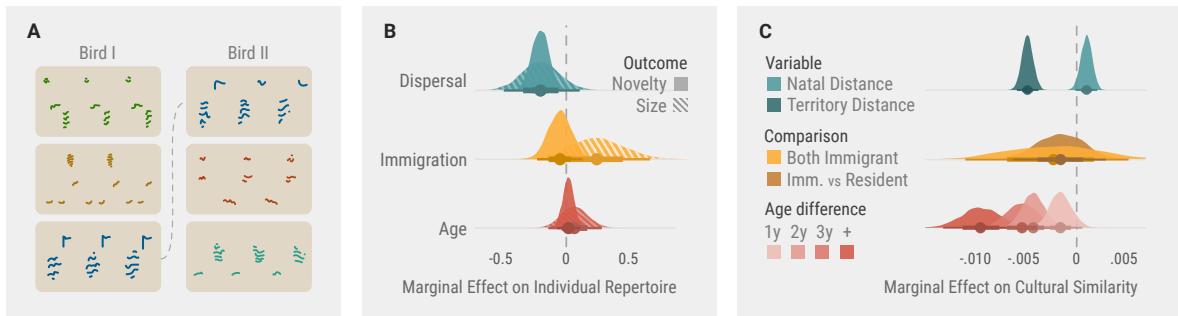


Figure 3. Individual and dyadic analysis of cultural diversity and similarity.

(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 S3), 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 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 S5, Table S3).

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 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 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 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%; specific values are contingent on the granularity of song type definitions, 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 greater stochasticity while common songs endure (Figure S4A). Indeed, some common song types documented over four decades

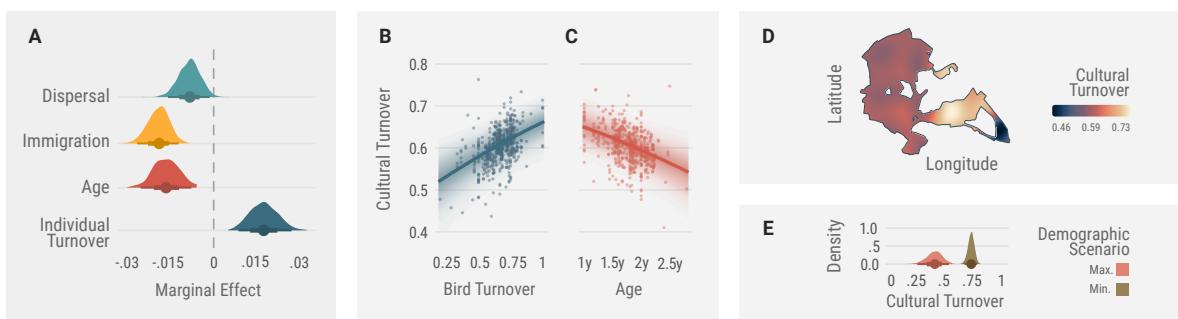


Figure 4. Influence of demographic variables on the rate of local cultural change.

(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.

ago persist within the population.^{42,48} This persistence may result from accurate, frequency-dependent learning and/or strong convergent biases.^{16,17,56,57}

After factoring in individual turnover, we examine how mean natal dispersal distance, the proportion of immigrant birds, and mean neighbourhood age affect cultural change within a neighbourhood. We find that higher levels of these factors correlate with slower cultural change (Figure 4A; Table S3). Specifically, when individuals have dispersed over greater distances to get to their breeding neighbourhood, there is a high influx of immigrants, and the distribution of age is skewed towards older individuals, the model predicts slower cultural change, at less than half the rate compared to the converse scenario (0.28 CI_{95%} [0.23, 0.34] vs. 0.61 CI_{95%} [0.49, 0.76], as illustrated in Figure 4E). This twofold difference in cultural turnover, based on realistic parameter values, is likely to significantly influence the cultural composition of neighbourhoods over time if it persists, highlighting the importance of the demographic structure of populations in also moderating the pace of cultural change.

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

Consequences for cultural structure, stability and diversity

Cultural traits, learnt bird song in this case, are shaped by many factors: some external, such as those discussed here, others intrinsic to learning and culture, and yet others that arise from selective processes driven by preference and function. Even within the confines of a relatively small population—Wytham Wood spans a mere four kilometres—we have recovered associations between heterogeneity in the demographic composition of neighbourhoods and cultural outcomes. This emphasises 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, which shape individuals' exposure to cultural variants and opportunities for learning and, therefore, emergent group-level cultural dynamics.

METHODS

Resource availability

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

Data collection

Study system and fieldwork

Great tits are small, short-lived birds—average lifespan: 1.9 years—that sing acoustically simple yet highly diverse songs. Each male great tit has a repertoire of one to over 10 song 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 standardized 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, which we account for in some of our analyses. In the years of our study, 261, 289 and 278 were occupied, with 173, 184 and 184 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).

216 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.

223 Data processing and annotation

We processed and annotated the song recordings, 109,963 in total, using custom software and scripts written in Python 3⁶⁷ 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

228 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

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

242 Characterising repertoire similarity

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

249 Continuous similarity

250 Traditional methods used to compare bird vocalisations include visual inspection of spectrograms and mea-
 251 surement of hand-picked acoustic features. However, these approaches have limitations in dealing with noise
 252 and variations in performance and can be extremely time-consuming. So, instead, we adopted a data-driven
 253 approach by training a Vision Transformer (ViT) model for feature extraction in a metric learning task on spec-
 254 trogram representations of great tit songs. Our goal was to create a similarity space based on inherent variation
 255 in the data, using categorical labels of song types sung by individual birds, which we know to be perceptu-
 256 ally and behaviourally significant.⁷² Further details, data, and code to reproduce this process are available at⁶⁸
 257 and,⁴⁴ we include a summary here.

258 We optimized model performance using Triplet loss, a loss function that ensures the projection of a positive
 259 sample (belonging to the same class as the anchor point) is closer to the anchor's projection than that of a
 260 negative sample (belonging to a different class) by a specified margin.^{73,74} During training, we mined hard
 261 triplets—where the negative sample is closer to the anchor than the positive—and used the Adam optimizer
 262 with a fixed learning rate of 1×10^{-5} .

263 To prevent the model from overfitting to irrelevant features within localized portions of the training data or
 264 background noise, we applied various train-time data augmentation techniques.^{75–77} These included random
 265 cropping in the time domain, dropping out parts of the spectrogram, adding Gaussian and multiplicative noise,
 266 equalization, sharpening, changes to brightness and contrast, blurring, and slight shifting in both time and
 267 frequency domains. This leads to a more robust model that can generalize better.

268 Finally, we used the resulting model to calculate feature vectors for each song in the dataset (109,963 samples
 269 x 384 dimensions), which serve as compressed representations that can be used to compare them. Great tits have
 270 variable repertoire sizes and there is no evidence that they ever learn them en bloc.^{42,78} Therefore, the simplest
 271 continuous measure (an average pairwise Euclidean distance between all songs) would mask any signatures of
 272 learning if the average repertoire similarity is similar across the population, and does not take into account the
 273 asymmetry in total repertoire size. To improve on this, we define repertoire similarity as the average minimum
 274 Euclidean distance (AMED), given by

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

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

281 Automated clustering

282 Instead of calculating a continuous measure of repertoire similarity, we can build a pairwise distance matrix for
 283 all songs, assign them to discrete clusters using a clustering algorithm, and then calculate the intersection be-
 284 tween repertoires by using the Jaccard coefficient or modelling it as a binomial process, with n = the combined
 285 repertoire size and s = the number of songs in the same cluster. Here we used UPGMA hierarchical cluster-
 286 ing and dynamic tree-cut techniques to classify the syllables into distinct types (since songs consist of repeated

287 syllables, syllable and song types are synonymous in this species). We allowed a minimum cluster size of 1 to
 288 ensure the representation of rare song types. The usefulness of this method relies on the global properties of the
 289 embedding space derived the [Continuous similarity](#) process. In a low-dimensional space where linear distances
 290 effectively capture meaningful variation, creating clusters by cutting the hierarchical tree at different heights
 291 yields varying cluster counts while maintaining meaningful groupings. However, in a high-dimensional space
 292 where global distances are not meaningful, only relatively small clusters of nearby points remain interpretable.
 293 This is the case with our dataset and embedding space: we find that the method reliably groups song rendi-
 294 tions by the same bird across different years, alone or together with other birds with highly similar songs, yet
 295 consistently splits songs that are similar by human (and perhaps great tit⁷⁹) standards, ultimately leading to a
 296 very large number of clusters (the most stable clustering solutions were close to the total number of different
 297 individual song types, >1000). Due to these issues, we did not use song types defined in this way.

298 ***Manual categorization***

299 All great tit song research has, to date, visually classified songs into population-level types.^{27,42,79–83} This process
 300 is both inevitable and very subjective. However, despite its clear problems, human perceptual judgments might
 301 be our best available substitute for those of the birds (but see recent work by Morfi et al.⁸⁴ and Zandberg et al.⁸⁵)
 302 for some tasks. Indeed, across fields, advanced classification algorithms are often evaluated against ground
 303 truth created by humans, and this is also the case in bird song research.

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

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

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

334 ***Quantification and statistical analysis***

335 ***Pairwise similarity and individual repertoire models***

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

342 **Individual repertoires** We first modelled individual repertoire size using Poisson and negative binomial models,
 343 but this led to poor performance as assessed through posterior predictive checks (both underestimation of mean
 344 values and either under or over-estimation of very low repertoire sizes). Instead, we built continuation ratio
 345 models, a type of sequential ordinal model where reaching a particular level (number of song types in the reper-
 346toire) requires first reaching all lower levels.^{86,87} rep_{m_1} , $rep_{m_{1,1}}$, and $rep_{m_{1,2}}$ estimate the association between immi-
 347 grant status, distance dispersed, age, and repertoire size. Three further log-normal models, $repnov_{m_1}$, $repnov_{m_{1,1}}$,
 348 $repnov_{m_{1,2}}$, do the same for the average cultural diversity of individual repertoires

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

361 **Group-level properties**

362 **Defining neighbourhoods and their demographic properties** Song turnover, diversity, and novelty are group-level
 363 properties. However, our study lacks naturally occurring distinct subpopulations that we can use as units for
 364 analysis. Rather than partitioning the population using a discrete polygonal grid or non-overlapping areas,
 365 we opted to model neighbourhoods continuously across space, with a radius of 200 m around each nest box
 366 occupied at least once during the study²⁷ which we sampled across the duration of the study. This radius is
 367 necessarily arbitrary but strikes a good compromise between describing the relevant spatial scale at which vocal
 368 interactions occur, which extends up to around 180 metres,^{88,89} and maintaining an adequate sample size in
 369 areas of low density. Neighbourhoods defined in this way are highly non-independent, so we model both this
 370 methodological spatial dependence and other sources of spatial autocorrelation intrinsic to the study site by
 371 including a 2D Gaussian process (GP), which estimates a length-scale parameter defining a variance-covariance
 372 matrix for the spatial locations based on their distance.^{90–92} We confirmed that this eliminated the residual
 373 spatial autocorrelation via Moran's I tests. Note that we fit a separate GP for each year, as treating the spatial
 374 dependence as fixed across the study duration, as is often done, risks further underestimating uncertainty.

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

383 **Operational definitions of cultural diversity, novelty, and turnover** We calculated a simple diversity index by dividing
 384 the number of different song types by the total number of songs in a neighbourhood. To calculate the novelty
 385 index, we computed the relative frequency of each song type in the current year in the entire population. We
 386 then took the mean of these relative frequencies for each song type in the neighbourhood, took the logarithm of
 387 the inverse of this proportion and scaled it between 0 and 1. In this way, 'diversity' describes the proportion of
 388 unique songs in a neighbourhood, and 'novelty' refers to how uncommon, on average, the songs of the birds in
 389 a neighbourhood are. These two ways of characterising cultural diversity are (as expected) anti-correlated in our
 390 study site due to the effect of sampling: more frequent songs are sampled more readily, causing larger sample
 391 sizes (neighbourhoods with more density and therefore songs) to yield lower average estimates of diversity and
 392 higher average estimates of novelty, in a nonlinear manner. Once this is adjusted for, diversity and novelty are
 393 positively correlated, as expected (see Figure S2; models nov_{m_2} and $nov_{m_{2,1}}$). All of our models adjust for this
 394 sampling effect.

395 **Models** To study the effect of dispersal and immigration on local cultural diversity and novelty, we built log-
 396 normal models (div_{m_1} , nov_{m_1}) and estimated the marginal effects of the proportion of immigrants, mean dis-

persal distance, and mean neighbourhood age, while also adjusting for individual turnover, year, and spatial dependence. Lastly, to examine whether the effects of immigration and dispersal on cultural diversity were related to individual differences in repertoire size and novelty, we fit two further models predicting the absolute number of unique songs in a neighbourhood while also adjusting for the number of birds (div_{m_2}) and the number of songs ($div_{m_{2,1}}$).

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

408 Model estimates and reporting

We built the models and approximated the posterior distributions of the parameters of interest using brms,⁹³ an interface to the Hamiltonian Monte Carlo engine Stan.⁹⁴ We then processed the posterior distributions with the help of the marginal effects package. We checked model convergence via the effective number of samples, visual inspection of the chain trace plots, and the Gelman-Rubin diagnostic. Estimation in a Bayesian framework returns a posterior distribution of possible values instead of point estimates. By convention, we report posterior central estimates (means or medians) and their 95% credible intervals, but also include plots with full posteriors. Note that categorical predictors are dummy-coded and continuous predictions z-score transformed.

For each parameter of interest, we calculated predictions or marginal effects at the means or other relevant values. Regression plots show predicted values of the mean and their credible intervals, as well as partial residuals adjusted to the means or other relevant values of the explanatory terms included in the model.^{95,96} We have tried to build reasonable models, but even then our estimates should not be interpreted causally. See the software section at the end for a complete list of libraries used in the various analyses and the code repository for full model specifications.

422 ACKNOWLEDGEMENTS

We thank all those who have contributed to the long-term nest box study in Wytham Woods and the collection of associated data. This work was supported by a Clarendon-Mary Frances Wagley Graduate Scholarship and an EGI scholarship to Nilo Merino Recalde, and made use of the University of Oxford Advanced Research Computing facility.⁹⁷

427 AUTHOR CONTRIBUTIONS

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

433 REFERENCES

- 434 1. Viciano, H. (2021). Animal Culture: But of Which Kind? *Studies in History and Philosophy of Science Part A* 90, 208–218. <https://doi.org/10.1016/j.shpsa.2021.10.012>.
- 435 2. Falótico, T., Proffitt, T., Ottoni, E. B., Staff, R. A., and Haslam, M. (2019). Three Thousand Years of Wild Capuchin Stone Tool Use. *Nature Ecology and Evolution*. <https://doi.org/10.1038/s41559-019-0904-4>.
- 436 3. Jesmer, B. R. et al. (2018). Is Ungulate Migration Culturally Transmitted? Evidence of Social Learning from Translocated Animals. *Science* 361, 1023–1025. <https://doi.org/10.1126/science.aat0985>.
- 437 4. Berdahl, A. M., Kao, A. B., Flack, A., Westley, P. A., Codling, E. A., Couzin, I. D., Dell, A. I., and Biro, D. (2018). Collective Animal Navigation and Migratory Culture: From Theoretical Models to Empirical Evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373, 20170009. <https://doi.org/10.1098/rstb.2017.0009>.
- 438 5. Byholm, P., Beal, M., Isaksson, N., Lötberg, U., and Åkesson, S. (2022). Paternal Transmission of Migration Knowledge in a Long-Distance Bird Migrant. *Nat Commun* 13, 1566. <https://doi.org/10.1038/s41467-022-29300-w>.
- 439 6. Allen, J., Weinrich, M., Hoppitt, W., and Rendell, L. (2013). Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales. *Science* 340, 485–488. <https://doi.org/10.1126/science.1231976>.
- 440 7. Rendell, L. and Whitehead, H. (2001). Culture in Whales and Dolphins. *Behavioral and Brain Sciences* 24, 309–324. <https://doi.org/10.1017/S0140525X0100396X>.

- 449 8. Potvin, D. A. and Clegg, S. M. (2015). The Relative Roles of Cultural Drift and Acoustic Adaptation in Shaping Syllable
450 Repertoires of Island Bird Populations Change with Time since Colonization. *Evolution* 69, 368–380. <https://doi.org/10.1111/evo.12573>.
- 452 9. Williams, H. and Lachlan, R. F. (2021). Evidence for Cumulative Cultural Evolution in Bird Song. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377, 20200322. <https://doi.org/10.1098/rstb.2020.0322>.
- 454 10. Tchernichovski, O., Feher, O., Fimiarz, D., and Conley, D. (2017). How Social Learning Adds up to a Culture: From
455 Birdsong to Human Public Opinion. *Journal of Experimental Biology* 220, 124–132. <https://doi.org/10.1242/jeb.142786>.
- 456 11. Deffner, D., Kandler, A., and Fogarty, L. (2022). Effective Population Size for Culturally Evolving Traits. *PLOS Computational Biology* 18, e1009430. <https://doi.org/10.1371/journal.pcbi.1009430>.
- 458 12. Kandler, A., Wilder, B., and Fortunato, L. (2017). Inferring Individual-Level Processes from Population-Level Patterns in
459 Cultural Evolution. *Royal Society Open Science* 4, 170949. <https://doi.org/10.1098/rsos.170949>.
- 460 13. Pike, T. W. and Laland, K. N. (2010). Conformist Learning in Nine-Spined Sticklebacks' Foraging Decisions. *Biology Letters* 6, 466–468. <https://doi.org/10.1098/rsbl.2009.1014>.
- 462 14. Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., and Hoppitt, W. (2015). Chimpanzees
463 Copy Dominant and Knowledgeable Individuals: Implications for Cultural Diversity. *Evolution and Human Behavior*
464 36, 65–72. <https://doi.org/10.1016/j.evolhumbehav.2014.09.002>.
- 465 15. Aplin, L. M., Sheldon, B. C., and McElreath, R. (2017). Conformity Does Not Perpetuate Suboptimal Traditions in a Wild
466 Population of Songbirds. *Proceedings of the National Academy of Sciences of the United States of America* 114, 7830–
467 7837. <https://doi.org/10.1073/pnas.1621067114>.
- 468 16. Lachlan, R. F., Ratmann, O., and Nowicki, S. (2018). Cultural Conformity Generates Extremely Stable Traditions in Bird
469 Song. *Nature Communications* 9, 2417. <https://doi.org/10.1038/s41467-018-04728-1>.
- 470 17. Tchernichovski, O., Eisenberg-Edidin, S., and Jarvis, E. D. (2021). Balanced Imitation Sustains Song Culture in Zebra
471 Finches. *Nat Commun* 12, 2562. <https://doi.org/10.1038/s41467-021-22852-3>.
- 472 18. Deffner, D. and McElreath, R. (2022). When Does Selection Favor Learning from the Old? Social Learning in Age-
473 Structured Populations. *PLOS ONE* 17, e0267204. <https://doi.org/10.1371/journal.pone.0267204>.
- 474 19. Kandler, A., Fogarty, L., and Karsdorp, F. (2023). The Interplay between Age Structure and Cultural Transmission. *PLOS
475 Computational Biology* 19, e1011297. <https://doi.org/10.1371/journal.pcbi.1011297>.
- 476 20. Fogarty, L., Creanza, N., and Feldman, M. W. (2019). The Life History of Learning: Demographic Structure Changes
477 Cultural Outcomes. *PLOS Computational Biology* 15, e1006821. <https://doi.org/10.1371/journal.pcbi.1006821>.
- 478 21. Deffner, D. and McElreath, R. (2020). The Importance of Life History and Population Regulation for the Evolution of
479 Social Learning. *Philosophical Transactions of the Royal Society B: Biological Sciences* 375, 20190492. <https://doi.org/10.1098/rstb.2019.0492>.
- 481 22. Derex, M. and Boyd, R. (2016). Partial Connectivity Increases Cultural Accumulation within Groups. *Proceedings of the
482 National Academy of Sciences* 113, 2982–2987. <https://doi.org/10.1073/pnas.1518798113>.
- 483 23. Kirby, S. and Tamariz, M. (2021). Cumulative Cultural Evolution, Population Structure and the Origin of Combinatorial-
484 ity in Human Language. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377, 20200319. <https://doi.org/10.1098/rstb.2020.0319>.
- 486 24. Nunn, C. L., Thrall, P. H., Bartz, K., Dasgupta, T., and Boesch, C. (2009). Do Transmission Mechanisms or Social Systems
487 Drive Cultural Dynamics in Socially Structured Populations? *Animal Behaviour* 77, 1515–1524. <https://doi.org/10.1016/j.anbehav.2009.02.023>.
- 489 25. Barta, K. A., Garamszegi, L. Z., Scheuring, I., and Zsebk, S. (2023). Effects of Positive Frequency-Dependent Learning,
490 Learning Mistakes, and Immigration on Complex CulturesValidation on the Song of Collared Flycatcher (*Ficedula Albicollis*) by Individual-Based Modeling. *Frontiers in Ecology and Evolution* 11,
- 492 26. Chimento, M., Alarcón-Nieto, G., and Aplin, L. M. (2021). Population Turnover Facilitates Cultural Selection for Effi-
493 ciency in Birds. *Current Biology* 31, 2477–2483.e3. <https://doi.org/10.1016/j.cub.2021.03.057>.
- 494 27. Fayet, A. L., Tobias, J. A., Hintzen, R. E., and Seddon, N. (2014). Immigration and Dispersal Are Key Determinants of
495 Cultural Diversity in a Songbird Population. *Behavioral Ecology* 25, 744–753. <https://doi.org/10.1093/beheco/aru047>.
- 496 28. Environment Food, D. for and Affairs, R. (2020). Defra Data Services Platform. <https://environment.data.gov.uk/DefraDataDownload>.
- 497 29. Morgan-Wall, T. (2023). *rayshader: Create Maps and Visualize Data in 2D and 3D*.
- 498 30. Brakes, P. et al. (2019). Animal Cultures Matter for Conservation. *Science* 363, 1032–1034. <https://doi.org/10.1126/science.aaw3557>.
- 500 31. Brakes, P. et al. (2021). A Deepening Understanding of Animal Culture Suggests Lessons for Conservation. *Proceedings
501 of the Royal Society B: Biological Sciences* 288, 20202718. <https://doi.org/10.1098/rspb.2020.2718>.
- 502 32. Paxton, K. L., Sebastián-González, E., Hite, J. M., Crampton, L. H., Kuhn, D., and Hart, P. J. (2019). Loss of Cultural Song
503 Diversity and the Convergence of Songs in a Declining Hawaiian Forest Bird Community. *Royal Society Open Science* 6,
504 <https://doi.org/10.1098/rsos.190719>.
- 505 33. Crates, R., Langmore, N., Ranjard, L., Stojanovic, D., Rayner, L., Ingwersen, D., and Heinsohn, R. (2021). Loss of Vocal
506 Culture and Fitness Costs in a Critically Endangered Songbird. *Proceedings of the Royal Society B: Biological Sciences*
507 288, 20210225. <https://doi.org/10.1098/rspb.2021.0225>.

- 508 34. Lack, D. (1964). A Long-Term Study of the Great Tit (*Parus Major*). *Journal of Animal Ecology* 33, 159–173. <https://doi.org/10.2307/2437>.
- 510 35. Laland, K. N. and Janik, V. M. (2006). The Animal Cultures Debate. *Trends in Ecology & Evolution* 21, 542–547. <https://doi.org/10.1016/j.tree.2006.06.005>.
- 512 36. Suárez, D., Arribas, P., Jiménez-García, E., and Emerson, B. C. (2022). Dispersal Ability and Its Consequences for Population Genetic Differentiation and Diversification. *Proceedings of the Royal Society B: Biological Sciences* 289, 20220489. <https://doi.org/10.1098/rspb.2022.0489>.
- 515 37. Claramunt, S., Derryberry, E. P., Remsen, J. V., and Brumfield, R. T. (2011). High Dispersal Ability Inhibits Speciation in a Continental Radiation of Passerine Birds. *Proceedings of the Royal Society B: Biological Sciences* 279, 1567–1574. <https://doi.org/10.1098/rspb.2011.1922>.
- 518 38. Papadopoulou, A., Anastasiou, I., Keskin, B., and Vogler, A. P. (2009). Comparative Phylogeography of Tenebrionid Beetles in the Aegean Archipelago: The Effect of Dispersal Ability and Habitat Preference. *Molecular Ecology* 18, 2503–2517. <https://doi.org/10.1111/j.1365-294X.2009.04207.x>.
- 521 39. Whitehead, H. and Lusseau, D. (2012). Animal Social Networks as Substrate for Cultural Behavioural Diversity. *Journal of Theoretical Biology* 294, 19–28. <https://doi.org/10.1016/j.jtbi.2011.10.025>.
- 523 40. Planqué, R., Britton, N. F., and Slabbekoorn, H. (2014). On the Maintenance of Bird Song Dialects. *Journal of Mathematical Biology* 68, 505–531. <https://doi.org/10.1007/s00285-012-0632-8>.
- 525 41. Searcy, W. A., Soha, J., Peters, S., and Nowicki, S. (2021). Variation in Vocal Production Learning across Songbirds. *Phil. Trans. R. Soc. B* 376, 20200257. <https://doi.org/10.1098/rstb.2020.0257>.
- 527 42. McGregor, P. K. and Krebs, J. R. (1982a). Song Types in a Population of Great Tits (*Parus Major*): Their Distribution, Abundance and Acquisition by Individuals. *Behaviour* 79, 126–152.
- 529 43. Rivera-Gutierrez, H. F., Pinxten, R., and Eens, M. (2011). Difficulties When Assessing Birdsong Learning Programmes under Field Conditions: A Re-Evaluation of Song Repertoire Flexibility in the Great Tit. *PLoS ONE* 6, ed. by M. Giurfa, e16003. <https://doi.org/10.1371/journal.pone.0016003>.
- 532 44. Merino Recalde, N., Estandía, A., Pichot, L., Vansse, A., Cole, E. F., and Sheldon, B. C. (2023). A Densely Sampled and Richly Annotated Acoustic Dataset from a Wild Bird Population. *bioRxiv*. <https://doi.org/10.1101/2023.07.03.547484>.
- 534 45. Greenwood, P. J., Harvey, P. H., and Perrins, C. M. (1979). The Role of Dispersal in the Great Tit (*Parus Major*): The Causes, Consequences and Heritability of Natal Dispersal. *Journal of Animal Ecology* 48, 123–142. <https://doi.org/10.2307/4105>.
- 536 46. Dhondt, A. A. (1979). Summer Dispersal and Survival of Juvenile Great Tits in Southern Sweden. *Oecologia* 42, 139–157. <https://doi.org/10.1007/BF00344854>.
- 538 47. Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., and Drent, P. J. (2003). Natal Dispersal and Personalities in Great Tits (*Parus Major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270, 741–747. <https://doi.org/10.1098/rspb.2002.2300>.
- 541 48. Keen, S. C. (2020). The Role of Social Environment in Shaping Vocal Communication Systems in Wild Songbirds. Cornell University, PhD Thesis. <https://doi.org/10.7298/qz29-2v92>.
- 543 49. Graham, B. A., Heath, D. D., Walter, R. P., and Mennill, D. J. (2018). Immigrant Song: Males and Females Learn Songs after Dispersal in a Tropical Bird. *Behavioral Ecology* 29, 711–723. <https://doi.org/10.1093/beheco/ary029>.
- 545 50. Verhulst, S., Perrins, C. M., and Riddington, R. (1997). Natal Dispersal of Great Tits in a Patchy Environment. *Ecology* 78, 864–872. [https://doi.org/10.1890/0012-9658\(1997\)078\[0864:NDOGT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0864:NDOGT]2.0.CO;2).
- 547 51. Payne, R. B. (1983). The Social Context of Song Mimicry: Song-matching Dialects in Indigo Buntings (*Passerina Cyanea*). *Animal Behaviour* 31, 788–805. [https://doi.org/10.1016/S0003-3472\(83\)80236-X](https://doi.org/10.1016/S0003-3472(83)80236-X).
- 549 52. Baker, M. C., Thompson, D. B., and Sherman, G. L. (1981). Neighbor/Stranger Song Discrimination in White-Crowned Sparrows. *The Condor* 83, 265–267. <https://doi.org/10.2307/1367322>.
- 551 53. Mortega, K. G., Flinks, H., and Helm, B. (2014). Behavioural Response of a Migratory Songbird to Geographic Variation in Song and Morphology. *Frontiers in Zoology* 11, 85. <https://doi.org/10.1186/s12983-014-0085-6>.
- 553 54. Lachlan, R. F., Anderson, R. C., Peters, S., Searcy, W. A., and Nowicki, S. (2014). Typical Versions of Learned Swamp Sparrow Song Types Are More Effective Signals than Are Less Typical Versions. *Proceedings of the Royal Society B: Biological Sciences* 281, <https://doi.org/10.1098/rspb.2014.0252>.
- 556 55. Beecher, M. D. (2008). Chapter 4 Function and Mechanisms of Song Learning in Song Sparrows*. *Advances in the Study of Behavior*. Vol. 38. Academic Press, 167–225. [https://doi.org/10.1016/S0065-3454\(08\)00004-1](https://doi.org/10.1016/S0065-3454(08)00004-1).
- 558 56. James, L. S. and Sakata, J. T. (2017). Learning Biases Underlie “Universals” in Avian Vocal Sequencing. *Current Biology* 27, 3676–3682. <https://doi.org/10.1016/j.cub.2017.10.019>.
- 560 57. Claidière, N. and Sperber, D. (2007). Commentary: The Role of Attraction in Cultural Evolution. *Journal of Cognition and Culture* 7, 89–111. <https://doi.org/10.1163/156853707X171829>.
- 562 58. Hinde, R. A. (1952). The Behaviour of the Great Tit (*Parus Major*) and Some Other Related Species. *Behaviour. Supplément*, III–201.
- 564 59. Perrins, C. M. (1965). Population Fluctuations and Clutch-Size in the Great Tit, *Parus Major* L. *Journal of Animal Ecology* 34, 601–647.

- 566 60. Cresswell, W. and McCleery, R. (2003). How Great Tits Maintain Synchronization of Their Hatch Date with Food Supply in
567 Response to Long-Term Variability in Temperature. *Journal of Animal Ecology* 72, 356–366. [https://doi.org/10.1046/j.1365-
568 2656.2003.00701.x](https://doi.org/10.1046/j.1365-2656.2003.00701.x).
- 569 61. Gibb, J. (1950). The Breeding Biology of the Great and Blue Titmice. *Ibis* 92, 507–539. [https://doi.org/10.1111/j.1474-
570 919X.1950.tb01759.x](https://doi.org/10.1111/j.1474-919X.1950.tb01759.x).
- 571 62. Mace, R. (1987). The Dawn Chorus in the Great Tit *Parus Major* Is Directly Related to Female Fertility. *Nature* 330, 745–
572 746. <https://doi.org/10.1038/330745a0>.
- 573 63. Rivera-Gutierrez, H. F., Pinxten, R., and Eens, M. (2012). Tuning and Fading Voices in Songbirds: Age-dependent Changes
574 in Two Acoustic Traits across the Life Span. *Animal Behaviour* 83, 1279–1283. [https://doi.org/10.1016/j.anbehav.2012.03.
575 001](https://doi.org/10.1016/j.anbehav.2012.03.001).
- 576 64. Van Duyse, E., Pinxten, R., Snoeijns, T., and Eens, M. (2005). Simultaneous Treatment with an Aromatase Inhibitor and
577 an Anti-Androgen Decreases the Likelihood of Dawn Song in Free-Living Male Great Tits, *Parus Major*. *Hormones and
578 Behavior* 48, 243–251. <https://doi.org/10.1016/j.yhbeh.2005.02.013>.
- 579 65. Halfwerk, W., Bot, S., and Slabbekoorn, H. (2012). Male Great Tit Song Perch Selection in Response to Noise-Dependent
580 Female Feedback. *Functional Ecology* 26, 1339–1347. <https://doi.org/10.1111/j.1365-2435.2012.02018.x>.
- 581 66. Hill, A. P., Prince, P., Snaddon, J. L., Doncaster, C. P., and Rogers, A. (2019). AudioMoth: A Low-Cost Acoustic Device for
582 Monitoring Biodiversity and the Environment. *HardwareX* 6, e00073. <https://doi.org/10.1016/j.hsx.2019.e00073>.
- 583 67. van Rossum, G. (1995). Python Reference Manual. CWI.
- 584 68. Merino Recalde, N. (2023a). Pykanto: A Python Library to Accelerate Research on Wild Bird Song. *Methods in Ecology
585 and Evolution* 00, 1–9. <https://doi.org/10.1111/2041-210X.14155>.
- 586 69. Merino Recalde, N. (2023b). nilomr/Ggreat-tit-hits-setup: V0.1.0. Zenodo. <https://doi.org/10.5281/zenodo.8092397>.
- 587 70. Quinn, J. L., Cole, E. F., Patrick, S. C., and Sheldon, B. C. (2011). Scale and State Dependence of the Relationship between
588 Personality and Dispersal in a Great Tit Population. *Journal of Animal Ecology* 80, 918–928.
- 589 71. Woodman, J. P., Cole, E. F., Firth, J. A., Perrins, C. M., and Sheldon, B. C. (2023). Disentangling the Causes of Age-
590 Assortative Mating in Bird Populations with Contrasting Life-History Strategies. *Journal of Animal Ecology* 92, 979–990.
591 <https://doi.org/10.1111/1365-2656.13851>.
- 592 72. Lind, H., Dabelsteen, T., and McGregor, P. K. (1996). Female Great Tits Can Identify Mates by Song. *Animal Behaviour*
593 52, 667–671. <https://doi.org/10.1006/anbe.1996.0211>.
- 594 73. Hermans, A., Beyer, L., and Leibe, B. (2017). In Defense of the Triplet Loss for Person Re-Identification. <https://doi.org/10.48550/arXiv.1703.07737>.
- 596 74. Hoffer, E. and Ailon, N. (2018). Deep Metric Learning Using Triplet Network. <https://doi.org/10.48550/arXiv.1412.6622>.
- 597 75. Mumuni, A. and Mumuni, F. (2022). Data Augmentation: A Comprehensive Survey of Modern Approaches. *Array* 16,
598 100258. <https://doi.org/10.1016/j.array.2022.100258>.
- 599 76. Perez, L. and Wang, J. (2017). The Effectiveness of Data Augmentation in Image Classification Using Deep Learning.
600 <https://doi.org/10.48550/arXiv.1712.04621>.
- 601 77. Shorten, C. and Khoshgoftaar, T. M. (2019). A Survey on Image Data Augmentation for Deep Learning. *Journal of Big
602 Data* 6, 60. <https://doi.org/10.1186/s40537-019-0197-0>.
- 603 78. Rivera-Gutierrez, H. F., Matthysen, E., Adriaensen, F., and Slabbekoorn, H. (2010). Repertoire Sharing and Song Similarity
604 between Great Tit Males Decline with Distance between Forest Fragments. *Ethology* 116, 951–960. <https://doi.org/10.1111/j.1439-0310.2010.01813.x>.
- 606 79. Falls, J. B., Krebs, J. R., and McGregor, P. K. (1982). Song Matching in the Great Tit (*Parus Major*): The Effect of Similarity
607 and Familiarity. *Animal Behaviour* 30, 997–1009. [https://doi.org/10.1016/S0003-3472\(82\)80188-7](https://doi.org/10.1016/S0003-3472(82)80188-7).
- 608 80. Baker, M. C., McGregor, P. K., and Krebs, J. R. (1987). Sexual Response of Female Great Tits to Local and Distant Songs.
609 *Ornis Scandinavica* 18, 186. <https://doi.org/10.2307/3676765>.
- 610 81. Hutfluss, A., Bermúdez-Cuamatzin, E., Mouchet, A., Briffa, M., Slabbekoorn, H., and Dingemanse, N. J. (2022). Male Song
611 Stability Shows Cross-Year Repeatability but Does Not Affect Reproductive Success in a Wild Passerine Bird. *Journal of
612 Animal Ecology* 91, 1507–1520. <https://doi.org/10.1111/1365-2656.13736>.
- 613 82. McGregor, P. K. and Krebs, J. R. (1982b). Mating and Song Sharing in the Great Tit. *Nature* 297, 60–61. <https://doi.org/10.1038/297060a0>.
- 615 83. McGregor, P. K., Krebs, J. R., and Perrins, C. M. (1981). Song Repertoires and Lifetime Reproductive Success in the Great
616 Tit (*Parus Major*). *The American Naturalist* 118, 149–159. <https://doi.org/918>.
- 617 84. Morfi, V., Lachlan, R. F., and Stowell, D. (2021). Deep Perceptual Embeddings for Unlabelled Animal Sound Events. *The
618 Journal of the Acoustical Society of America* 150, 2–11. <https://doi.org/10.1121/10.0005475>.
- 619 85. Zandberg, L., Morfi, V., George, J., Clayton, D. F., Stowell, D., and Lachlan, R. F. (2022). Bird Song Comparison Using
620 Deep Learning Trained from Avian Perceptual Judgments. <https://doi.org/10.1101/2022.12.23.521425>.
- 621 86. Chambers, M. and Drovandi, C. (2023). Many-Levelled Continuation Ratio Models for Frequency of Alcohol and Drug
622 Use Data.

- 623 87. Warti, R., Kurnia, A., and Sadik, K. (2020). Evaluation of Proportional Odds and Continuation Ratio Models for Smoker
624 in Indonesia. Proceedings of the 1st International Conference on Statistics and Analytics, ICSA 2019, 2-3 August 2019,
625 Bogor, Indonesia.
- 626 88. Bircher, N., van Oers, K., and Naguib, M. (2021). Anyone Listening? No Evidence for Eavesdropping on Male Singing
627 Interactions in the Great Tit, *Parus Major*. *Animal Behaviour* 176, 67–76. <https://doi.org/10.1016/j.anbehav.2021.03.009>.
- 628 89. Blumenrath, S. H. and Dabelsteen, T. (2004). Degradation of Great Tit (*Parus Major*) Song before and after Foliation:
629 Implications for Vocal Communication in a Deciduous Forest. *Behaviour* 141, 935–958.
- 630 90. Dearmon, J. and Smith, T. E. (2016). Gaussian Process Regression and Bayesian Model Averaging: An Alternative Ap-
631 proach to Modeling Spatial Phenomena: Gaussian Process Regression and BMA. *Geogr Anal* 48, 82–111. <https://doi.org/10.1111/gean.12083>.
- 633 91. Gelfand, A. E. and Schliep, E. M. (2016). Spatial Statistics and Gaussian Processes: A Beautiful Marriage. *Spatial Statistics*.
634 *Spatial Statistics Avignon: Emerging Patterns* 18, 86–104. <https://doi.org/10.1016/j.sposta.2016.03.006>.
- 635 92. Wright, W. J., Irvine, K. M., Rodhouse, T. J., and Litt, A. R. (2021). Spatial Gaussian Processes Improve Multi-Species
636 Occupancy Models When Range Boundaries Are Uncertain and Nonoverlapping. *Ecology and Evolution* 11, 8516–8527.
637 <https://doi.org/10.1002/ece3.7629>.
- 638 93. Bürkner, P.-C. (2017). Brms : An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80,
639 <https://doi.org/10.18637/jss.v080.i01>.
- 640 94. Stan Development Team (2023). Stan Modeling Language Users Guide and Reference Manual, Version 2.18.0. URL: <http://mc-stan.org/>.
- 642 95. Fox, J. and Weisberg, S. (2018). Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots
643 and Partial Residuals. *Journal of Statistical Software* 87, 1–27. <https://doi.org/10.18637/jss.v087.i09>.
- 644 96. Larsen, W. A. and McCleary, S. J. (1972). The Use of Partial Residual Plots in Regression Analysis. *Technometrics* 14,
645 781–790. <https://doi.org/10.1080/00401706.1972.10488966>.
- 646 97. Richards, A. (2015). *University of Oxford Advanced Research Computing*. Manual. <https://doi.org/10.5281/zenodo.22558>.

647 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

648

649

Table S2. Model variable key

Variable	Description
repertoire_size	Number of distinct song types sung by an individual
immigrant	Immigrant status (hatched in the population / not hatched in the population)
sampling_effort	Total number of recordings obtained for this individual
year	Year in which the repertoire was recorded
father	ID of the male; BTO (British Trust for Ornithology) ring number
dispersal_distance	Postnatal dispersal distance, in metres, from the natal nest box to the breeding nest box
age	The age of the bird. This is exact if the bird was ringed as a pullus in the population, or approximate (based on plumage moult) otherwise
average_frequency	The mean of the frequency of each song in a bird's repertoire in a given year
mean_dist1	Average minimum Euclidean distance between the repertoires of two birds
natal_distance	Distance in metres at which two birds were born
nest_distance	Distance in metres at which two birds bred
year_born_diff	The absolute difference between the birth years of two birds
mm(...)	Multi-membership grouping term for the similarity network
resident_status	Origin of a pair of birds: both, one or neither were hatched in the population
prop_immigrant	Proportion of the birds in a neighbourhood that were not hatched inside the population
mean_dispersal_distance	Mean postnatal dispersal distance, in metres, of the birds in the neighbourhood
prop_same_birds	Proportion of the birds in a neighbourhood that were already there the year before
mean_age	Mean age of the birds in a neighbourhood
n_current_songs	Absolute number of song types in a neighbourhood (not unique song types)
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
prop_shared	Proportion of the song types in a neighbourhood that were already present. Reported as 1-prop_shared: 'song turnover'

650

651

Table S3. Model estimates

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

652

Continued on next page

Table S3. Model estimates (Continued)

Model	Hypothesis	Estimate^a	Evid. Ratio	Post. Prob
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

653 ^a Estimates are Medians and 95% Credible Intervals

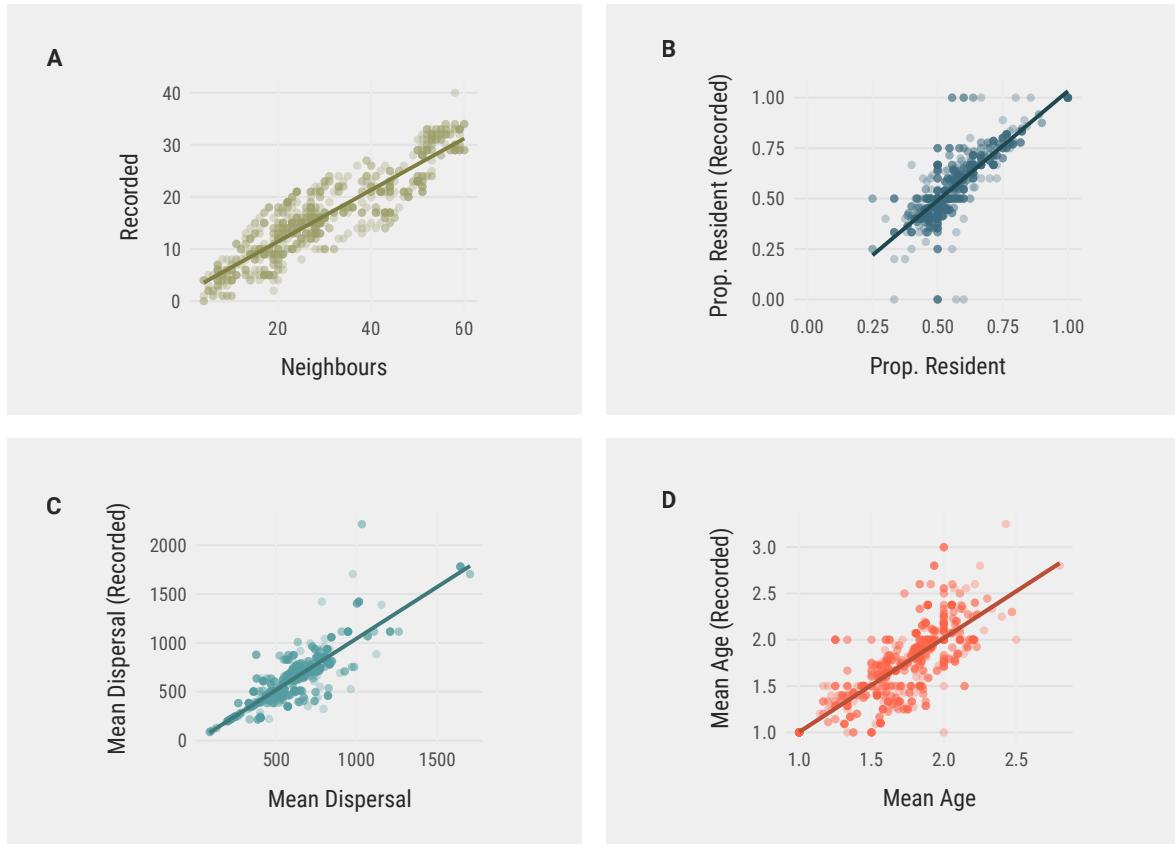


Figure S1. Absence of bias in the sampling of neighbourhood properties.

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.

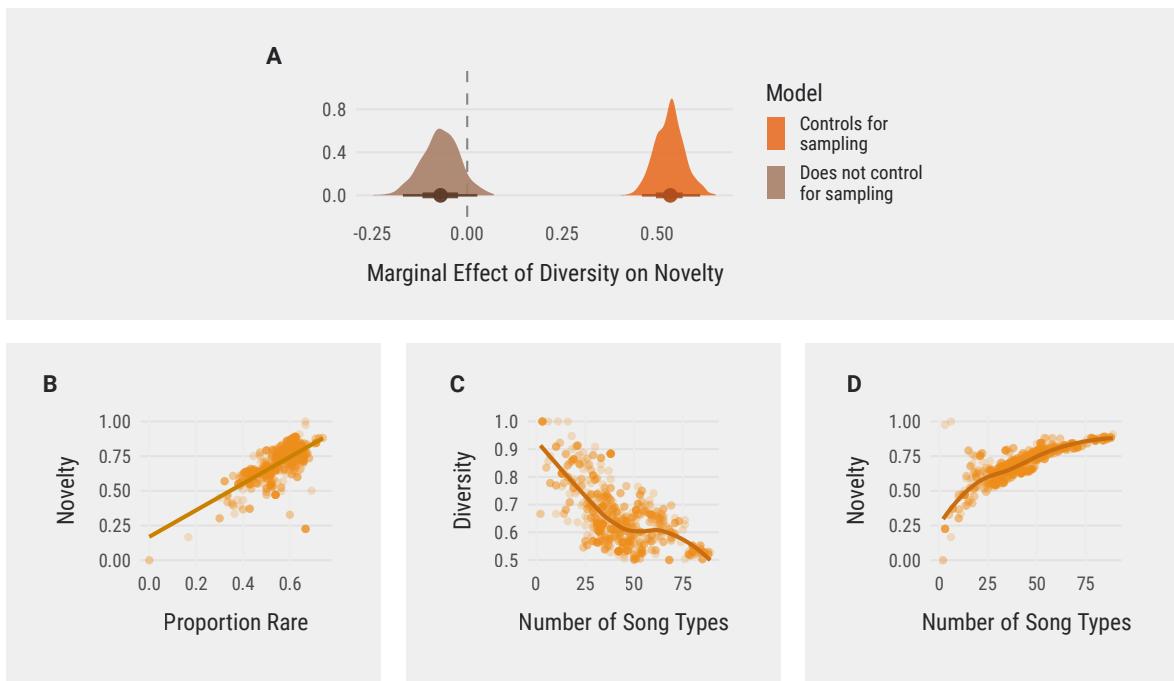


Figure S2. Relationships among outcome variables and sampling effects.

(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.

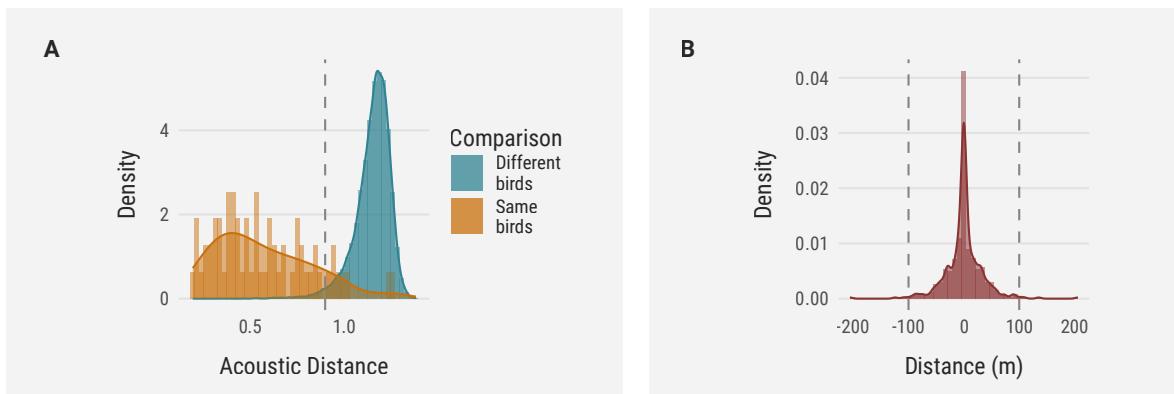


Figure S3. Thresholds used during the process of reidentifying individual birds based on their songs.

(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.

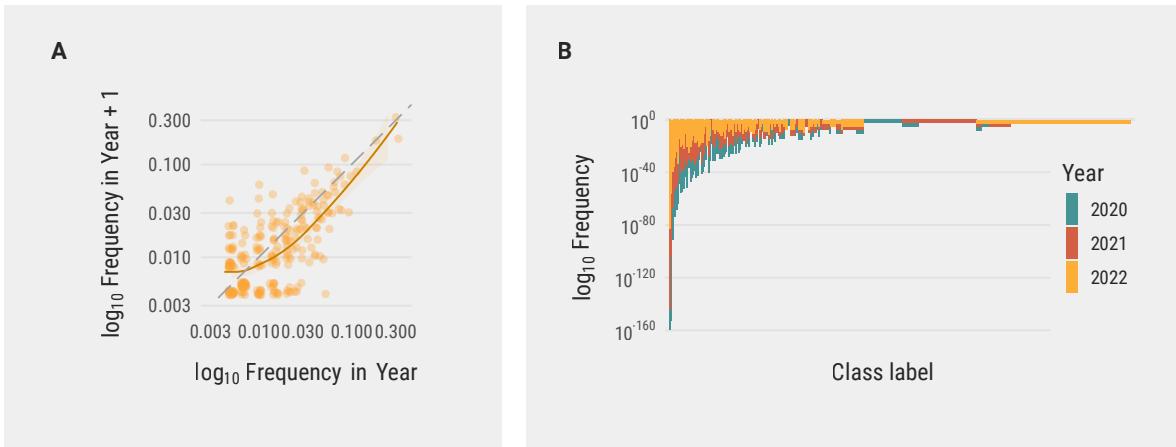


Figure S4. Song frequencies and their relationship with abundance in the following year.

(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.

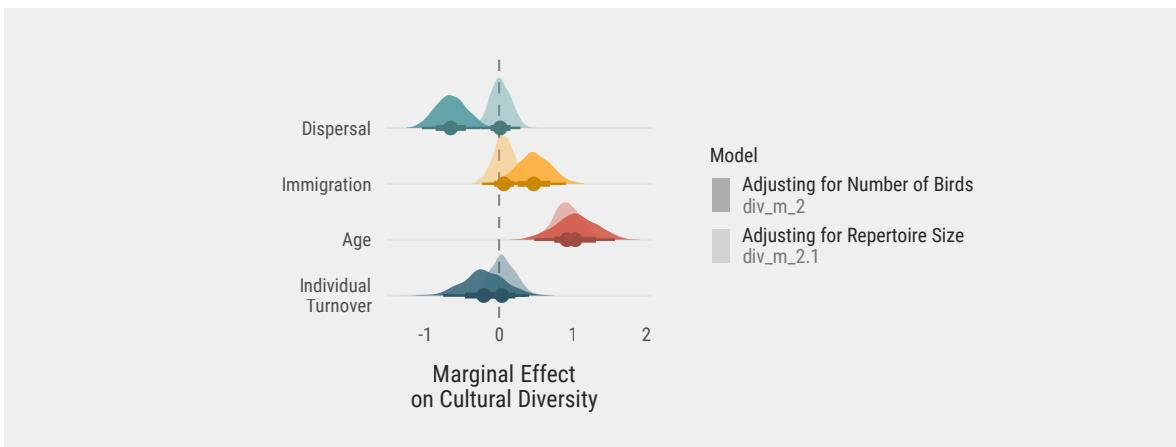


Figure S5. Marginal effects of demographic variables on absolute cultural diversity.

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, $div_m_2.1$).

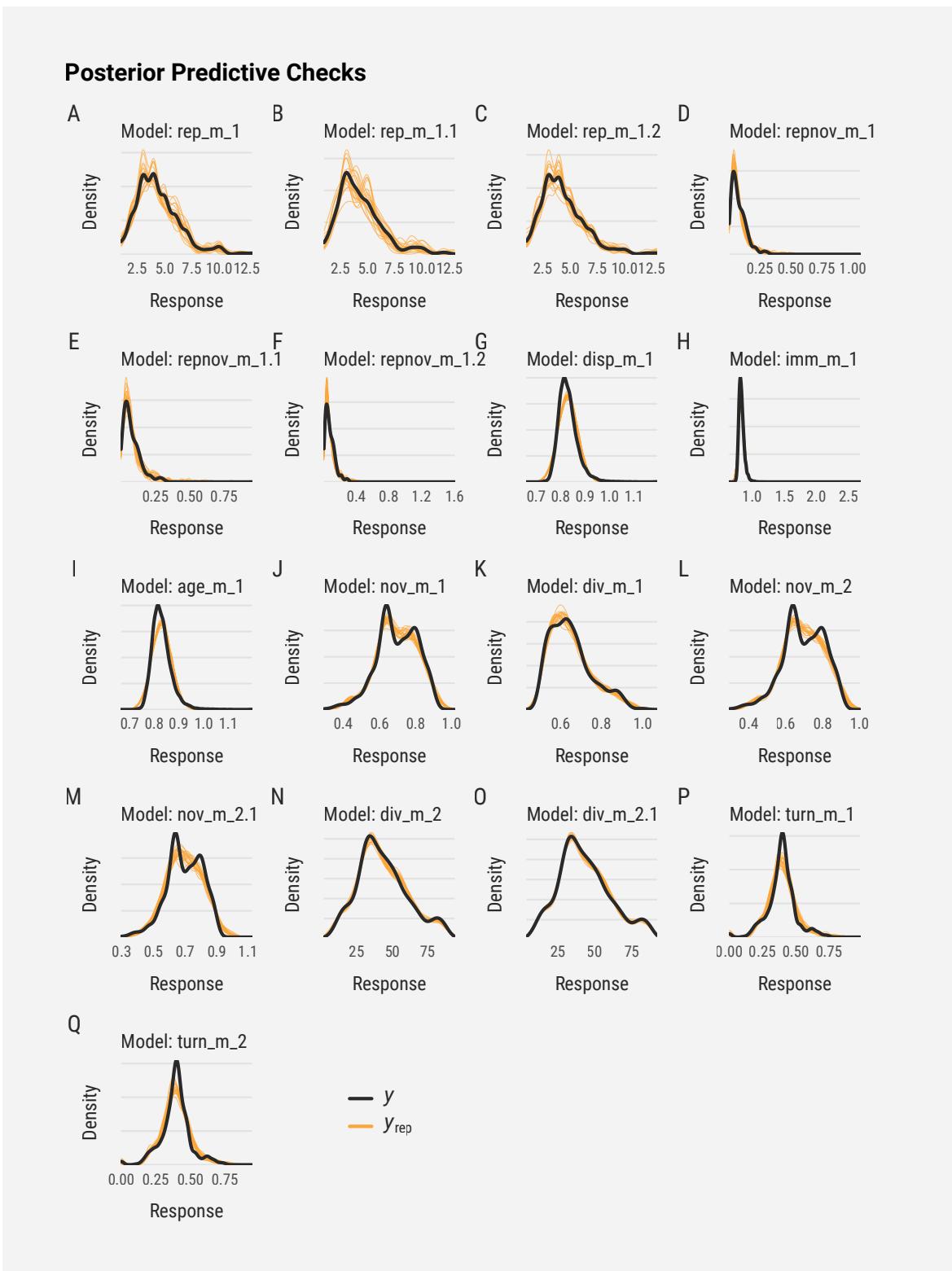


Figure S6. Posterior predictive checks for the main models in the study.

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.