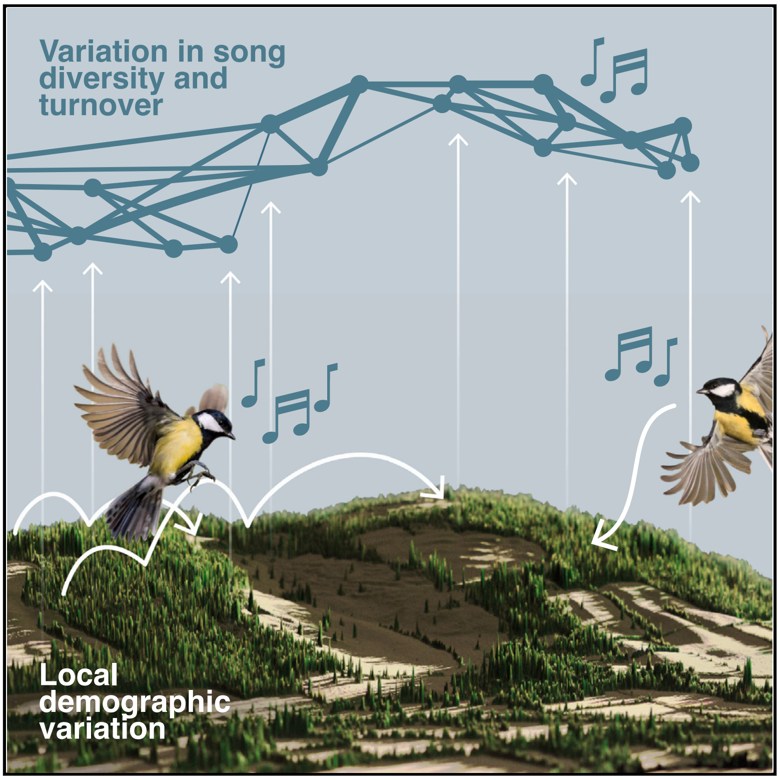
Current Biology

Report

The demographic drivers of cultural evolution in bird song

Graphical abstract



Highlights

- Analyzed over 100,000 great tit songs using deep learning to study vocal culture
- Tested if local demographic variation and processes impact song culture in the wild
- Showed that age, dispersal, and turnover affect cultural diversity and change

Authors

Nilo Merino Recalde, Andrea Estandía,
Sara C. Keen, Ella F. Cole,
Ben C. Sheldon

Correspondence

nilo.recalde@biology.ox.ac.uk

In brief

Merino Recalde et al. analyze over 100,000 great tit songs to study how demographic factors and processes like turnover, immigration, and age structure shape vocal culture. Their findings reveal complex interactions between these processes, advancing our understanding of how population dynamics influence cultural evolution in animal communities.

Merino Recalde et al., 2025, Current Biology *35*, 1631–1640
April 7, 2025
https://doi.org/10.1016/j.cub.2025.02.016

Current Biology

CellPress
OPEN ACCESS

Report

The demographic drivers of cultural evolution in bird song

Nilo Merino Recalde,[1,3,*] 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 OX1 3RB, UK
[2]Earth Species Project, 1536 Oxford St., Berkeley, CA 94709, USA
[3]Lead contact
*Correspondence: nilo.recalde@biology.ox.ac.uk

https://doi.org/10.1016/j.cub.2025.02.016

SUMMARY

Social learning can give rise to shared behavioral patterns that persist as culture within animal communities,[1,2] such as bird and whale songs and cetacean feeding techniques.[3–5] These cultural traits evolve[6–9] and can impact individual survival, population structure, and conservation efforts.[10] Although theoretical work indicates that demographic processes—like population turnover, immigration, and age structure—significantly influence cultural evolution,[11–13] empirical evidence from natural populations is limited. Using deep metric learning to analyze over 100,000 songs from >400 repertoires in great tits (Parus major), we show that demographic variation affects vocal cultures within the small spatial and temporal scales where learning occurs. Within-population dispersal homogenizes song culture, and immigrant birds adopt local songs while increasing neighborhood diversity through larger repertoires. Birds of similar age tend to have more similar repertoires, which provides evidence of cultural change, with mixed-age neighborhoods showing higher cultural diversity. We estimate that individual turnover is a main driver of cultural change and that its pace is also moderated by dispersal, immigration, and population age structure. These findings 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 and mode of song acquisition.

RESULTS AND DISCUSSION

Culture is increasingly recognized as both a fundamental aspect of many animals' lives and a valuable tool in monitoring and conservation efforts.[14–16] 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[10,17] and can be lost when habitat fragmentation and population decline lead to reduced learning opportunities.[18,19] Neutral and selective mechanisms drive cultural evolution,[6,7,20–22] resulting in "traditions" that differ considerably in their diversity and stability.[23] While the effects of social learning strategies—such as frequency dependence and tutor biases—on the diversity and stability of cultures are well-documented,[24–28] our understanding of how demography affects cultural traits within wild populations is less well developed. Processes such as the recruitment of juveniles, immigration, emigration, mortality, and variation in age structure are likely to strongly affect an individual's opportunities for learning and exposure to different cultural variants, as it has been amply emphasized by theoretical work.[11,13,29–39] However, translating theoretical expectations into empirical evidence remains a challenge (see Chimento et al.,[40] Fayet et al.,[41] Payne and Payne,[42] Graham et al.,[43] and Laiolo et al.[44] for exceptions). A comprehensive understanding of cultural dynamics in the wild requires examining both intrinsic factors—social, cultural, and cognitive, which have received greater attention—and extrinsic, ecological, and demographic processes. This includes identifying the spatial and temporal scales at which these processes operate and evaluating their relative significance within natural populations.

To contribute to this goal, we built a comprehensive dataset that spans 3 years and documents the dawn songs produced by male great tit birds during 454 breeding attempts in a single population located in Wytham Woods, UK. The population's marked variation in individual turnover, postnatal dispersal distances, age structure, and immigration across space—known through ongoing long-term monitoring[45]—allowed us to estimate their effects on song cultural repertoires at individual and group levels. First, we assigned more than 109,000 songs in 330 song repertoires to 242 individual birds through direct physical capture, radio frequency identification microchips, and a novel song-based re-identification method that uses a deep metric learning model. Then, we quantified individual and group-level traits and analyzed variation in song cultural similarity, diversity, and turnover (see definitions) using network and spatially explicit Bayesian multilevel regression models. See Figure 1 for a visual abstract of the study.

Our results reveal an interplay of demographics and song cultural dynamics that, albeit complex, largely matches theoretical expectations. This work also demonstrates that bird song, which already provides what is perhaps the largest body of evidence for cultural change in animals,[48] also has the potential to help us shed light on the impact of other population processes on

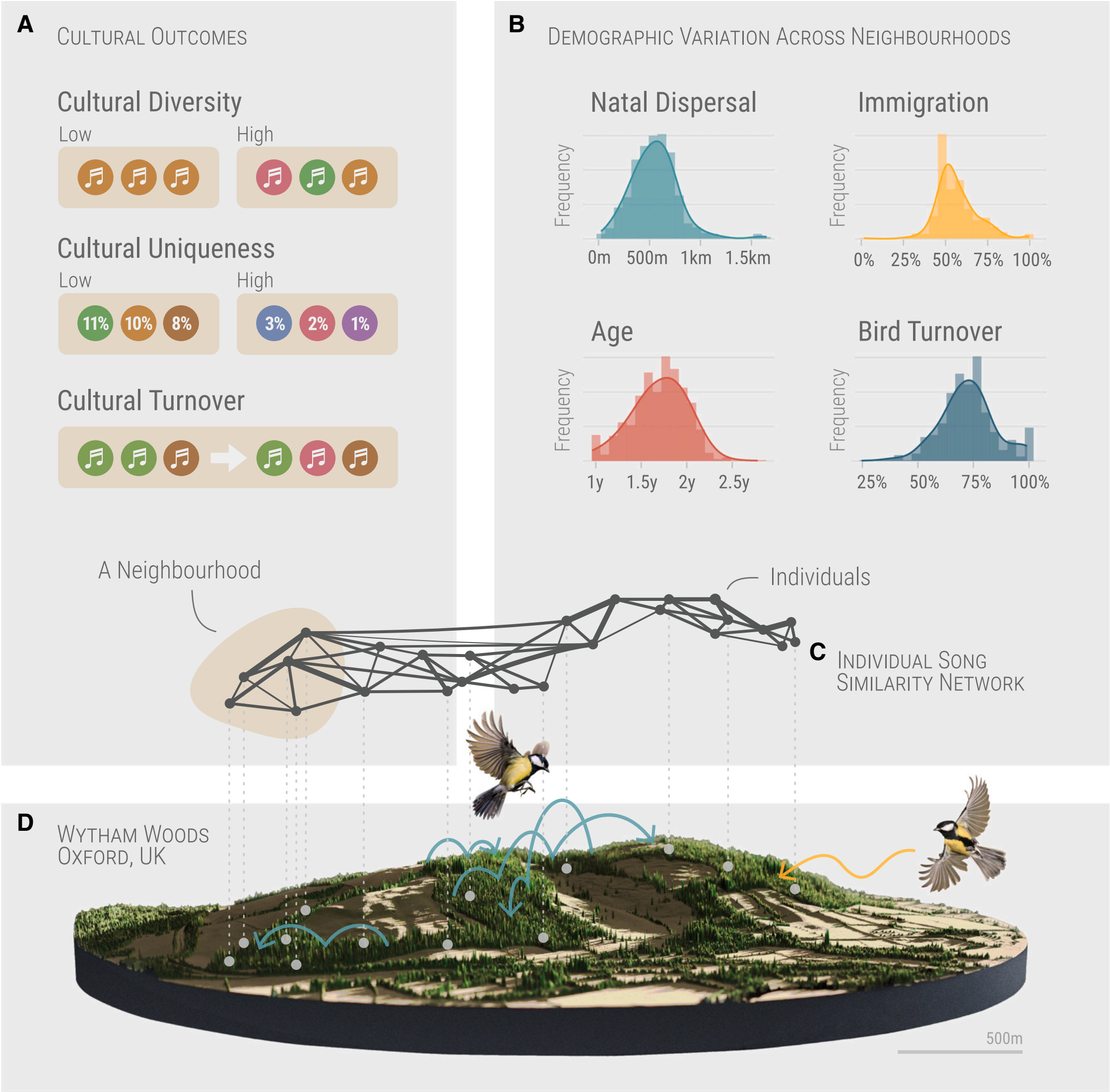


Figure 1. Study system and main variables in our analysis

(A) Cultural variables measured at the neighborhood level. Higher values of cultural diversity indicate that there are more distinct song types in the neighborhood relative to the total song output. Higher cultural uniqueness indicates that the songs in the neighborhood are, on average, less common in the population, and higher cultural turnover indicates that the neighborhood's song repertoire has changed more from 1 year to the next. See definitions for full definitions.

(B) Variation in the demographic properties and composition of neighborhoods 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[46] and made with rayshader.[47] 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.

animal cultures, owing to the fact that we can sample individual song repertoires with relative ease.

Reduced dispersal, higher immigration, 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.[49–51] 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.[36] This, in turn, should result in the maintenance of distinct behavioral patterns within populations if learning is somewhat accurate, leading to a greater number of cultural variants unique to

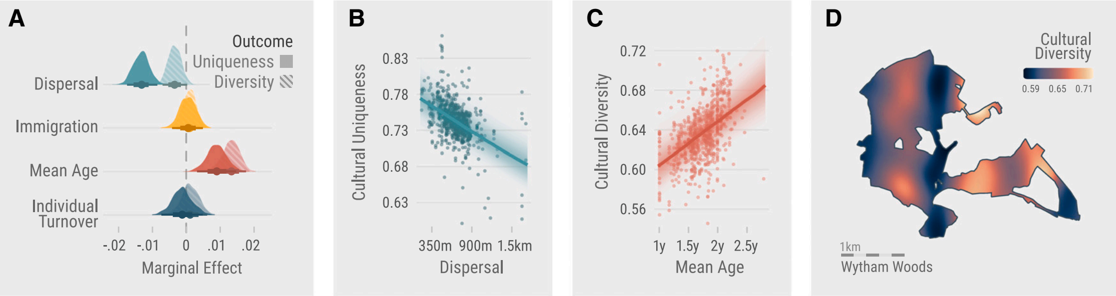


Figure 2. Influence of demographic variables on cultural diversity and uniqueness within neighborhoods

(A) Marginal effects at the mean of neighborhood characteristics, including mean dispersal distance, proportion of immigrant birds, average age, and individual turnover. See STAR Methods for full definitions. See also Figures S7E and S5.

(B) Adjusted predictions and partial residuals of the effect of mean neighborhood dispersal distance on cultural uniqueness. Low-dispersal neighborhoods are those in which birds hatched in the same area.

(C) Adjusted predictions and partial residuals of the effect of the mean age of the neighborhood on cultural diversity. A neighborhood 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.

a neighborhood or region.[52,53] Our analysis indeed indicates that neighborhoods (see here) where more birds have remained in proximity to their natal areas harbor greater and more unique cultural diversity (diversity: $P(\beta_{disp(\overline{m})} \langle 0|D) = 1, mem = -0.018$, $CI_{95\%} [-0.023, -0.012]$; uniqueness: $P(\beta_{disp(\overline{m})} \langle 0|D) = 0.96$, $mem = -0.005$, $CI_{95\%} [-0.01, 0]$; Figures 2A and 2B; Table S3; see subsection modeling group-level outcomes), which is in line with prior research at a much coarser grain.[41]

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 from their parents and early in life, in a manner reminiscent of genetic inheritance, while others learn continuously from their neighbors or only after dispersal (see Searcy et al.[54] 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 10 different song types.[55–57] 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: $P(\beta_{disp(m)} \langle 0|D) = 1, mem = -0.2, CI_{95\%} [-0.3, -0.09]$; Figure 3B; Table S3), and possibly smaller repertoires as well (repertoire size: $P(\beta_{disp(m)} \langle 0|D) = 0.91, mem = -0.2, CI_{95\%} [-0.44, 0.05]$; 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 positive frequency-dependent learning or a process leading to similar acquisition curves (see Figure S8; 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 program, 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,[56] and become chiefly sedentary as adults.[58–60] 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.[61,62]

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 critical period learners that learn primarily from territorial neighbors after dispersal.[55,56]

However, immigrant birds, while not acoustically distinct, tend to have larger repertoires compared with their resident counterparts (Figure 3B; $P(\beta_{\overline{imm.}} > 0|D) = 0.87, mem = 0.24$, $CI_{95\%} [-0.098, 0.593]$; Table S3). At the group level, this small and uncertain effect amplifies, such that neighborhoods 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 3B) but do have

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

(A) Illustrative example showing the repertoires of two different birds in the population, with three songs in each, one of which is shared. Each sub-panel shows a cartoon spectrogram, with time on the horizontal axis and frequency on the vertical. Units not shown.

(B) Marginal effects of dispersal, immigration status, and age on individual song repertoires, described in terms of their absolute size (the total number of distinct song types sung by that bird) and their uniqueness (how rare, on average, the song types are in the population within that year).

(C) Marginal effects of dispersal, immigration status, and age on song repertoire similarity between individuals. Dispersal: birds that are close neighbors are more culturally similar, regardless of where they hatched, whereas natal distance may have a weak positive effect on cultural similarity. Immigration: there is no strong evidence that birds that hatched outside the population are dissimilar from resident birds. Age difference: birds are less culturally similar the greater the difference in their birth years, which evidences cultural change.

higher absolute cultural diversity—above what would be expected based solely on the number of birds ($P(\beta_{\overline{imm.}} > 0|D) = 0.98, mem = 0.47, CI_{95\%}$ [0.1, 0.84]; Figure S7E; Table S3).

Previous research[63] has revealed that most birds arriving from outside the population disperse over 2 kilometers, significantly farther than the typical distances observed within the population (median for males = 558 meters[56]). 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, and then, a heightened pressure to adopt vocalizations similar to those of territorial neighbors to avoid any social or reproductive costs associated with non-local signals, as seen in other species.[64–68]

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 neighborhoods: those with a higher proportion of older individuals have higher levels of cultural diversity and uniqueness (Figures 3A, 3C, and S7E). Conversely, in areas where the majority of the population comprises younger birds surrounded by similar-aged peers, individual birds tend to sing fewer song types, and those song types tend to be more common within the population (diversity: $P(\beta_{\overline{age}} \langle 0|D) = 1, mem = 0.021, CI_{95\%}$ [0.014, 0.027]; uniqueness: $P(\beta_{\overline{age}} \langle 0|D) = 0.99, mem = 0.012, CI_{95\%}$ [0.005, 0.019]; Figures 2A and 2C; Table S3).

Demographic processes moderate the rate of cultural change at small spatiotemporal scales

We now shift our focus from static measures of cultural diversity to cultural turnover, examining how quickly song types disappear from neighborhoods and the consequences this has for their cultural makeup. The primary driver of cultural turnover within neighborhoods is individual turnover (total effect $mem = 0.072\ CI_{95\%}$ [0.051, 0.093]). When birds leave or die, many song types disappear with them, and, as modeling suggests, the young birds that replace them might speed up the adoption of new song types.[38] Across the 3-year study period, now considering the entire population, cultural turnover between consecutive years averages 0.45 (0.47 and 0.44; note that specific values are contingent on the granularity of song type definitions; see manual categorization). If all variants faced an equal chance of disappearing, this would quickly lead to complete cultural replacement. However, after a 2-year gap (2020–2023), turnover only slightly increases to 0.59 (compared with an expected 0.7; estimating the variance around these figures would require longer-term data). We anticipate this rate to taper further over longer periods, as rare variants encounter greater stochasticity while common songs endure, likely placing a ceiling on the long-term rate of cultural turnover (Figure S7C). Indeed, some common song types documented over four decades ago persist within the population.[55,61] This persistence might be due to different factors, like accurate learning based on song frequency or strong tendencies to converge on certain song types.[27,28,69,70]

After factoring in individual turnover, we examine how mean natal dispersal distance, the proportion of immigrant birds, and mean neighborhood age affect cultural change within a neighborhood. 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 neighborhood, there is a high influx of immigrants, and the distribution of age is skewed toward older individuals. The model predicts slower cultural change at less than half the rate compared with the converse scenario ($0.39\ CI_{95\%}$ [0.24, 0.51] vs. $0.72\ CI_{95\%}$[0.66, 0.77], 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 neighborhoods over time if it persists, highlighting the importance of the demographic structure of populations in also moderating the pace of cultural change.

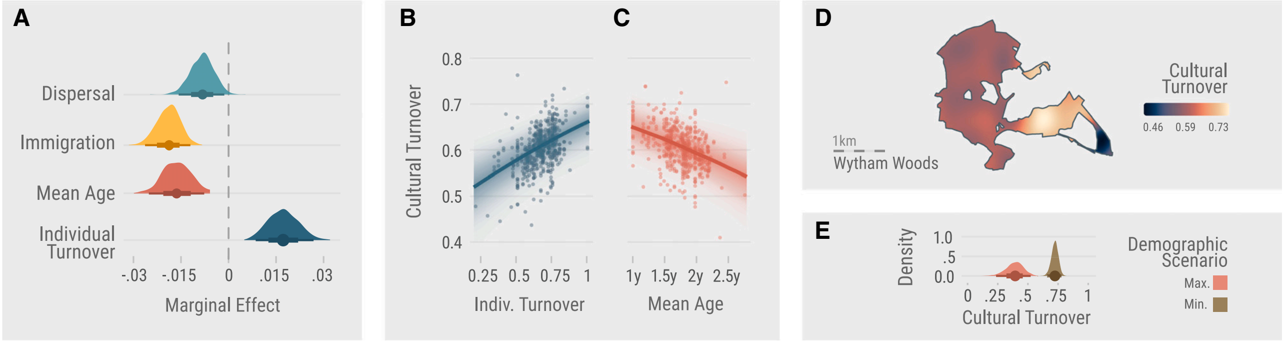


Figure 4. Influence of demographic variables on cultural turnover within neighborhoods

(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 neighborhoods.

(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 neighborhood age on cultural turnover within neighborhoods (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 neighborhood dispersal, immigration, and age are low, as they slow down cultural change.

The observed slowdown in cultural change due to dispersal and immigration aligns with our findings that dispersal homogenizes song repertoires and that immigrants tend to adopt the existing population's variants rather than introducing new ones (see Figures 2A and 3A). At the same time, our estimate for the effect of neighborhood age ($P(\beta_{\overline{age}} \langle 0|D) = 1$, $mem = -0.044$, $CI_{95\%}$ $[-0.063, -0.026]$; Figure 4C) aligns with modeling work suggesting that learning from older individuals should slow down cultural change.[35] Indeed, age may serve as a brake on change, as older birds continue to sing song types that are becoming less frequent in the population, an idea supported by the observation that individual birds' repertoires are least similar when there is a large age difference (Figure 3C). The differences between the older and younger birds' repertoires also increase cultural diversity and uniqueness within neighborhoods that include many older birds, as discussed above, suggesting an important role of age structure in shaping both cultural diversity and turnover.

Consequences for cultural structure, stability, and diversity

Cultural traits, learned bird song in this case, are shaped by many factors: some external, such as those discussed here, others intrinsic to learning and culture, and yet others that arise from selective processes driven by preference and function. Even within the confines of a relatively small population—Wytham Woods spans a mere 4 kilometers—we have been able to document associations between heterogeneity in the demographic composition of neighborhoods and cultural outcomes using a large dataset of song repertoires. These outcomes are most likely driven by differences in individual learning and exposure to cultural variants. In particular, we find that dispersal within the population reduces cultural diversity and uniqueness. Birds that hatched outside the population seem to adopt existing song types rather than introduce new ones but tend to have larger repertoires and so increase the absolute diversity of neighborhoods. Birds of the same age tend to share similar song types, while neighborhoods comprising both older and younger birds are more likely to have 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, older-age neighborhoods have slower cultural turnover. The main driver of cultural turnover is individual turnover, while longer postnatal dispersal distances, a higher proportion of immigrant birds, and an older population slow it down.

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

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to the lead contact, Nilo Merino Recalde (nilo.recalde@biology.ox.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The complete Wytham great tit song dataset has been deposited at OSF and is publicly available at osf.io/n8ac9.[71] Documentation for the dataset is available at nilomr.github.io/great-tit-hits/.
- All original code and data used to reproduce the analyses and figures in this article have been deposited at Zenodo and are publicly available at https://doi.org/10.5281/zenodo.12800735.[72] The repository can also be accessed at github.com/nilomr/birdsong-demography.

- Any additional information required to reanalyze the data reported in this paper is available from the lead contact.

ACKNOWLEDGMENTS

We thank all those who have contributed to the long-term nest box study in Wytham Woods and the collection of associated data. We also thank three anonymous reviewers for their constructive feedback. This work was supported by a Clarendon-Mary Frances Wagley Graduate Scholarship and an EGI scholarship to N.M.R. and made use of the University of Oxford Advanced Research Computing facility.[73]

AUTHOR CONTRIBUTIONS

N.M.R.: conceptualization, methodology, software, formal analysis, investigation, data curation, writing—original draft, writing—review and editing, and visualization; A.E.: investigation, data curation, and writing—review and editing; S.C.K.: writing—review & editing; E.F.C.: supervision and project administration; B.C.S.: supervision, project administration, writing—review and editing, and funding acquisition.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
  - Data collection
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Data processing and annotation
  - Characterizing repertoire similarity
  - Re-identifying individuals from their songs
  - Modelling pairwise similarity and individual repertoires
  - Modelling group-level outcomes
  - Model estimates and reporting
  - Software

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.02.016.

Received: December 1, 2023
Revised: December 12, 2024
Accepted: February 11, 2025
Published: March 7, 2025

REFERENCES

1. Viciana, H. (2021). Animal Culture: But of Which Kind? Stud. Hist. Philos. Sci. A *90*, 208–218. https://doi.org/10.1016/jshpsa.2021.10.012.
2. Whiten, A. (2019). Cultural Evolution in Animals. Annu. Rev. Ecol. Evol. Syst. *50*, 1–26. https://doi.org/10.1146/annurev-ecolsys-110218-025040.
3. Aplin, L.M. (2019). Culture and Cultural Evolution in Birds: A Review of the Evidence. Anim. Behav. *147*, 179–187. https://doi.org/10.1016/j.anbehav.2018.05.001.
4. 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.
5. Garland, E.C., and McGregor, P.K. (2020). Cultural Transmission, Evolution and Revolution in Vocal Displays: Insights from Bird and Whale Song. Front. Psychol. *11*, 544929. https://doi.org/10.3389/fpsyg.2020.544929.
6. Potvin, D.A., and Clegg, S.M. (2015). The Relative Roles of Cultural Drift and Acoustic Adaptation in Shaping Syllable Repertoires of Island Bird Populations Change with Time since Colonization. Evolution *69*, 368–380. https://doi.org/10.1111/evo.12573.
7. Williams, H., and Lachlan, R.F. (2022). Evidence for cumulative cultural evolution in bird song. Philos. Trans. R. Soc. Lond. B Biol. Sci. *377*, 20200322. https://doi.org/10.1098/rstb.2020.0322.
8. Ju, C., Geller, F.C., Mundinger, P.C., and Lahti, D.C. (2019). Four Decades of Cultural Evolution in House Finch Songs. Auk *136*. https://doi.org/10.1093/auk/uky012.
9. Riebel, K., Lachlan, R.F., and Slater, P.J.B. (2015). Learning and Cultural Transmission in Chaffinch Song. Adv. Study Behav. *47*, 181–227. https://doi.org/10.1016/bs.asb.2015.01.001.
10. Brakes, P., Dall, S.R.X., Aplin, L.M., Bearhop, S., Carroll, E.L., Ciucci, P., Fishlock, V., Ford, J.K.B., Garland, E.C., Keith, S.A., et al. (2019). Animal Cultures Matter for Conservation. Science *363*, 1032–1034. https://doi.org/10.1126/science.aaw3557.
11. Deffner, D., Kandler, A., and Fogarty, L. (2022). Effective Population Size for Culturally Evolving Traits. PLoS Comput. Biol. *18*, e1009430. https://doi.org/10.1371/journal.pcbi.1009430.
12. Hudson, E.J., and Creanza, N. (2022). Modeling How Population Size Drives the Evolution of Birdsong, a Functional Cultural Trait. Evolution *76*, 1139–1152. https://doi.org/10.1111/evo.14489.
13. Kandler, A., Fogarty, L., and Karsdorp, F. (2023). The Interplay between Age Structure and Cultural Transmission. PLoS Comput. Biol. *19*, e1011297. https://doi.org/10.1371/journal.pcbi.1011297.
14. Laiolo, P., and Jovani, R. (2007). The Emergence of Animal Culture Conservation. Trends Ecol. Evol. *22*, 5. https://doi.org/10.1016/j.tree.2006.10.007.
15. Brakes, P., Carroll, E.L., Dall, S.R.X., Keith, S.A., McGregor, P.K., Mesnick, S.L., Noad, M.J., Rendell, L., Robbins, M.M., Rutz, C., et al. (2021). A deepening understanding of animal culture suggests lessons for conservation. Proc. Biol. Sci. *288*, 20202718. https://doi.org/10.1098/rspb.2020.2718.
16. Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., Hurley, M.A., McWhirter, D.E., Miyasaki, H.M., Monteith, K.L., 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.
17. Garland, E.C., Goldizen, A.W., Lilley, M.S., Rekdahl, M.L., Garrigue, C., Constantine, R., Hauser, N.D., Poole, M.M., Robbins, J., and Noad, M.J. (2015). Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. Conserv. Biol. *29*, 1198–1207. https://doi.org/10.1111/cobi.12492. https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/cobi.12492.
18. Paxton, K.L., Sebastián-González, E., Hite, J.M., Crampton, L.H., Kuhn, D., and Hart, P.J. (2019). Loss of Cultural Song Diversity and the Convergence of Songs in a Declining Hawaiian Forest Bird Community. R. Soc. Open Sci. *6*, 190719. https://doi.org/10.1098/rsos.190719.
19. Crates, R., Langmore, N., Ranjard, L., Stojanovic, D., Rayner, L., Ingwersen, D., and Heinsohn, R. (2021). Loss of Vocal Culture and Fitness Costs in a Critically Endangered Songbird. Proc. Biol. Sci. *288*, 20210225. https://doi.org/10.1098/rspb.2021.0225.
20. Williams, H., Levin, I.I., Norris, D.R., Newman, A.E.M., and Wheelwright, N.T. (2013). Three Decades of Cultural Evolution in Savannah Sparrow Songs. Anim. Behav. *85*, 213–223. https://doi.org/10.1016/j.anbehav.2012.10.028.
21. Youngblood, M., and Lahti, D.C. (2022). Content Bias in the Cultural Evolution of House Finch Song. Anim. Behav. *185*, 37–48. https://doi.org/10.1016/j.anbehav.2021.12.012.

22. Williams, H., Scharf, A., Ryba, A.R., Ryan Norris, D., Mennill, D.J., Newman, A.E.M., Doucet, S.M., and Blackwood, J.C. (2022). Cumulative cultural evolution and mechanisms for cultural selection in wild bird songs. Nat. Commun. *13*, 4001. https://doi.org/10.1038/s41467-022-31621-9.
23. Tchernichovski, O., Feher, O., Fimiarz, D., and Conley, D. (2017). How Social Learning Adds up to a Culture: From Birdsong to Human Public Opinion. J. Exp. Biol. *220*, 124–132. https://doi.org/10.1242/jeb.142786.
24. Pike, T.W., and Laland, K.N. (2010). Conformist Learning in Nine-Spined Sticklebacks' Foraging Decisions. Biol. Lett. *6*, 466–468. https://doi.org/10.1098/rsbl.2009.1014.
25. Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J., and Hoppitt, W. (2015). Chimpanzees Copy Dominant and Knowledgeable Individuals: Implications for Cultural Diversity. Evol. Hum. Behav. *36*, 65–72. https://doi.org/10.1016/j.evolhumbehav.2014.09.002.
26. Aplin, L.M., Sheldon, B.C., and McElreath, R. (2017). Conformity Does Not Perpetuate Suboptimal Traditions in a Wild Population of Songbirds. Proc. Natl. Acad. Sci. USA *114*, 7830–7837. https://doi.org/10.1073/pnas.1621067114.
27. Lachlan, R.F., Ratmann, O., and Nowicki, S. (2018). Cultural Conformity Generates Extremely Stable Traditions in Bird Song. Nat. Commun. *9*, 2417. https://doi.org/10.1038/s41467-018-04728-1.
28. Tchernichovski, O., Eisenberg-Edidin, S., and Jarvis, E.D. (2021). Balanced Imitation Sustains Song Culture in Zebra Finches. Nat. Commun. *12*, 2562. https://doi.org/10.1038/s41467-021-22852-3.
29. Deffner, D., and McElreath, R. (2022). When Does Selection Favor Learning from the Old? Social Learning in Age-Structured Populations. PLoS One *17*, e0267204. https://doi.org/10.1371/journal.pone.0267204.
30. Kandler, A., Wilder, B., and Fortunato, L. (2017). Inferring Individual-Level Processes from Population-Level Patterns in Cultural Evolution. R. Soc. Open Sci. *4*, 170949. https://doi.org/10.1098/rsos.170949.
31. Fogarty, L., Creanza, N., and Feldman, M.W. (2019). The Life History of Learning: Demographic Structure Changes Cultural Outcomes. PLoS Comput. Biol. *15*, e1006821. https://doi.org/10.1371/journal.pcbi.1006821.
32. Deffner, D., and McElreath, R. (2020). The Importance of Life History and Population Regulation for the Evolution of Social Learning. Philos. Trans. R. Soc. Lond. B Biol. Sci. *375*, 20190492. https://doi.org/10.1098/rstb.2019.0492.
33. Derex, M., and Boyd, R. (2016). Partial Connectivity Increases Cultural Accumulation within Groups. Proc. Natl. Acad. Sci. USA *113*, 2982–2987. https://doi.org/10.1073/pnas.1518798113.
34. Derex, M., Perreault, C., and Boyd, R. (2018). Divide and Conquer: Intermediate Levels of Population Fragmentation Maximize Cultural Accumulation. Philos. Trans. R. Soc. Lond. B Biol. Sci. *373*, 20170062. https://doi.org/10.1098/rstb.2017.0062.
35. Kirby, S., and Tamariz, M. (2022). Cumulative Cultural Evolution, Population Structure and the Origin of Combinatoriality in Human Language. Philos. Trans. R. Soc. Lond. B Biol. Sci. *377*, 20200319. https://doi.org/10.1098/rstb.2020.0319.
36. Nunn, C.L., Thrall, P.H., Bartz, K., Dasgupta, T., and Boesch, C. (2009). Do Transmission Mechanisms or Social Systems Drive Cultural Dynamics in Socially Structured Populations? Anim. Behav. *77*, 1515–1524. https://doi.org/10.1016/j.anbehav.2009.02.023.
37. Barta, K.A., Garamszegi, L.Z., Scheuring, I., and Zsebők, S. (2023). Effects of Positive Frequency-Dependent Learning, Learning Mistakes, and Immigration on Complex Cultures–Validation on the Song of Collared Flycatcher (Ficedula Albicollis) by Individual-Based Modeling. Front. Ecol. Evol. *11*. https://doi.org/10.3389/fevo.2023.1040550.
38. Dyble, M., and Micheletti, A.J.C. (2024). Population Turnover, Behavioral Conservatism, and Rates of Cultural Evolution. Behav. Ecol. *35*, arae003. https://doi.org/10.1093/beheco/arae003.
39. Chimento, M., and Aplin, L.M. (2024). Understanding the Role of Naive Learners in Cultural Change. Am. Nat. *203*, 695–712. https://doi.org/10.1086/730110. https://www.journals.uchicago.edu/doi/10.1086/730110.
40. Chimento, M., Alarcón-Nieto, G., and Aplin, L.M. (2021). Population Turnover Facilitates Cultural Selection for Efficiency in Birds. Curr. Biol. *31*, 2477–2483.e3. https://doi.org/10.1016/j.cub.2021.03.057.
41. Fayet, A.L., Tobias, J.A., Hintzen, R.E., and Seddon, N. (2014). Immigration and Dispersal Are Key Determinants of Cultural Diversity in a Songbird Population. Behav. Ecol. *25*, 744–753. https://doi.org/10.1093/beheco/aru047.
42. Payne, R.B., and Payne, L.L. (1993). Song Copying and Cultural Transmission in Indigo Buntings. Anim. Behav. *46*, 1045–1065. https://doi.org/10.1006/anbe.1993.1296.
43. Graham, B.A., Heath, D.D., and Mennill, D.J. (2017). Dispersal Influences Genetic and Acoustic Spatial Structure for Both Males and Females in a Tropical Songbird. Ecol. Evol. *7*, 10089–10102. https://doi.org/10.1002/ece3.3456.
44. Laiolo, P., Vögeli, M., Serrano, D., and Tella, J.L. (2008). Song Diversity Predicts the Viability of Fragmented Bird Populations. PLoS One *3*, e1822. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0001822.
45. Lack, D. (1964). A Long-Term Study of the Great Tit (Parus Major). J. Anim. Ecol. *33*, 159–173. https://doi.org/10.2307/2437.
46. Department for Environment Food and Rural Affairs (2020). Defra Data Services Platform. https://environment.data.gov.uk/DefraDataDownload.
47. Morgan-Wall, T. (2023). rayshader: Create Maps and Visualize Data in 2D and 3D (GitHub).
48. Laland, K.N., and Janik, V.M. (2006). The Animal Cultures Debate. Trends Ecol. Evol. *21*, 542–547. https://doi.org/10.1016/j.tree.2006.06.005.
49. Suárez, D., Arribas, P., Jiménez-García, E., and Emerson, B.C. (2022). Dispersal Ability and Its Consequences for Population Genetic Differentiation and Diversification. Proc. Biol. Sci. *289*, 20220489. https://doi.org/10.1098/rspb.2022.0489.
50. Claramunt, S., Derryberry, E.P., Remsen, J.V., and Brumfield, R.T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. Proc. Biol. Sci. *279*, 1567–1574. https://doi.org/10.1098/rspb.2011.1922.
51. 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. Mol. Ecol. *18*, 2503–2517. https://doi.org/10.1111/j.1365-294X.2009.04207.x.
52. Whitehead, H., and Lusseau, D. (2012). Animal Social Networks as Substrate for Cultural Behavioural Diversity. J. Theor. Biol. *294*, 19–28. https://doi.org/10.1016/j.jtbi.2011.10.025.
53. Planqué, R., Britton, N.F., and Slabbekoorn, H. (2014). On the Maintenance of Bird Song Dialects. J. Math. Biol. *68*, 505–531. https://doi.org/10.1007/s00285-012-0632-8.
54. Searcy, W.A., Soha, J., Peters, S., and Nowicki, S. (2021). Variation in Vocal Production Learning across Songbirds. Philos. Trans. R. Soc. Lond. B Biol. Sci. *376*, 20200257. https://doi.org/10.1098/rstb.2020.0257.
55. McGregor, P.K., and Krebs, J.R. (1982). Song Types in a Population of Great Tits (Parus Major): Their Distribution, Abundance and Acquisition by Individuals. Behaviour *79*, 126–152. https://doi.org/10.1163/156853982X00210.
56. 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. M. Giurfa, ed. *6*, e16003. https://doi.org/10.1371/journal.pone.0016003.
57. Merino Recalde, N., Estandía, A., Pichot, L., Vansse, A., Cole, E.F., and Sheldon, B.C. (2024). A densely sampled and richly annotated acoustic data set from a wild bird population. Anim. Behav. *211*,

111–122. https://doi.org/10.1016/j.anbehav.2024.02.008. https://www.sciencedirect.com/science/article/pii/S0003347224000587.

58. 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. J. Anim. Ecol. *48*, 123–142. https://doi.org/10.2307/4105.

59. 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.

60. 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). Proc. Biol. Sci. *270*, 741–747. https://doi.org/10.1098/rspb.2002.2300.

61. Keen, S.C. (2020). The Role of Social Environment in Shaping Vocal Communication Systems in Wild Songbirds. PhD Thesis (Cornell University). https://doi.org/10.7298/qz29-2v92.

62. 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. Behav. Ecol. *29*, 711–723. https://doi.org/10.1093/beheco/ary029.

63. 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:NDOGTI]2.0.CO;2.

64. Payne, R.B. (1983). The Social Context of Song Mimicry: Song-matching Dialects in Indigo Buntings (Passerina Cyanea). Anim. Behav. *31*, 788–805. https://doi.org/10.1016/S0003-3472(83)80236-X.

65. Baker, M.C., Thompson, D.B., and Sherman, G.L. (1981). Neighbor/Stranger Song Discrimination in White-Crowned Sparrows. Condor *83*, 265–267. https://doi.org/10.2307/1367322.

66. Mortega, K.G., Flinks, H., and Helm, B. (2014). Behavioural Response of a Migratory Songbird to Geographic Variation in Song and Morphology. Front. Zool. *11*, 85. https://doi.org/10.1186/s12983-014-0085-6.

67. 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. Proc. Biol. Sci. *281*, 20140252. https://doi.org/10.1098/rspb.2014.0252.

68. Beecher, M.D. (2008). Function and Mechanisms of Song Learning in Song Sparrows. Advances in the Study of Behavior, 167–225. https://doi.org/10.1016/S0065-3454(08)00004-1.

69. James, L.S., and Sakata, J.T. (2017). Learning Biases Underlie “Universals” in Avian Vocal Sequencing. Curr. Biol. *27*, 3676–3682.e4. https://doi.org/10.1016/j.cub.2017.10.019.

70. Claidière, N., and Sperber, D. (2007). Commentary: The Role of Attraction in Cultural Evolution. J. Cogn. Cult. *7*, 89–111. https://doi.org/10.1163/156853707X171829.

71. Merino Recalde, N. (2023). Wytham Great Tit Song Dataset. https://doi.org/10.17605/OSF.IO/N8AC9.

72. Merino Recalde, N. (2024). nilomr/birdsong-demography: Publication-ready release. Version v1.0.0. https://doi.org/10.5281/zenodo.12800736.

73. Richards, A. (2015). University of Oxford Advanced Research Computing. Manual. https://doi.org/10.5281/zenodo.22558.

74. Merino Recalde, N. (2023). pykanto: a python library to accelerate research on wild bird song. Methods Ecol. Evol. *14*, 1994–2002. https://doi.org/10.1111/2041-210X.14155.

75. Hill, A.P., Prince, P., Snaddon, J.L., Doncaster, C.P., and Rogers, A. (2019). AudioMoth: A Low-Cost Acoustic Device for Monitoring Biodiversity and the Environment. HardwareX *6*, e00073. https://doi.org/10.1016/j.ohx.2019.e00073.

76. Nottebohm, F. (1999). The Anatomy and Timing of Vocal Learning in Birds. In The Design of Animal Communication, M.D. Hauser, and M. Konishi, eds. (The MIT Press), pp. 63–110. https://doi.org/10.7551/mitpress/2359.003.0005.

77. Thorpe, W.H. (1958). The Learning of Song Patterns by Birds, with Especial Reference to the Song of the Chaffinch Fringilla Coelebs. Ibis *100*, 535–570. https://doi.org/10.1111/j.1474-919X.1958.tb07960.x. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1474-919X.1958.tb07960.x.

78. McGregor, P.K., and Avery, M.I. (1986). The Unsung Songs of Great Tits (Parus Major): Learning Neighbours’ Songs for Discrimination. Behav. Ecol. Sociobiol. *18*, 311–316. https://doi.org/10.1007/BF00300009.

79. Lind, H., Dabelsteen, T., and McGregor, P.K. (1996). Female Great Tits Can Identify Mates by Song. Anim. Behav. *52*, 667–671. https://doi.org/10.1006/anbe.1996.0211.

80. Hinde, R.A. (1952). The Behaviour of the Great Tit (Parus Major) and Some Other Related Species. Supplement. Behaviour. III–201.

81. Perrins, C.M. (1965). Population Fluctuations and Clutch-Size in the Great Tit, Parus Major L. Journal of Animal Ecology *34*, 601–647.

82. Cresswell, W., and Mccleery, R. (2003). How Great Tits Maintain Synchronization of Their Hatch Date with Food Supply in Response to Long-Term Variability in Temperature. J. Anim. Ecol. *72*, 356–366. https://doi.org/10.1046/j.1365-2656.2003.00701.x.

83. Gibb, J. (1950). The Breeding Biology of the Great and Blue Titmice. Ibis *92*, 507–539. https://doi.org/10.1111/j.1474-919X.1950.tb01759.x.

84. Mace, R. (1987). The Dawn Chorus in the Great Tit Parus Major Is Directly Related to Female Fertility. Nature *330*, 745–746. https://doi.org/10.1038/330745a0.

85. Rivera-Gutierrez, H.F., Pinxten, R., and Eens, M. (2012). Tuning and Fading Voices in Songbirds: Age-dependent Changes in Two Acoustic Traits across the Life Span. Anim. Behav. *83*, 1279–1283. https://doi.org/10.1016/j.anbehav.2012.03.001.

86. Van Duyse, E., Pinxten, R., Snoeijs, T., and Eens, M. (2005). Simultaneous Treatment with an Aromatase Inhibitor and an Anti-Androgen Decreases the Likelihood of Dawn Song in Free-Living Male Great Tits, Parus Major. Horm. Behav. *48*, 243–251. https://doi.org/10.1016/j.yhbeh.2005.02.013.

87. Halfwerk, W., Bot, S., and Slabbekoorn, H. (2012). Male Great Tit Song Perch Selection in Response to Noise-Dependent Female Feedback. Funct. Ecol. *26*, 1339–1347. https://doi.org/10.1111/j.1365-2435.2012.02018.x.

88. Naguib, M., Diehl, J., Van Oers, K., and Snijders, L. (2019). Repeatability of Signalling Traits in the Avian Dawn Chorus. Front. Zool. *16*, 27. https://doi.org/10.1186/s12983-019-0328-7.

89. Snijders, L., van Rooij, E.P., Henskens, M.F.A., van Oers, K., and Naguib, M. (2015). Dawn Song Predicts Behaviour during Territory Conflicts in Personality-Typed Great Tits. Anim. Behav. *109*, 45–52. https://doi.org/10.1016/j.anbehav.2015.07.037.

90. Boucaud, I.C.A., Aguirre Smith, M.L.N., Valère, P.A., and Vignal, C. (2016a). Incubating Females Signal Their Needs during Intrapair Vocal Communication at the Nest: A Feeding Experiment in Great Tits. Anim. Behav. *122*, 77–86. https://doi.org/10.1016/j.anbehav.2016.09.021.

91. Boucaud, I.C.A., Valère, P.A., Aguirre Smith, M.L.N., Doligez, B., Cauchard, L., Rybak, F., and Vignal, C. (2016b). Interactive Vocal Communication at the Nest by Parent Great Tits Parus Major. Ibis *158*, 630–644. https://doi.org/10.1111/ibi.12374.

92. Quinn, J.L., Cole, E.F., Patrick, S.C., and Sheldon, B.C. (2011). Scale and State Dependence of the Relationship between Personality and Dispersal in a Great Tit Population. J. Anim. Ecol. *80*, 918–928. https://doi.org/10.1111/j.1365-2656.2011.01835.x.

93. Woodman, J.P., Cole, E.F., Firth, J.A., Perrins, C.M., and Sheldon, B.C. (2023). Disentangling the Causes of Age-Assortative Mating in Bird Populations with Contrasting Life-History Strategies. J. Anim. Ecol. *92*, 979–990. https://doi.org/10.1111/1365-2656.13851.

94. van Rossum, G. (1995). Python Reference Manual (CWI).

95. Merino Recalde, N. (2023c). nilomr/Ggeat-tit-hits-setup: V0.1.0. Zenodo. https://doi.org/10.5281/zenodo.8092397.

96. Hermans, A., Beyer, L., and Leibe, B. (2017). In Defense of the Triplet Loss for Person Re-Identification. Preprint at arXiv. https://doi.org/10.48550/arXiv.1703.07737.

97. Hoffer, E., and Ailon, N. (2018). Deep Metric Learning Using Triplet Network. Preprint at arXiv. https://doi.org/10.48550/arXiv.1412.6622.

98. Mumuni, A., and Mumuni, F. (2022). Data Augmentation: A Comprehensive Survey of Modern Approaches. Array *16*, 100258. https://doi.org/10.1016/j.array.2022.100258.

99. Perez, L., and Wang, J. (2017). The Effectiveness of Data Augmentation in Image Classification Using Deep Learning. Preprint at arXiv. https://doi.org/10.48550/arXiv.1712.04621.

100. Shorten, C., and Khoshgoftaar, T.M. (2019). A Survey on Image Data Augmentation for Deep Learning. J. Big Data *6*, 60. https://doi.org/10.1186/s40537-019-0197-0.

101. Rivera-Gutierrez, H.F., Matthysen, E., Adriaensen, F., and Slabbekoorn, H. (2010). Repertoire Sharing and Song Similarity 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.

102. Falls, J.B., Krebs, J.R., and McGregor, P.K. (1982). Song Matching in the Great Tit (Parus Major): The Effect of Similarity and Familiarity. Anim. Behav. *30*, 997–1009. https://doi.org/10.1016/S0003-3472(82)80188-7.

103. 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.

104. McGregor, P.K., Krebs, J.R., and Perrins, C.M. (1981). Song Repertoires and Lifetime Reproductive Success in the Great Tit (Parus Major). Am. Nat. *118*, 149–159. https://doi.org/10.1086/283811.

105. Baker, M.C., McGregor, P.K., and Krebs, J.R. (1987). Sexual Response of Female Great Tits to Local and Distant Songs. Ornis Scand. *18*, 186. https://doi.org/10.2307/3676765.

106. Hutfluss, A., Bermúdez-Cuamatzin, E., Mouchet, A., Briffa, M., Slabbekoorn, H., and Dingemanse, N.J. (2022). Male Song Stability Shows Cross-Year Repeatability but Does Not Affect Reproductive Success in a Wild Passerine Bird. J. Anim. Ecol. *91*, 1507–1520. https://doi.org/10.1111/1365-2656.13736.

107. Morfi, V., Lachlan, R.F., and Stowell, D. (2021). Deep Perceptual Embeddings for Unlabelled Animal Sound Events. J. Acoust. Soc. Am. *150*, 2. https://doi.org/10.1121/10.0005475.

108. Zandberg, L., Morfi, V., George, J.M., Clayton, D.F., Stowell, D., and Lachlan, R.F. (2024). Bird song comparison using deep learning trained from avian perceptual judgments. PLoS Comput. Biol. *20*, e1012329. https://doi.org/10.1371/journal.pcbi.1012329.

109. Chambers, M., and Drovandi, C. (2023). Many-Levelled Continuation Ratio Models for Frequency of Alcohol and Drug Use Data. Preprint at arXiv.

110. Warti, R., Kurnia, A., and Sadik, K. (2020). Evaluation of Proportional Odds and Continuation Ratio Models for Smoker in Indonesia. In Proceedings of the 1st International Conference on Statistics and Analytics, ICSA 2019, 2–3 August 2019, Bogor, Indonesia. https://doi.org/10.4108/eai.2-8-2019.2290483.

111. Bircher, N., van Oers, K., and Naguib, M. (2021). Anyone Listening? No Evidence for Eavesdropping on Male Singing Interactions in the Great Tit, Parus Major. Anim. Behav. *176*, 67–76. https://doi.org/10.1016/j.anbehav.2021.03.009.

112. Blumenrath, S.H., and Dabelsteen, T. (2004). Degradation of Great Tit (Parus Major) Song before and after Foliation: Implications for Vocal Communication in a Deciduous Forest. Behaviour *141*, 935–958. https://doi.org/10.1163/1568539042360152.

113. Dearmon, J., and Smith, T.E. (2016). Gaussian Process Regression and Bayesian Model Averaging: An Alternative Approach to Modeling Spatial Phenomena: Gaussian Process Regression and BMA. Geogr. Anal. *48*, 82–111. https://doi.org/10.1111/gean.12083.

114. Gelfand, A.E., and Schliep, E.M. (2016). Spatial Statistics and Gaussian Processes: A Beautiful Marriage. Spatial Statistics. Spat. Stat. *18*, 86–104. https://doi.org/10.1016/j.spasta.2016.03.006.

115. Wright, W.J., Irvine, K.M., Rodhouse, T.J., and Litt, A.R. (2021). Spatial Gaussian Processes Improve Multi-Species Occupancy Models When Range Boundaries Are Uncertain and Nonoverlapping. Ecol. Evol. *11*, 8516–8527. https://doi.org/10.1002/ece3.7629.

116. Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. J. Stat. Software *80*, 1–28. https://doi.org/10.18637/jss.v080.i01.

117. Stan Development Team (2023). Stan Modeling Language Users Guide and Reference Manual, Version 2.18.0. http://mc-stan.org/.

118. Arel-Bundock, V. (2023). marginaleffects: predictions, Comparisons, Slopes, Marginal Means, and Hypothesis Tests. https://CRAN.R-project.org/package=marginaleffects.

119. Fox, J., and Weisberg, S. (2018). Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. J. Stat. Software *87*, 1–27. https://doi.org/10.18637/jss.v087.i09.

120. Larsen, W.A., and McCleary, S.J. (1972). The Use of Partial Residual Plots in Regression Analysis. Technometrics *14*, 781–790. https://doi.org/10.1080/00401706.1972.10488966.

121. Harris, C.R., Millman, K.J., van der Walt, S.J., Gommers, R., Virtanen, P., Cournapeau, D., Wieser, E., Taylor, J., Berg, S., Smith, N.J., et al. (2020). Array Programming with NumPy. Nature *585*, 357–362. https://doi.org/10.1038/s41586-020-2649-2.

122. Virtanen, P., Gommers, R., Oliphant, T.E., Haberland, M., Reddy, T., Cournapeau, D., Burovski, E., Peterson, P., Weckesser, W., Bright, J., et al. (2020). SciPy 1.0: Fundamental Algorithms for Scientific Computing in Python. Nat. Methods *17*, 261–272. https://doi.org/10.1038/s41592-019-0686-2.

123. The pandas development team (2023). Pandas-Dev/Pandas: Pandas (Zenodo). https://doi.org/10.5281/zenodo.7549438.

124. Lam, S.K., Pitrou, A., and Seibert, S. (2015). Numba: A LLVM-based Python JIT Compiler. In Proceedings of the Second Workshop on the LLVM Compiler Infrastructure in HPC. LLVM ’15. New York, NY, USA (Association for Computing Machinery), pp. 1–6. https://doi.org/10.1145/2833157.2833162.

125. Paszke, A., Gross, S., Massa, F., Lerer, A., Bradbury, J., Chanan, G., Killeen, T., Lin, Z., Gimelshein, N., Anti, L., et al. (2019). PyTorch: An Imperative Style, High-Performance Deep Learning Library. In Adv. Neural Inf. Process. Syst., *32*, H. Wallach, H. Larochelle, A. Beygelzimer, F. dAlché-Buc, E. Fox, and R. Garnett, eds. (Curran Associates, Inc.), pp. 8024–8035.

126. TorchVision maintainers and contributors. (2016). TorchVision: PyTorch’s Computer Vision Library. GitHub.

127. Falcon, W.; The PyTorch Lightning team; PyTorch Lightning (2019). https://doi.org/10.5281/zenodo.3828935.

128. da Costa-Luis, C.O. (2019). Tqdm: A Fast, Extensible Progress Meter for Python and CLI. J. Open Source Software *4*, 1277. https://doi.org/10.21105/joss.01277.

129. Moritz, P., Nishihara, R., Wang, S., Tumanov, A., Liaw, R., Liang, E., Elibol, M., Yang, Z., Paul, W., Jordan, M.I., et al. (2018). Ray: A Distributed Framework for Emerging AI Applications. In Proceedings of the 13th USENIX Conference on Operating Systems Design and Implementation. OSDI’18. USA (USENIX Association), pp. 561–577.

130. Bechtold, B. and Geier, M. (2022). Soundfile.

131. McInnes, L., Healy, J., Saul, N., and Großberger, L. (2018). UMAP: Uniform Manifold Approximation and Projection for Dimension Reduction. J. Open Source Software *3*, 861. https://doi.org/10.21105/joss.00861.

132. Joblib Development Team. (2020). Joblib: Running Python Functions as Pipeline Jobs.

133. McInnes, L., Healy, J., and Astels, S. (2017). Hdbscan: Hierarchical Density Based Clustering. J. Open Source Software *2*, 205. https://doi.org/10.21105/joss.00205.

134. Waskom, M.L. (2021). Seaborn: Statistical Data Visualization. J. Open Source Software *6*, 3021. https://doi.org/10.21105/joss.03021.

135. van der Walt, S., Schönberger, J.L., Nunez-Iglesias, J., Boulogne, F., Warner, J.D., Yager, N., Gouillart, E., and Yu, T.; scikit-image contributors (2014). scikit-image: image processing in Python. PeerJ *2*, e453. https://doi.org/10.7717/peerj.453.
136. McFee, B., Raffel, C., Liang, D., Ellis, D., McVicar, M., Battenberg, E., and Nieto, O. (2015). Librosa: Audio and Music Signal Analysis in Python. In Proceedings of the Python in Science Conference, pp. 18–24. https://doi.org/10.25080/Majora-7b98e3ed-003.
137. Bokeh Development Team (2018). Bokeh: Python Library for Interactive Visualization. Manual.
138. van Kemenade, H., et al. (2023). Ultrajson (Zenodo). https://doi.org/10.5281/zenodo.7510698.
139. Rodola, G. (2023). Psutil. https://psutil.readthedocs.io/en/latest/.
140. Schlawack, H. (2019). Attrs. https://www.attrs.org/en/stable/.
141. R Core Team (2022). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing). https://www.R-project.org/.
142. Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., and Gelman, A. (2019). Visualization in Bayesian workflow. J. R. Stat. Soc. A *182*, 389–402. https://doi.org/10.1111/rssa.12378.
143. Gabry, J., and Mahr, T. (2022). bayesplot: Plotting for Bayesian Models. https://mc-stan.org/bayesplot/.
144. Rudolph, K. (2023). box: Write Reusable, Composable and Modular R Code. https://CRAN.R-project.org/package=box.
145. Bürkner, P.-C. (2021). Bayesian Item Response Modeling in R with brms and Stan. J. Stat. Software *100*, 1–54. https://doi.org/10.18637/jss.v100.i05.
146. Chavent, M., Kuentz, V., Labenne, A., and Saracco, J. (2021). ClustGeo: Hierarchical Clustering with Spatial Constraints. https://CRAN.R-project.org/package=ClustGeo.
147. Zeileis, A., Fisher, J.C., Hornik, K., Ihaka, R., McWhite, C.D., Murrell, P., Stauffer, R., and Wilke, C.O. (2020). colorspace: A Toolbox for Manipulating and Assessing Colors and Palettes. J. Stat. Software *96*, 1–49. https://doi.org/10.18637/jss.v096.i01.
148. Allaire, J. (2020). config: Manage Environment Specific Configuration Values. https://CRAN.R-project.org/package=config.
149. Wickham, H., Hester, J., Chang, W., and Bryan, J. (2022). devtools: Tools to Make Developing R Packages Easier. https://CRAN.R-project.org/package=devtools.
150. Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. https://CRAN.R-project.org/package=DHARMa.
151. Hester, J., Wickham, H., and Csárdi, G. (2023). fs: Cross-Platform File System Operations Based on ‘libuv’. https://CRAN.R-project.org/package=fs.
152. Kay, M. (2023). ggdist: Visualizations of Distributions and Uncertainty. https://doi.org/10.5281/zenodo.3879620. https://mjskay.github.io/ggdist/.
153. Pedersen, T.L. (2022a). ggraph: An Implementation of Grammar of Graphics for Graphs and Networks. https://CRAN.R-project.org/package=ggraph.
154. Rupprecht, F. (2023). httpgd: A ‘HTTP’ Server Graphics Device. https://CRAN.R-project.org/package=httpgd.
155. Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. InterJournal Complex Systems, 1695. https://igraph.org.
156. Csárdi, G., Nepusz, T., Traag, V., Horvát, S., Zanini, F., Noom, D., and Müller, K. (2024). igraph: Network Analysis and Visualization in R. https://doi.org/10.5281/zenodo.7682609. https://CRAN.R-project.org/package=igraph.
157. Lüdecke, D., Waggoner, P., and Makowski, D. (2019). insight: A Unified Interface to Access Information from Model Objects in R. JOSS *4*, 1412. https://doi.org/10.21105/joss.01412.
158. Zhu, H. (2021). kableExtra: Construct Complex Table with ‘kable’ and Pipe Syntax. https://CRAN.R-project.org/package=kableExtra.
159. Lai, R. (2023). languageserver: Language Server Protocol. https://CRAN.R-project.org/package=languageserver.
160. Arel-Bundock, V. (2022). modelsummary: data and Model Summaries in R. Journal of Statistical. Software *103*, 1–23. https://doi.org/10.18637/jss.
161. Pedersen, T.L. (2022b). patchwork: the Composer of Plots. https://CRAN.R-project.org/package=patchwork.
162. Csárdi, G., and FitzJohn, R. (2019). progress: Terminal Progress Bars. https://CRAN.R-project.org/package=progress.
163. Ushey, K., and Wickham, H. (2023). renv: Project Environments. https://CRAN.R-project.org/package=renv.
164. Müller, K. (2022). rprojroot: Finding Files in Project Subdirectories. https://CRAN.R-project.org/package=rprojroot.
165. Wickham, H., and Seidel, D. (2022). scales: Scale Functions for Visualization. https://CRAN.R-project.org/package=scales.
166. Pedersen, T.L., and Crameri, F. (2023). scico: Colour Palettes Based on the Scientific Colour-Maps. https://CRAN.R-project.org/package=scico.
167. Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. R J. *10*, 439–446. https://doi.org/10.32614/RJ-2018-009.
168. Pebesma, E., and Bivand, R. (2023). Spatial Data Science: With applications in R (Chapman and Hall/CRC). https://r-spatial.org/book/.
169. Wickham, H., Henry, L., Pedersen, T.L., Luciani, T.J., Decorde, M., and Lise, V. (2023). svglite: An ‘SVG’ Graphics Device. https://CRAN.R-project.org/package=svglite.
170. Hijmans, R.J. (2023). terra: Spatial Data Analysis. https://CRAN.R-project.org/package=terra.
171. Pedersen, T.L. (2023). tidygraph: A Tidy API for Graph Manipulation. https://CRAN.R-project.org/package=tidygraph.
172. Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., et al. (2019). Welcome to the tidyverse. J. Open Source Software *4*, 1686. https://doi.org/10.21105/joss.01686.
173. Garnier (2023). viridis(Lite) - Colorblind-Friendly Color Maps for R.. https://doi.org/10.5281/zenodo.4679424 https://sjmgarnier.github.io/viridis/.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Wytham great tit song dataset	Merino Recalde[71]	https://osf.io/n8ac9; osf.io/n8ac9
Experimental models: Organisms/strains		
Great tit (Parus major)	Wild population at Wytham Woods, Oxford, UK	N/A
Software and Algorithms		
Analysis code and data	Merino Recalde[72]	https://github.com/nilomr/birdsong-demography; github.com/nilomr/birdsong-demography
pykanto	Merino Recalde[74]	https://github.com/nilomr/pykanto; github.com/nilomr/pykanto
Other		
AudioMoth recorders	Hill[75]	https://www.openacousticdevices.info; openacousticdevices.info

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Great tits are small, short-lived birds—average lifespan: 1.9 years—that sing acoustically simple yet highly diverse songs. Each male great tit has a repertoire of one to over 10 song types, also referred to as syllable types, which are repeated multiple times in short bursts separated by longer periods of silence. Although detailed studies on how individual great tits learn their songs are limited, existing evidence suggests several key points. First, it appears that great tits do not learn their song repertoires from their fathers.[55] Instead, their song development is influenced by the songs they encounter during their early life until they establish a territory and breed for the first time. We do not currently know how precisely great tits learn songs, or how social interactions affect the process. At 10-11 months of age, before their first breeding season begins, vocal learning culminates in a final crystallised song repertoire that remains relatively stable afterward[56]—a process known as critical period learning.[76,77] Additionally, while there is evidence that birds can continue to learn to recognize new songs later in life (that is, learning for discrimination, as opposed to learning for production), this ability seems to be limited compared to their early learning experiences.[78] Females are able to individually recognize males based on their songs[79] and, even across a large population, individual song renditions can accurately indicate the identity of the bird producing them.[57,74]

During the breeding season, from March to June, great tit pairs are socially monogamous and defend territories around their nests.[80] In Wytham Woods, Oxfordshire, UK (51°46 N, 1°20 W), a population of these birds has been the focus of a long-term study since 1947.[45] 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. The birds were not provided with supplementary sources of food during the study.

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).

METHOD DETAILS

Data collection

Breeding data monitoring

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,[81] 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 the number of eggs present on the day of observation. In cases where we did not observe the chicks on their day of hatching, the hatching date was determined by assessing the weight of the heaviest chicks and extrapolating their age from established growth curves.[82,83]

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 as described in the sections below. In the years of our study, 261, 289, and 278 nest boxes were occupied by pairs of great tits, with 173, 184, and 184 that led to successful breeding attempts where at least one chick fledged. See Figure S1 for a map of the study site and sampling locations.

Song recording protocol

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.[84] Collectively, this vocal display is referred to as the dawn chorus, and it has been demonstrated to yield a reliable estimation of the song repertoire of individuals when recorded in full.[85,86] 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.

We used 60 (30 in 2020) AudioMoth automated recorders,[75] 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. The microphone faced upwards and slightly away from the nest box, aligning with the nest box entrance hole's direction. The birds sang near the recorder: although we did not gather data on the singer's location, our anecdotal observations were in line with a different population where the average distance to the nest box while singing was 10 metres.[87] 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.

This approach is supported by previous studies on great tit dawn song,[61,88–91] as well as our observations that: (a) recordings from consecutive days contain renditions of the same song types clearly sung by a single individual cycling through its repertoire, (b) performances of the same song types across different days can be assigned to a single individual by our deep metric learning model (see deep metric learning model training), and (c) when we recapture the same bird in a different field season (often in the same location due to high adult site fidelity), we can easily match its songs to the ones on record, which would not happen if we were misattributing songs to individuals.

To further ensure that we were recording the correct birds, we discarded recordings with more than one vocalizing bird unless one was distinctly louder than the others during the segmentation process. Additionally, we excluded all songs with a maximum amplitude below -16 dB, calculated as $20\log_{10}\left(\frac{A}{A_0}\right)$, with $A = 5000$ and $A_0 = 32767$ (the maximum value for 16-bit digital audio). This threshold was established based on observations showing that an amplitude cutoff greater than 4000 unambiguously differentiated the focal bird from its closest neighbours when simultaneous recordings from nearby spatial locations captured multiple birds. It is important to note that these values are not calibrated and are relative to our recording equipment and settings, as well as other factors like sound directionality and vegetation cover. Although variation in sound amplitude due to distance and direction of the singer could affect which songs were recorded clearly enough to analyse, we did not observe any systematic bias that might have resulted in low signal-to-noise ratios causing exclusion of song types.

Sampling density and representativeness

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

Dispersal distance and age determination

For this study, we calculated postnatal dispersal distance as the straight-line distance from the natal site to the breeding site. The dispersal distances of birds classed as immigrants (not ringed as chicks in the population) are not known, but most are thought to come from other populations at least 1 km, and likely more than 2.5 km, away.[63,92] We determined age based on the year of hatching for birds hatched in the population and using plumage characteristics for immigrants, which are most often caught as yearlings (76%)—allowing us to age them accurately.[93]

QUANTIFICATION AND STATISTICAL ANALYSIS

Data processing and annotation

We processed and annotated the song recordings, 109,963 in total, from 299 repertoires belonging to 242 known birds, using custom software and scripts written in Python 3[94] and the open source package pykanto.[74] These are available from github.com/nilomr/great-tit-hits-setup.[95] Our annotated data set and a detailed description of the process can be found in Merino Recalde et al.[57] Below we provide a narrative summary of the subsequent characterisation of song similarity and song types.

Characterizing repertoire similarity

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

Continuous similarity (individual-level analyses)

Traditional methods used to compare bird vocalisations include visual inspection of spectrograms and measurement of hand-picked acoustic features. However, these approaches have limitations in dealing with noise and variations in performance, and can be extremely time-consuming. So, instead, we adopted a data-driven approach by training a Vision Transformer (ViT) model for feature extraction in a metric learning task on spectrogram representations of great tit songs. Our goal was to create a similarity space based on inherent variation in the data, using categorical labels of song types sung by individual birds, which we know to be perceptually and behaviourally significant.[79] Further details, data, and code to reproduce this process are available at[74] and[57]; we include a summary here.

We optimized model performance using Triplet loss, a loss function that ensures the projection of a positive sample (belonging to the same class as the anchor point) is closer to the anchor's projection than that of a negative sample (belonging to a different class) by a specified margin.[96,97] During training, we mined hard triplets—where the negative sample is closer to the anchor than the positive—and used the Adam optimizer with a fixed learning rate of 1×10^{-5}.

To prevent the model from overfitting to irrelevant features within localized portions of the training data or learning background noise, we applied various data augmentation techniques during model training.[98–100] These included random cropping in the time domain, dropping out parts of the spectrogram, adding Gaussian and multiplicative noise, equalization, sharpening, changes to brightness and contrast, blurring, and slight shifting in both time and frequency domains. This leads to a more robust model that can generalize better and is not influenced by differences in background noise.

Finally, we used the resulting model to calculate feature vectors for each song in the data set (109,963 samples x 384 dimensions), which serve as compressed representations that can be used to compare them. Great tits have variable repertoire sizes and there is no evidence that they learn them en bloc.[55,101] Therefore, the simplest continuous measure (an average Euclidean distance between all pairs of songs) would mask any signatures of learning if the average repertoire similarity is similar across the population, and does not take into account the asymmetry in total repertoire size. To improve on this, we defined repertoire similarity as the average minimum Euclidean distance (AMED), given by

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

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

Automated clustering (first step for neighbourhood analyses)

If song learning is categorical and not very precise in terms of fine song structure, the continuous similarity method could underestimate or fail to detect similarities between repertoires. In addition, our neighbourhood-level analyses require that we define discrete cultural units (population-wide song types). To do this, we first calculated the distances between all songs in the data set using the feature vectors obtained from the ViT model, as described above. Then we used UPGMA hierarchical clustering and dynamic tree-cut techniques to assign the syllables to distinct types (since songs consist of repeated syllables, syllable and song types are synonymous in this species). We allowed a minimum cluster size of 1 to ensure the representation of rare song types. The usefulness of this method depends on the global properties of the embedding space derived from the continuous similarity process. In a low-dimensional space where linear distances effectively capture meaningful variation, creating clusters by cutting the hierarchical tree at different heights yields varying cluster counts while maintaining meaningful groupings. However, in a high-dimensional space where global distances are not meaningful, only relatively small clusters of nearby points remain interpretable. This is the case with our data set and embedding space: we find that the method reliably groups song renditions by the same bird across different years, alone or together with other birds with highly similar songs, yet consistently splits songs that are similar by human (and perhaps great tit[102]) standards, ultimately leading to a very large number of clusters (the most stable clustering solutions were close to the total number of different individual song types, >1000). Due to these issues, we did not directly use song types defined by automated hierarchical clustering, but performed an additional manual categorization step.

Manual categorization (second step for neighborhood analyses)

With over 100,000 songs, our data set is very large and would have been impossible to label entirely manually as is common in the field. Instead, we used the output of the automated clustering process described above, consisting of 1920 labelled song clusters assigned to 422 larger clusters of highly similar songs (making the problem 57 times smaller), which we reviewed manually using the criteria followed by McGregor and Krebs[55,103,104] and subsequent work.[41,102,105,106] This process is both inevitable and partly subjective. However, despite its clear problems, human perceptual judgments might be our best available substitute for those of the birds for some tasks (but see recent work by Morfi et al.[107] and Zandberg et al.[108]). Indeed, across fields, advanced classification algorithms are routinely evaluated against ground truth created by humans, and this is also the case in bird song research.

Following common practice in the field, we statistically validated our resulting 335 manually assigned labels to evaluate whether they represented quantitatively robust clusters. To do this, we retrained the ResNet[50]-based classifier described in Merino Recalde[74] on a random subset of labelled song spectrograms data and obtained an accuracy of 0.87 on the validation set (see other metrics in the repository). For comparison, an equivalent process by Fayet et al.[41] was able to reach 0.71 accuracy for 374 songs. We further explored the result by creating a hierarchical clustering diagram (dendrogram) based on how often the model mistakenly classified one song type as another during evaluation. We then reviewed the song classes that weren't clearly distinguished by the model. Following Fayet et al.,[41] this led us to combine seven poorly differentiated classes into two more distinct categories. With the caveats already mentioned, this means that our classification following McGregor and Krebs[55] is successful at finding song type clusters that reduce intraclass variation.

Most of the great tits in our population sing some variation of the well-known 'tea-cher, tea-cher' song, These are harder to assign to discrete classes than rarer songs with more complex structures, a problem that is not restricted to our data set: regions of the acoustic space with more data are harder to cluster because they often contain more variation and overlap, making it difficult for algorithms (or humans) to find clear boundaries. As mentioned in the main body of the article, the consequence of this for any analysis is that the absolute estimates of cultural turnover depend on the granularity of this clustering process. Were we to lump most 'tea-cher' songs together, as McGregor and Krebs[55] do, the estimates of turnover would become lower—but, crucially, any relative differences across time or space remain the same. Indeed, precisely quantifying turnover using categorical metrics might be altogether impossible in some species, because song categories are not likely to be natural kinds beyond the scale of interacting neighbours.

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

Re-identifying individuals from their songs

In some cases, we failed to capture birds or identify them using PIT (Passive Integrated Transponder) tags, as tags sometimes malfunction, birds can be difficult to catch, or may have disappeared before their chicks were old enough for us to attempt capture at the next box. We were able to match an additional 31 song repertoires belonging to this subset of birds with existing individual IDs by using the deep metric learning model (ViT) described earlier to recognize individual songs. This increased the number of identified repertoires from 299 to 330, belonging to the same 242 unique birds. We summarise the process here, but see also Merino Recalde et al.[57] for details on model design and training.

Briefly, we calculated pairwise song distances using the feature vectors obtained from a vision transformer on a metric learning task. This model achieved a mean average precision at 5 (mAP5) of 0.98 and a cumulative matching characteristic at 1 (CMC1) of 0.98, which roughly means that in 98% of the queries made to the similarity space (on a held-out test data set of known songs) the candidate bird and song type returned by the model were correct. Given that the model was trained on almost 2000 classes, this means that there is enough individual information contained in each song type to distinguish between birds with very high confidence: even though many have likely copied tutor songs that were also in the data set, this model could still tell them apart.

We used the calculated song distances to determine if two song repertoires came from the same bird, even when the bird wasn't physically identified more than once. We set very conservative criteria for this: at least two songs in the repertoires had to be more similar than the 0.025 quantile of the distance distribution for songs from known different birds, or (distance score of 0.9), and the bird must be within 100 meters of the reference bird. When we applied the metric learning model to songs from the entire population, which increases the risk of false positives, we found that the percentage of wrongly assigned birds in our ground truth data (birds that we have physically re-identified across years) was 0.3%, or 34 out of 11,359 unique comparisons if we only used the acoustic distance criterion—further reduced to 0.04%, or 4 out of 11359, when we also added the spatial constraint (see Figures S7A and S7B for a graphic explanation).

Modelling pairwise similarity and individual repertoires

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

Individual repertoires

We first modelled individual repertoire size using Poisson and negative binomial models, but this led to poor performance as assessed through posterior predictive checks (both underestimation of mean values and either under or over-estimation of very low repertoire sizes). Instead, we built continuation ratio models, a type of sequential ordinal model where reaching a particular level (number of song types in the repertoire) requires first reaching all lower levels.[109,110] rep_{m_1}, $rep_{m_{1.1}}$, and $rep_{m_{1.2}}$ estimate the association between immigrant status, distance dispersed, age, and repertoire size. Three further log-normal models, $repnov_{m_1}$, $repnov_{m_{1.1}}$, $repnov_{m_{1.2}}$, do the same for the average cultural uniqueness of individual repertoires, defined as one minus the mean of the relative frequencies of each song type present in the repertoire.

Pairwise similarity

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

Modelling group-level outcomes

Defining neighbourhoods and their demographic properties

Song turnover, diversity, and uniqueness are group-level properties. However, our study lacks naturally occurring distinct subpopulations that we can use as units for analysis. Rather than partitioning the population using a discrete polygonal grid or non-overlapping areas, we opted to model neighbourhoods continuously across space, defining a radius of 200 m around each of 549 nest boxes that were occupied at least once during the study,[41] which we then sampled across the duration of the study. This radius is necessarily arbitrary but strikes a good compromise between capturing the relevant spatial scale at which vocal interactions occur, which extends up to around 180 metres,[111,112] and maintaining an adequate sample size in areas of low density (neighbourhood sizes range from 7 to 60, mean 30.3 ± 14.9). Importantly, neighbourhoods defined in this way are highly non-independent, so we modelled both this methodological spatial dependence and other sources of complex spatial autocorrelation intrinsic to the study site (such as edges, nest box density, etc.) by including a 2D Gaussian process (GP), which estimates a length-scale parameter defining a variance-covariance matrix for the spatial locations based on their distance.[113–115] We confirmed that this eliminated the residual spatial autocorrelation via Moran's I tests. Note that we fitted a separate GP for each year, as treating the spatial dependence as fixed across the study duration, as is often done, risks further underestimating uncertainty.

We defined our predictor variables in the following way:

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

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

Operational definitions of cultural diversity, uniqueness, and turnover

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

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

In this way, 'diversity' describes the relative proportion of distinct songs in a neighbourhood, and 'uniqueness' refers to how uncommon, on average, the songs of the birds in a neighbourhood are. These two ways of characterizing 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 density and therefore songs—to yield lower average estimates of diversity and higher average estimates of uniqueness, in a nonlinear manner. Once this is adjusted for, which we did by including a GAM term capturing the nonlinear effect of the sample size, diversity and uniqueness are positively correlated, as expected (see Figure S5; models nov_{m_2} and $nov_{m_{2.1}}$; spatial distribution of these variables in Figure S6). All the relevant models adjusted for these effects of neighbourhood density and sampling.

Models

To study the effect of dispersal and immigration on local cultural diversity and uniqueness, we built log-normal models (div_{m_1}, nov_{m_1}) and estimated the marginal effects of the proportion of immigrants, mean dispersal 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 uniqueness, we fit two further models predicting the absolute number of distinct song types in a neighbourhood while also adjusting for the number of birds (div_{m_2}) and the number of songs ($div_{m_{2.1}}$).

The rate of song cultural turnover 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.

Following the suggestion of one anonymous reviewer, we built a spatially explicit simulation of song learning with dispersal. The simulation models the relationship between pre-breeding bird movement and repertoire uniqueness, showing that the effects of dispersal that we estimate using regression models could arise under positively frequency-dependent learning or a similar acquisition process (see Figure S8 for details).

Model estimates and reporting

We built the models and approximated the posterior distributions of the parameters of interest using brms,[116] an interface to the Hamiltonian Monte Carlo engine Stan.[117] We then processed the posterior distributions with the help of the marginaleffects package.[118] 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 (see Table S3). Note that categorical predictors are dummy-coded and continuous predictors z-score transformed. Estimates in the text and tables are calculated as the posterior probability under a hypothesis (e.g., that a parameter estimate is greater than 0) against its alternative. Our figures include plots containing the posterior distributions of the marginal effect at the mean of each variable of interest. 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.[119,120] We have tried to build reasonable models, but even then our estimates should not be interpreted causally. Figure S9 shows posterior predictive checks for all models in the study. 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.

Software

Song processing and analyses were carried out using pykanto[74] and rely on the following open-source scientific libraries or tools: numpy,[121] scipy,[122] pandas,[123] numba,[124] pytorch,[125] torchvision,[126] pytorch lightning,[127] tqdm,[128] ray,[129] soundfile,[130] umap,[131] joblib,[132] hdbscan,[133] seaborn,[134] scikit-image,[135] librosa,[136] bokeh,[137] ujson,[138] psutil,[139] attrs.[140] We also used R version 4.2.1[141] and the following R packages: bayesplot,[142,143] box,[144] brms,[116,145] ClustGeo,[146] colorspace,[147] config,[148] devtools,[149] Dharma,[150] fs,[151] ggdist,[152] ggraph,[153] httpgd,[154] igraph,[155,156] insight,[157] kableExtra,[158] languageserver,[159] marginaleffects,[118] modelsummary,[160] patchwork,[161] progress,[162] renv,[163] rprojroot,[164] scales,[165] scico,[166] sf,[167,168] svglite,[169] terra,[170] tidygraph,[171] tidyverse,[172] viridis.[173] See the code repositories for specific versions of these libraries.

Current Biology, Volume *35*

Supplemental Information

The demographic drivers of cultural evolution in bird song

Nilo Merino Recalde, Andrea Estandía, Sara C. Keen, Ella F. Cole, and Ben C. Sheldon

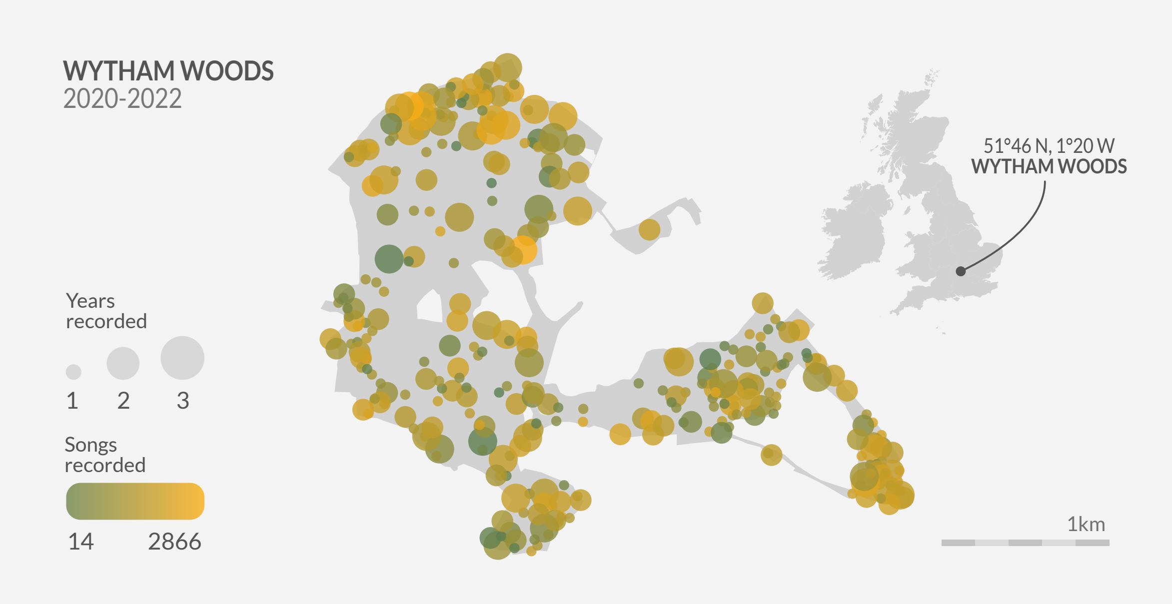


Figure S1. Map of the study site and sampling locations. Related to STAR Methods.
This study was conducted in Wytham Woods, a 385-hectare semi-natural woodland surrounded by farmland. Data was collected during the breeding seasons of 2020, 2021, and 2022 by regularly checking 1018 nest boxes, documenting information such as breeding pair identities, clutch initiation and hatching dates, clutch size, and fledgling details according to standardized protocols, and recording the songs of the birds in the population using 60 AudioMoth acoustic logger. Each dot on the map shows the locations of a nest box where we recorded song repertoires.

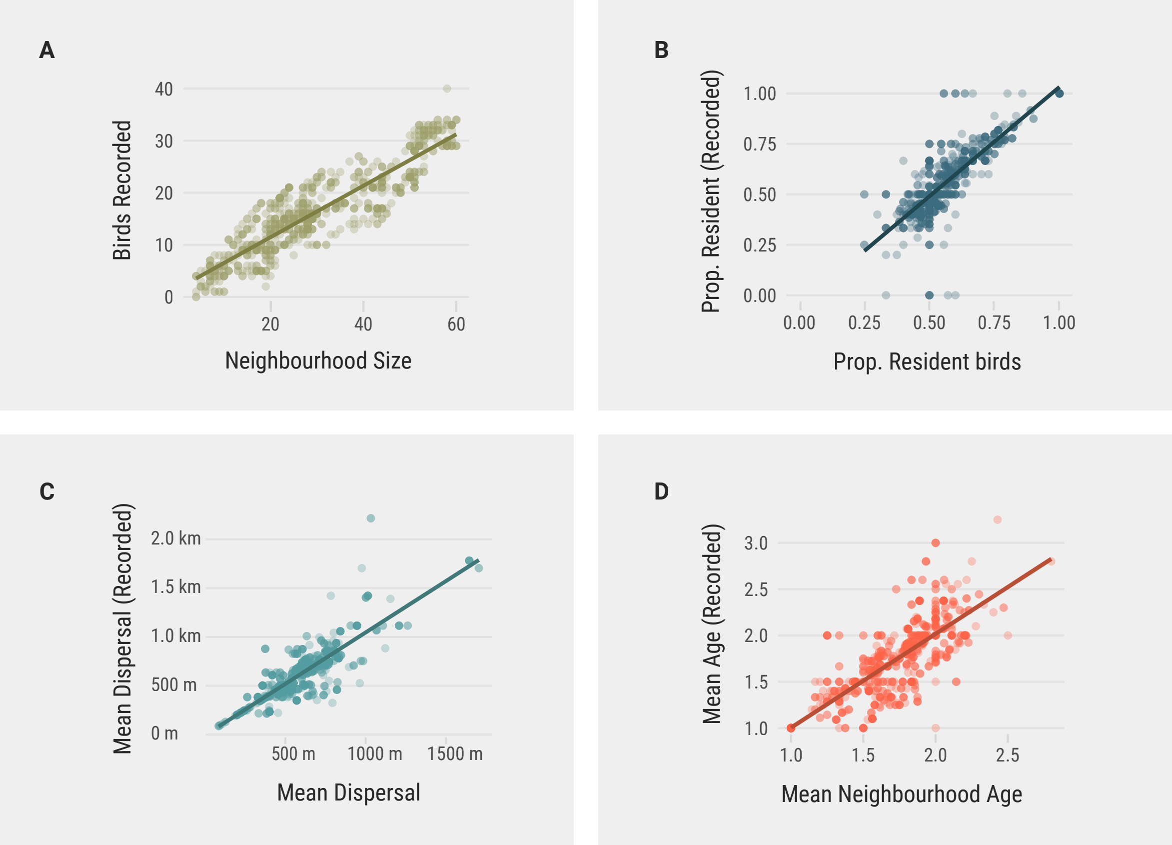


Figure S2. Demographic characteristics of recorded birds compared to those of all birds in the neighbourhood. Related to STAR Methods.
Comparison between the actual neighbourhood properties and neighbourhood properties estimated from birds for which we have song recordings. (A) Neighbourhood size (number 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.

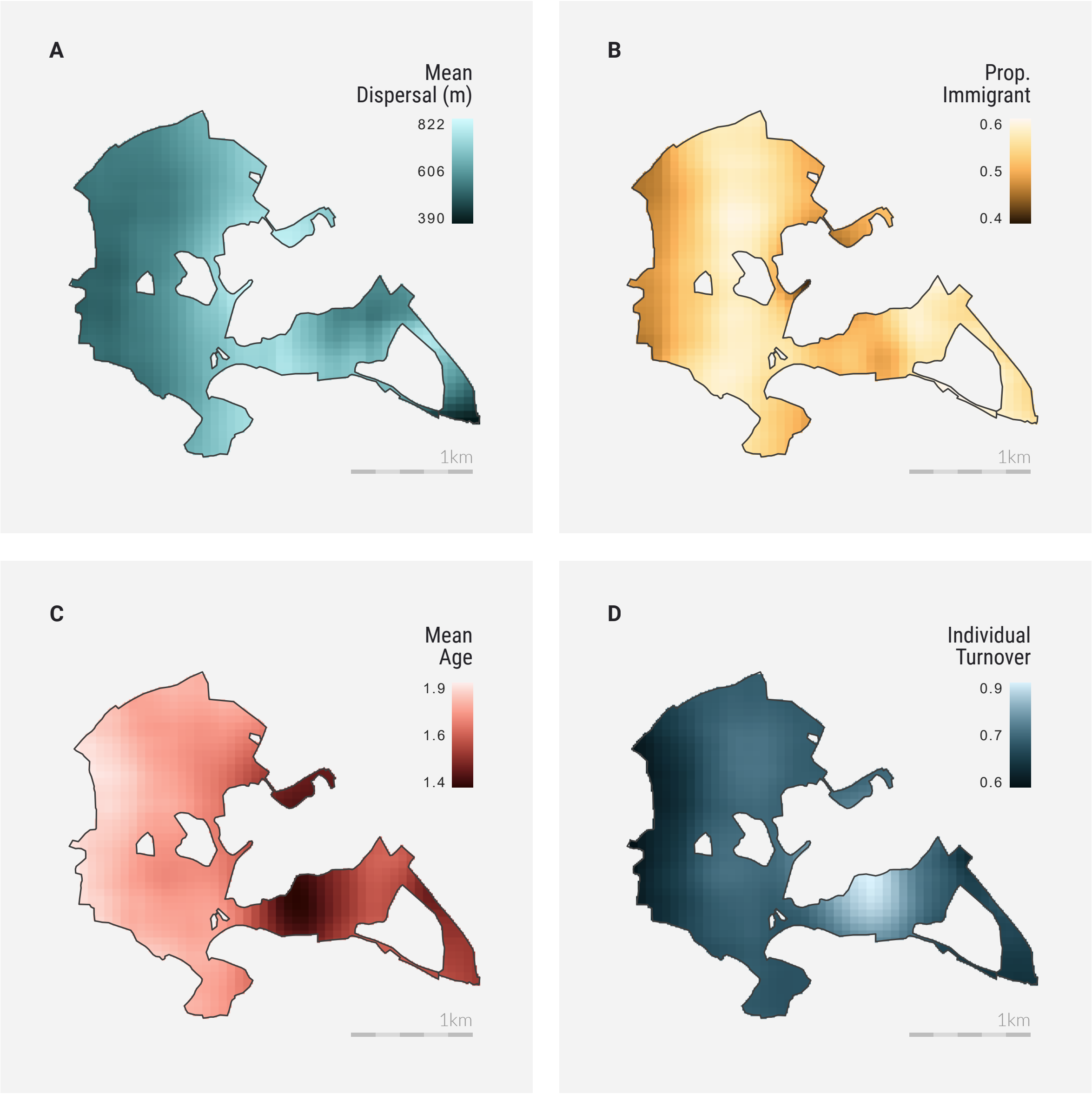


Figure S3. Spatial distribution of the neighbourhood-level predictor variables in the study. Related to STAR Methods.
(A) Mean natal dispersal distance, or the mean distance between the natal nest box and the breeding site for all birds in the neighbourhood. (B) Proportion of immigrant birds in the neighbourhood. (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.

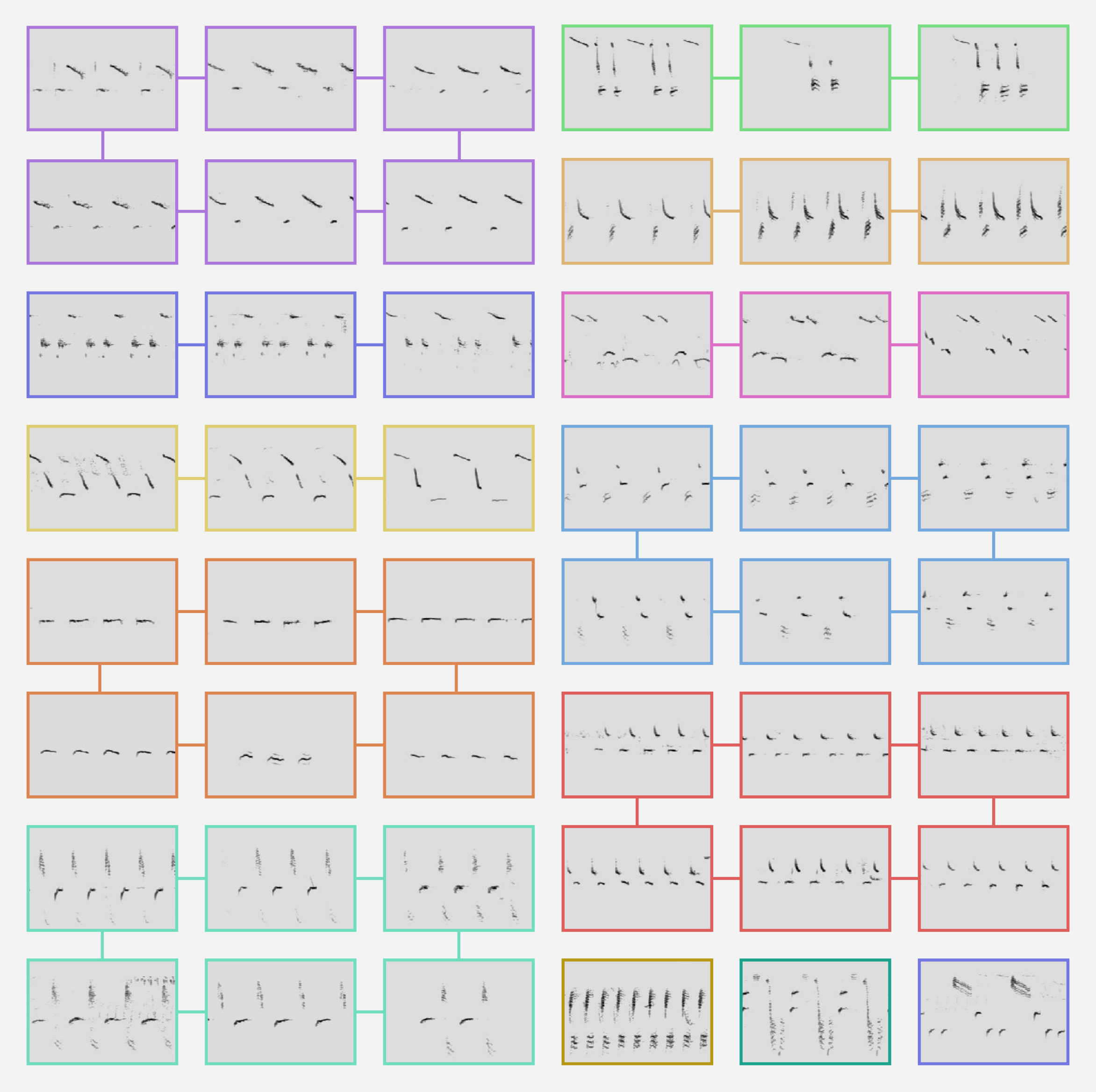


Figure S4. Examples of song type clusters in the study population. Related to STAR Methods.
Colours and connected lines represent the same song type cluster sung by different birds. Some song types are sung by many birds, while others are unique to a single bird. The clustering process is based on song similarity derived from a deep metric learning model and a manual categorization process following McGregor and Krebs, as described in the STAR methods.

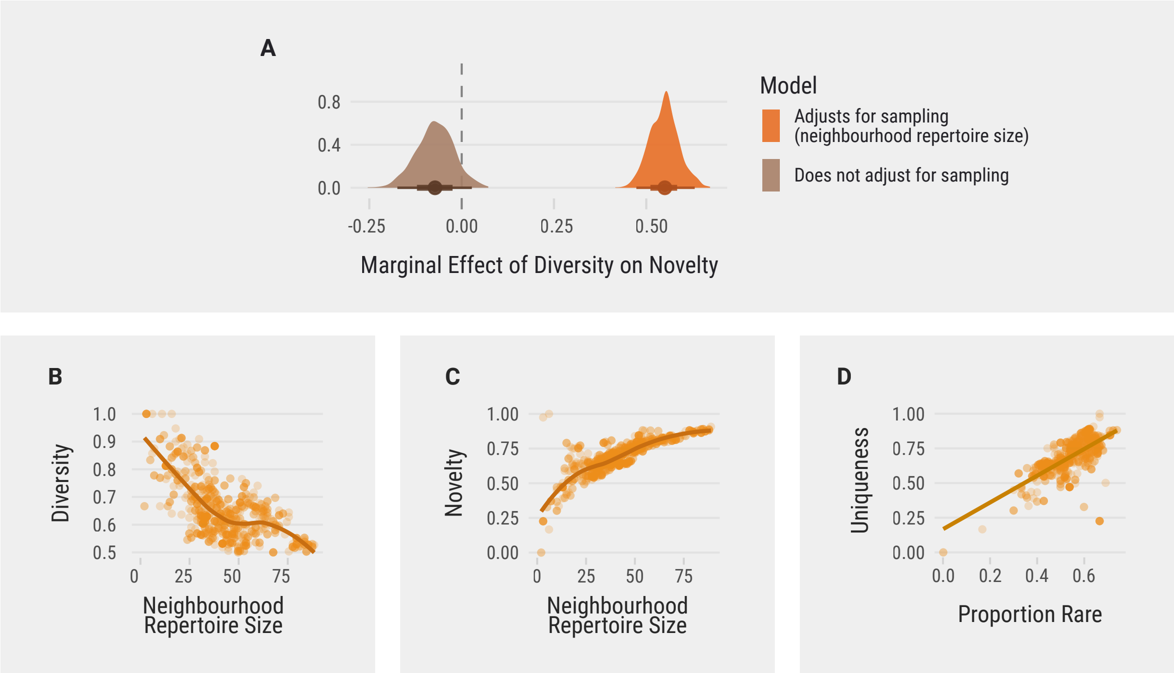


Figure S5. Estimates of cultural outcomes depend on the size of the neighbourhood repertoire. Related to STAR Methods and Figure 2.
(A) Marginal effect of diversity—which describes the proportion of distinct songs in a neighbourhood—on uniqueness, that is, how rare, on average, the songs of the birds in a neighbourhood are in the popualtion. These two ways of characterizing cultural diversity are anti-correlated in our study site due to the effect of sampling: more frequent songs are sampled more readily, causing larger sample sizes (neighbourhoods with more birds and therefore songs) to yield lower average estimates of diversity (B) and higher average estimates of uniqueness (C), in a nonlinear manner. Once this is adjusted for, which we do by including GAM terms capturing neighbourhood song density or number of birds, diversity and uniqueness are positively correlated, as expected. (D) Our measure of cultural uniqueness (y-axis) has the advantages of being continuous and not using an arbitrary cut-off, but is nonetheless correlated with definitions traditionally used in the literature, such as 'songs shared by fewer than 4 birds, here on the x-axis.

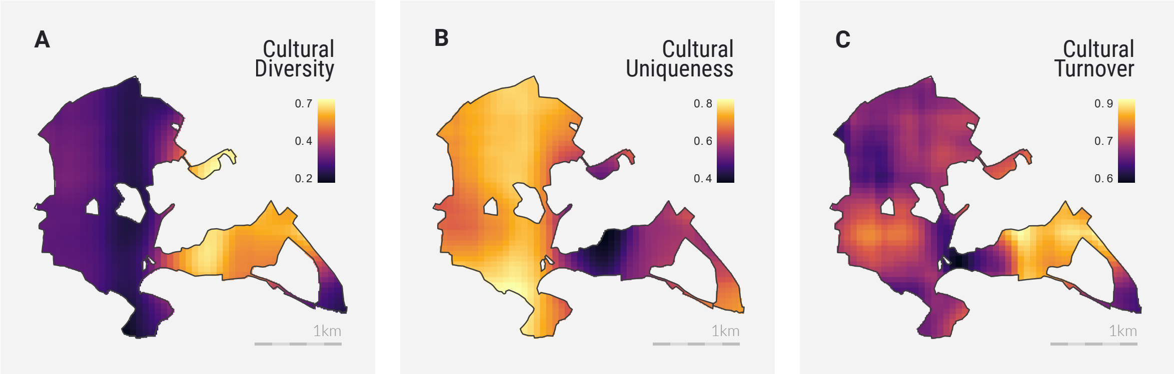


Figure S6. Spatial distribution of the neighbourhood-level cultural variables in the study. Related to STAR Methods.
(A) Relative cultural diversity ('diversity'): the ratio of distinct song types recorded in a neighbourhood to the total number of songs recorded in that neighbourhood. Higher values indicate that there are more distinct song types in the neighbourhood relative to its total song output. (B) Uniqueness index: the complement of the logarithm of the mean population-wide frequency of the song types present in a neighbourhood. Higher values indicate that the songs in the neighbourhood are on average less common in the population. (C) Cultural turnover: the proportion of distinct song types recorded in a neighbourhood that were not present in the previous year. Higher values indicate that the neighbourhood's song repertoire has changed more from one year to the next. As described in Figure S5, (A) and (B) are anti-correlated due to the effect of sampling, but once this is adjusted for, neighbourhoods with more cultural diversity also tend to have more distinct songs, as expected.

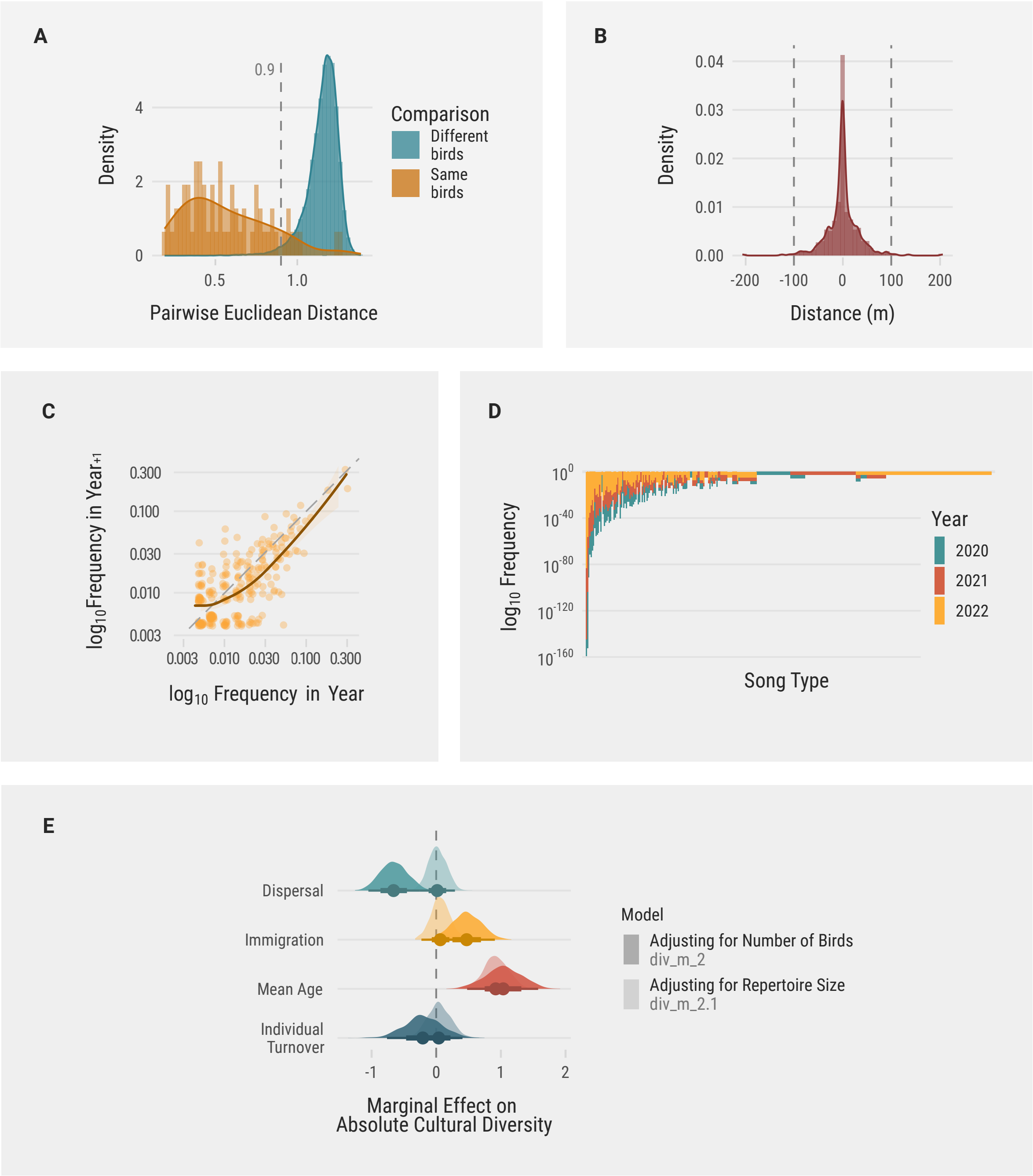


Figure S7. Overview of thresholds, song frequencies, and cultural diversity. Related to STAR Methods and Figure 2.
(A and B) Thresholds for re-identifying individual birds based on their songs. We used conservative criteria to infer when two repertoires belong to the same bird. Acoustic similarity: A minimum of two matching songs must be more similar than the 0.025 quantile of the distance distribution (an acoustic distance of 0.9). Spatial proximity: The bird must be no more than 100 meters apart from the reference bird. Accuracy of the method: Using only acoustic distance: 0.3% error rate (34 out of 11,359 unique comparisons). Using acoustic distance and spatial constraint: 0.04% error rate (4 out of 11,359 comparisons). These error rates were calculated using only ground truth data from physically re-identified birds across years.
(A) Distribution of acoustic distances. Orange: Same song type sung by the same known bird in different years. Blue: Minimum pairwise distance between different birds and years. Vertical dashed line: x-intercept at 0.9, representing the acoustic distance threshold.
(B) Distribution of distance changes between breeding sites for birds that bred more than once. Demonstrates high nest site fidelity in adult birds, which we use as an additional constraint for re-identification. Vertical dashed lines: 100 m threshold.

(C and D) Song frequencies and their relationship with abundance in the following year.
(C) The abundance of a song type in a year predicts its abundance in the following year, with higher stochasticity around rare songs.
(D) Histogram showing the frequency of individual song types in the study.

(E) Effect of demographic variation on absolute cultural diversity within neighbourhoods. To explore how the number of individuals and their repertoire sizes within a neighbourhood affect the total number of distinct song types recorded within a neighbourhood (as opposed to the relative diversity reported in Figure 2), we fit two models: one adjusting for the nonlinear effect of the number of individuals (higher opacity fill, corresponding to model *div_m_2*), and a second adjusting for the nonlinear effect of the number of song types, including repeated variants (lower opacity fill, *div_m_2.1*). See Table S1 for full model specifications.

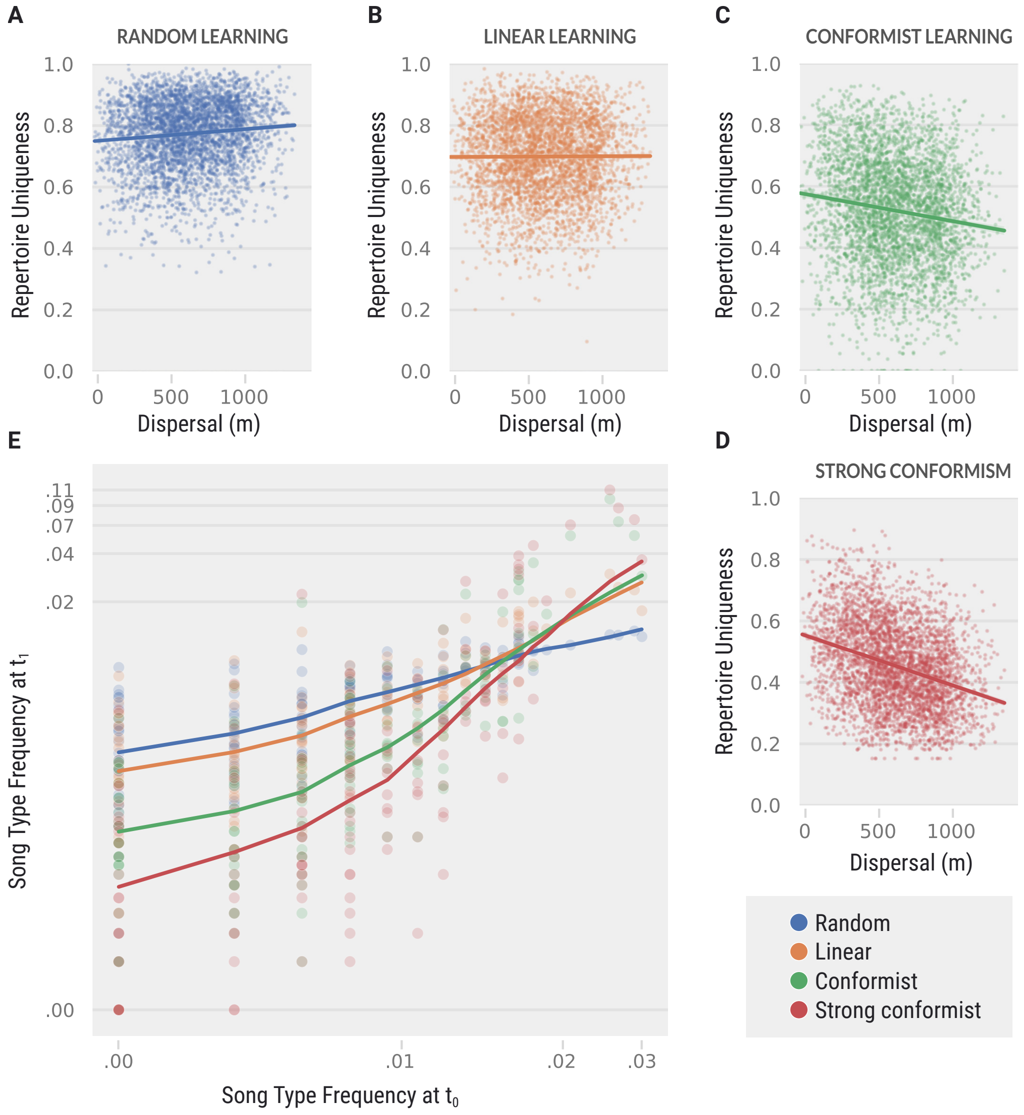


Figure S8. Simulation of the effect of natal dispersal on repertoire uniqueness. Related to STAR Methods.
We simulate the relationship between pre-breeding bird movement and the uniqueness of songs in their repertoires (relative to the population). We initialize 200 birds in a 1500 x 1500 square, each capable of singing 4 songs selected from a pool of 200 song types. Birds do not initially move. New birds hatch and move based on a log-normal distribution parametrized to represent realistic dispersal behaviour in our population. Each bird can learn the songs it hears within a 200 m radius as it moves. At the end of their movement, a bird's crystallized repertoire is determined by its learning mechanism: (A) random learning of songs, (B) linearly frequency-dependent learning, (C) positively frequency-dependent learning, or (D) learn the most popular songs (strong conformism). The simulation is repeated n times per learning strategy, and we record the average uniqueness of songs in each bird's repertoire, which is a transformation of the average frequency of the bird's songs, as well as the distance that each bird has moved. The results show that the relationship between dispersal and repertoire uniqueness depends on the learning mechanism, and that the effect of dispersal detected in our study might be expected to arise if being exposed to a larger number of songs influences learning in a nonlinear frequency-dependent manner.

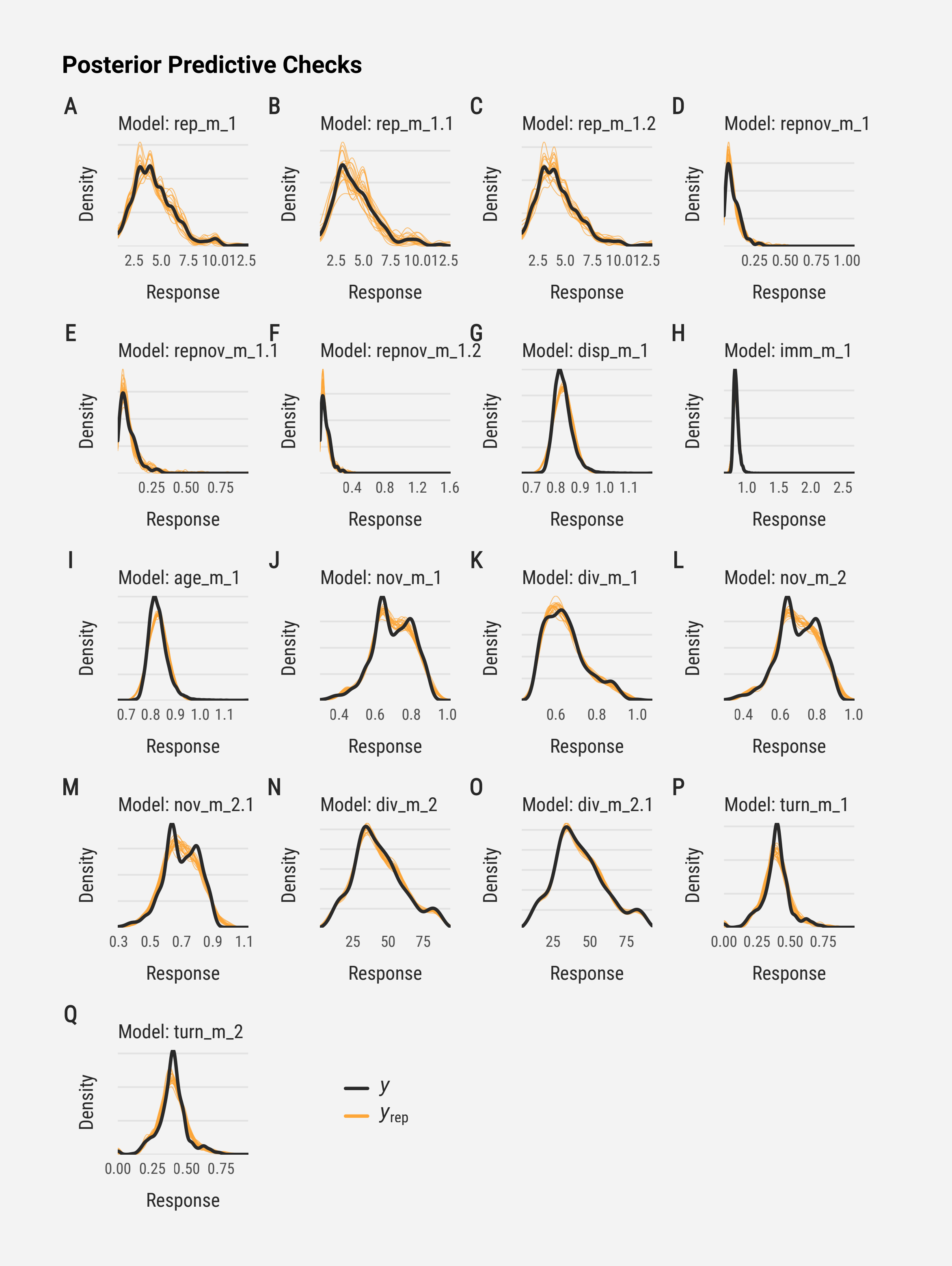


Figure S9. Posterior predictive checks for the main models in the study. Related to STAR Methods.
Comparing simulations from the posterior predictive distribution y^{rep} (thin orange lines) with the outcome y (black lines) using Kernel density estimates. The posterior predictive distribution is a distribution 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.

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	uniqueness ∼ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(n_current_songs) + year + gp(x, y, by = year)	lognormal	791	GP
div_m_1	diversity ∼ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(n_current_songs) + year + gp(x, y, by = year)	lognormal	791	GP
nov_m_2	uniqueness ∼ 0 + diversity + s(n_current_songs) + year + gp(x, y, by = year)	lognormal	791	GP
nov_m_2.1	uniqueness ∼ 0 + diversity + year + gp(x, y, by = year)	lognormal	791	GP
div_m_2	n_unique_current_songs ∼ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(recorded) + year + gp(x, y, by = year)	Gaussian	791	GP
div_m_2.1	n_unique_current_songs ∼ 0 + prop_immigrant + mean_dispersal_distance + prop_same_birds + mean_age + s(n_current_songs) + year + gp(x, y, by = year)	Gaussian	791	GP
Cultural Turnover				
turn_m_1	prop_shared ∼ 0 + prop_same_birds + year + gp(x, y, by = year, k = 25, c = 5/4)	hurdle lognormal	544	GP
turn_m_2	prop_shared ∼ 0 + prop_immigrant + mean_dispersal_distance + mean_age + prop_same_birds + year + gp(x, y, by = year, k = 25, c = 5/4)	hurdle lognormal	544	GP

Table S1. Model information. Related to STAR methods.

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

Continued on next page

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

Table S2. Model variable key. Related to STAR methods.

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

Continued on next page

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

[a] Estimates are Medians and 95% Credible Intervals

Table S3. Model-derived estimates. Related to main text and STAR methods.