

1. Supplementary Methods

“It is the most closely-allied forms,—varieties of the same species, and species of the same genus or related genera,—which, from having nearly the same structure, constitution and habits, generally come into the severest competition with each other. Consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred” C. Darwin, *The Origin of Species*¹

Definitions

The term ‘adaptive radiation’ is sometimes restricted to early bursts of evolution within lineages undergoing rapid ecological diversification. We apply the more general definition² that refers to the pattern of species and trait evolution in lineages that have diversified into a variety of ecological roles (e.g. Extended Data Fig. 1).

‘Character displacement’ is sometimes defined as a geographical pattern determined intraspecifically by comparing between sympatric and allopatric parts of ranges. However, this approach makes it difficult to assess whether the mechanism is general across species, and raises the problem that spatial variation may be explained by many alternative processes³⁻⁵. We follow previous studies⁶⁻⁸ in defining character displacement as the process of selection driving phenotypic evolution as a result of species interactions. This framework is more general, being relevant to all interacting species rather than only those with partially overlapping ranges⁴.

The term ‘convergence’ implies decreasing trait differences between lineages over time. However, we also define convergence as the failure of lineages to diverge (‘non-divergence’), which leads to convergence of traits relative to the normal trajectory of divergence. Our approach is logical given that increased differences in coexisting lineages are routinely interpreted as ‘divergence’ in both ecological⁹ and social traits¹⁰. Although we follow this convention in interpreting reduced trait differences as trait convergence, the extent to which this pattern is caused by classic convergence or non-divergence is unclear.

Background to methods and sampling

Sample size. Numerous studies investigating size assortment or size evolution in island reptiles [e.g.¹¹⁻¹³] include low numbers of species interactions (often two species per island, < 10 species overall). The most extensive time-calibrated analysis of character divergence⁹ included 50 pairs of sister species, of which only 17 were sympatric (as defined here). Meanwhile, many field studies have also focused on small numbers of lineages—typically a pair of interacting

species [e.g.¹⁴⁻¹⁷]. While this approach has demonstrated the existence of ecological (ECD), reproductive (RCD) and agonistic character displacement (ACD), it is difficult to draw firm conclusions about the generality of these processes. In particular, it is hard to rule out the role of chance and environmental drivers³⁻⁵.

Evolutionary and geographical biases. Samples in most empirical studies of character displacement are not only small, but appear to target a non-random set of species. Studies reporting ECD have focused on recent speciation events in radiations such as Darwin's finches (*Geospiza*), salamanders (*Plethodon*), sticklebacks (*Gasterosteus*) and spadefoot toads (*Spea*). Demonstrations of RCD derive from studies of young species, including tree-frogs (*Litoria*), flycatchers (*Ficedula*) and flies (*Drosophila*). In both cases (ECD and RCD), molecular data suggest that most study lineages are very young, typically 0.0001 to 0.5 million years old.

A disproportionate number of studies focusing on ECD have also focused on (i) insular radiations (e.g. *Anolis* lizards in the Caribbean, *Phelsuma* geckos in the Seychelles, *Cnemidophorus* lizards on Mexican islands, *Tribolonotus* skinks in the Pacific), and (ii) lake communities. These cases are characterised by few interacting species with early sympatry, and may tell us little about macroevolutionary patterns.

Ecological biases. Comparative studies of character displacement rarely consider the influence of ecological niches. Niche divergence may be greater in sympatric lineages, reflecting ecological sorting mechanisms¹⁸. Thus, functional trait divergence associated with habitat or diet divergence provides weaker evidence for ECD than trait divergence in species sharing similar niches. For example, a study of Carnivora⁹ included sympatric pairings so ecologically divergent—e.g. *Eupleres goudotii* (invertebrate diet) and *Fossa fossana* (vertebrate diet), and *Arctitis binturong* (arboreal frugivore) and *Paguma larvata* (terrestrial omnivore)—that it is difficult to ascribe phenotypic divergence to competition. These contrasts tend to have unusually high leverage in models of trait divergence⁹.

Strengths of Furnariidae as a study system

Ovenbirds are a diverse continental radiation: 97% of 295 species and 100% of 69 genera occur in South America, and only 2 species occur exclusively on islands¹⁹. Most clades are uniform in foraging substrate and strata^{20,21}. Ovenbirds offer highly resolved data on geographical range, phylogenetic relationships and social signals. This is an advantage in comparison with other

temporal frameworks, including the fossil record, which tends to suffer from patchy sampling of lineages and incomplete geographic data. Additionally, mating or territorial signals are rarely preserved in fossils, which therefore usually provide no insight into social traits.

Functional traits: In suboscine birds, beak morphology is a key functional trait reflecting dietary and foraging niche^{20,21}, and song is the primary social signal functioning in competition for mates and territories²². Species from all major ovenbird clades appear to use song in courtship and advertisement, as well as in aggressive interactions^{20,21}. These songs are relatively consistent within species (Extended Data Fig. 2), but vary among species, ranging from slow whistles to rapid trills and complex coordinated duets (Extended Data Fig. 3).

Song development: Song in some avian lineages (e.g. parrots, hummingbirds, oscine passerines) develops by learning—an imprinting-like process that generates geographical and individual variation²³. Learning introduces three major problems for studies of character displacement²⁴. First, the acoustic structure of learned songs is often complex, making it difficult to quantify and interpret. Second, it is regularly influenced by heterospecific copying in sympatry. Third, it may lack a genetic basis, one of the essential properties of character displacement^{3,8}. In contrast, field and experimental studies indicate that suboscine passerines develop song without learning²⁵. Non-learning is an advantage as it means that ovenbird song structure is relatively simple and stereotyped within species, and within and between individuals (Extended Data Fig. 2). This facilitates acoustic analysis, and reduces the need for large samples of songs to capture variation²⁶. Most importantly, ovenbird song structure is likely to be genetically determined, and thus free of the potentially confounding influence of cultural evolution and heterospecific copying²⁴.

Taxonomy and sample sizes

Ovenbirds and woodcreepers were previously classified as two separate families, but recent studies revealed that woodcreepers are embedded within the ovenbirds^{19,27,28}. Both groups are now treated as a single family (Furnariidae), containing 295 species, 69 genera, and three major subfamilies (Sclerurinae, Dendrocolaptinae and Furnariinae) (see SI Database 1).

We compiled data from 350 lineages (279 species). Species excluded from analysis lacked genetic data (12 species: *Asthenes berlepschi*, *Asthenes heterura*, *Cranioleuca henricae*, *Lepidocolaptes squamatus*, *Phacellodomus erythrophthalmus*, *Philydor novaesi*, *Pseudoseisura cristata*, *Synallaxis beverlyae*, *Synallaxis fusciorufa*, *Synallaxis infuscata*, *Synallaxis whitneyi*, *Thripophaga macroura*), song samples (4 species: *Asthenes coryi*, *Cinclodes taczanowskii*,

Siptornis striaticollis, *Xenerpestes minlosi*), or both (1 species: *Aphrastura masafuerae*). We also included 72 intraspecific lineages, some of which contained multiple subspecies (if these were geographically contiguous, and song or genetic variation indicated a close relationship). Taxonomy and nomenclature follows standard treatments (see SI Database 1).

Phylogenetic framework

To develop a robust temporal framework, we constructed a multilocus phylogenetic tree using published molecular data for 279 (95%) of 295 extant ovenbird species, along with a further six intraspecific lineages¹⁹. To capture the complete timespan of phenotypic divergence in younger lineages, we added genes for a further 65 intraspecific lineages. Of the total of 71 lineages currently considered intraspecific, we treated 4 lineages as species in our analyses on the basis of our phylogenetic results, which indicated that traditional treatment as subspecies rendered parent lineages polyphyletic (*Phacellodomus* taxon nov., *Cranioleuca dissita*, *Xiphorhynchus chunchotambo*, *Xiphorhynchus eytoni*). The final tree included all 350 lineages, representing 68 of 69 recognised genera (see SI Database 1).

Molecular data

Extraction, sequencing, alignment and partitioning followed protocols described by Derryberry et al.¹⁹. For most individuals, we amplified and sequenced three mitochondrial genes (*NADH dehydrogenase subunit 3* [ND3; 350 bp], *cytochrome oxidase subunit 2* [CO2; 684 bp], *NADH dehydrogenase subunit 2* [ND2; 1041 bp]), and one nuclear intron (*β-fibrinogen intron 7* [Bf7; ~840 bp]). For at least one individual per genus, we also included a large portion of the single exons of two *recombination activating genes* (RAG-1 [2904bp] and RAG-2 [1152bp]). RAG sequences were obtained from Moyle et al.²⁷. The final alignment included 6,954 base pairs and is available in TreeBASE (available from the authors on request). All sequences are deposited in GenBank (see SI Database 1). To root and calibrate the phylogeny, we included 15 species from related suboscine families as outgroups.

Phylogenetic inference and divergence times

We estimated topology and divergence times in a Bayesian framework, following Derryberry et al.¹⁹. Substitution model, rate heterogeneity, and base frequencies were unlinked across partitions. We used a Yule prior for tree shape, and the default priors for the substitution model and relaxed clock parameters. A UPGMA tree was used as the starting tree. No restrictions

were placed on the topology so that topological uncertainty was factored into the divergence date estimates. Tree calibration was based on Derryberry et al.¹⁹. We placed a prior distribution on the age of the root (split of Tyrannoidea and Furnarioidea) and used biogeographic events to place further priors on the divergence times of the most recent common ancestor (tMRCA) of 10 sets of lineages. These included 6 Panamanian Isthmus tMRCAs: (1) *Synallaxis candei*, *S. erythrothorax*, (2) *Cranioleuca antisiensis*, *C. baroni*, *C. curtata*, *C. dissita*, *C. erythroptis*, (3) *Lepidocolaptes lacrymiger*, *L. leucogaster*, *L. affinis*, (4) *Margarornis rubiginosus*, *M. squamiger*, *M. stellatus*, (5) *Thripadectes melanorhynchus*, *T. rufobrunneus*, and (6) *Anabacerthia variegaticeps variegaticeps*, *A. v. temporalis*; and 4 Andean tMRCAs: (1) *Hylocichla ustulata virgatus*, *H. s. ustulata*; (2) *Automolus rubiginosus rubiginosus*, *A. r. obscurus*, *A. r. nigricauda*, *A. r. watkinsi*, *A. rufipectus*, *Hylocichla erythrocephalus*; (3) *Philydor erythrocerum lyra*, *P. e. ochrogaster*, *P. fuscipennis*; and (4) *Dendrocolaptes certhia certhia*, *D. c. concolor*, *D. c. juruanus*, *D. c. radiolatus*, *D. sanctithomae*.

To optimize Markov Chain Monte Carlo (MCMC) operators, we performed incrementally longer runs and adjusted the scale factors for the operators. Once scale factors stabilised, we ran analyses for a total of 200 million generations across eleven independent runs. Using Tracer 1.5²⁹, we determined that replicate analyses converged, and all parameters met benchmark effective sample size values (>200). We combined 11 independent, converged runs, each between 10 and 18 million generations. The total combined length was 156 million generations, and we discarded ~21 million generations as burn-in across the different chains, making the total final length 135 million generations. Converged runs were combined in LogCombiner²⁹ and used to estimate the posterior distributions of topologies and divergence times. We used a sample of 1000 trees from the posterior distribution to estimate the maximum clade credibility (MCC) tree (see Fig. 2).

Ecological trait dataset

To model ECD we quantified variation in beak shape and tarsus length. Variation in beak design has profound impacts on the ability of birds to forage and survive in the wild³⁰, and beak morphology is a classic trait for the study of foraging ecology and competition in birds³¹⁻³³. However, beak and song may undergo correlated evolution because shifts in beak shape driven by ecological selection can influence the acoustic structure of songs^{34,35}. We therefore included tarsus as an independent ecological trait in our analyses. In ovenbirds, variation in tarsus length is related to habitat and foraging niche³⁶, but has no direct influence on beaks or songs (it is

indirectly related as a correlate of body size), and represents the best univariate index of overall body size in birds³⁰.

We took ~5,000 measurements of beaks and tarsi from museum specimens using digital calipers (see Fig. 1a). Beaks were measured (to the nearest 0.01 mm) in three ways: (1) length from the anterior edge of the nostrils to the tip; (2) depth (vertical height) at the anterior edge of nostrils; and (3) width at the anterior edge of the nostrils. Tarsus length was measured from the middle of the rear ankle joint (i.e. the notch between the tibia and tarsus) to the end of the last scale of the acrotarsium (usually the last undivided scale). One researcher (S. Claramunt) took all measurements.

A total of 1281 museum specimens representing 349 ovenbird lineages were sampled for this study. For the only missing lineage, *Thripadectes virgaticeps klagesi*, we assigned biometric data from a close relative: *T. v. virgaticeps*. We sampled a mean \pm SD of 4.6 ± 2.6 specimens per species and a mean of 3.7 ± 1.5 specimens per lineage. Most (76.9%) specimens came from the collections of Louisiana State University Museum of Natural Science (LSUMZ). Other contributing institutions are listed in the Supporting Acknowledgments. See Database S1 for a list of specimens and sources.

Song dataset

Song sampling: We used >5000 digital sound files to identify primary songs of each study lineage. Files were compiled from: (1) global sound archives, including Xeno-canto (<http://xeno-canto.org>) and Macaulay Library (<http://macaulaylibrary.org>); (2) commercial recordings; and (3) private collections. We discarded non-song vocalizations and poor quality cuts (i.e. those with high amounts of overlapping noise). In all cases, we verified that we had sampled the primary song using published descriptions and reference to sound archive material (see SI Database 1). We focused on homologous signals (those with most similar structure) and selected only adult male songs, where available. We checked song samples to ensure they were consistent. In duetting species, we restricted our analysis to the loudest or most complex contribution, assuming these were produced by the male^{22,37}. We discarded all duets and choruses with temporal overlaps between male and female contributions.

Our sample contained 1854 high quality sound files of ovenbird songs: 1079 (58.2%) from Macaulay Library, 315 (17.0%) from commercial sources, 262 (14.1%) from private collections, and 198 (10.7%) from Xeno-canto (see SI Database 1, and Supporting Acknowledgments). All files were saved as 44.1 kHz wav files. Using ADOBE AUDITION, we

sampled the highest quality song per individual (i.e. highest signal-to-noise ratio, least sign of degradation, and no overlap with background noise), and at least three individuals per species, wherever possible. Some lineages were included on the basis of songs from two individuals if recordings were very high quality and song structure was consistent across a further sample of discarded cuts. The final sample (SI Database 1) included ~50,000 measurements for 350 ovenbird lineages, with a mean (\pm SD) of 5.3 ± 3.0 individuals sampled per lineage.

Identification

Our song analyses rest on accurate identification of sounds, as misidentifications may give an inaccurate impression of song similarity. Most of our data are extracted from files held in the Macaulay Library (Cornell University) and xeno-canto online archive (www.xeno-canto.org) which are open access, containing multiple song examples per species, verified by numerous experts. To maximise accuracy, all identifications were cross-checked against these resources by a single observer (JAT) with two decades of experience recording and identifying Neotropical bird sounds.

Song processing and analysis

We processed songs using the MatLab signal processing toolbox (Mathworks, Natick, MA). All songs were filtered using a 10th order highpass Butterworth filter (cut-off frequency = 400 Hz) before final broadband spectrograms were generated (window = Hann, bandwidth = 256 Hz, Fast Fourier Transform = 1024, overlap = 0.875). Spectrograms were visualized with a custom graphical user interface (GUI) and manually segmented using on-screen cursors to record sample number at note onset and offset (see Extended Data Fig. 3). A note was defined as a continuous trace on the spectrogram with amplitude much greater than that of background noise. We used 10% of peak energy as a threshold for the temporal extent of a note. Rapid trills were classed as series of separate notes unless intervals between individual notes were imperceptible against background noise. A few species had long songs, i.e. >100 notes. In these cases, note number and song duration were measured from the entire recording, but all other measures were taken from 30 notes from the middle section of the song. Where songs consisted of a series of repeated units of stereotyped structure, e.g. a series of descending trills, we ensured that the sample encompassed one unit (i.e. not necessarily 30 notes). Segmented songs were analysed using a custom MatLab script code (available from the authors on request). This automatically extracted a total of 12 raw acoustic measures (5 spectral and 7 temporal), from

which we generated an additional 20 composite acoustic variables (SI Table 1). Final data used for analysis are presented in SI Database 1.

Habitat niche divergence

To test for the role of ecology in driving ecological and social trait divergence in ovenbirds, we used habitat scores in Stotz et al.³⁸ to classify primary habitat of all lineages in this study as (1) dense, closed-canopy forest [categories F1–F15 in Stotz et al.³⁸], (2) open-canopy woodland and shrubland (N1–N4, N11, N12, N14), (3) grasslands and desert (N5–N10, N13). No lineage occurred in both (1) and (3); some species occupied intermediate habitats qualifying as both (1) and (2), or (2) and (3). In virtually all cases, however, a clear association with one category was evident from published habitat scores. In the few ambiguous cases (and for more recently described lineages) we used recent habitat descriptions [^{20,21}] to assign habitat categories. Our scoring system provided an index of ecological divergence for pairwise comparisons between sympatric and allopatric species. We included ecological contrasts in models: no habitat contrasts (1 vs 1; 2 vs 2; 3 vs 3), moderate contrasts (1 vs 2; 2 vs 3) and large contrast (1 vs 3).

Geographic relationships

To facilitate interpretation in our core analyses, we treated sympatry and allopatry as binary variables using a three-step process.

First, we used standard digital range polygons downloaded from NatureServe³⁹ to quantify overlap (sympatry) for all pairwise comparisons between lineages. Degree of overlap was calculated as the proportion of the smaller range that occurred within the larger range. Where our dataset contained more than one intraspecific lineage, we subdivided range polygons according to published range descriptions for each lineage^{20,21}—available online at <http://ibc.lynxeds.com>. All intraspecific lineages were distributed allopatrically. All calculations were made using ArcGIS 9.1 (ESRI, Redlands, CA).

Second, we converted range overlap to a binary variable by categorizing each pairwise comparison as either allopatric or sympatric, following established thresholds for ‘substantial sympatry’^{40,41}: allopatric species were defined as those with mutually exclusive or narrowly (< 20%) overlapping breeding ranges; sympatric species were defined as those with broadly (> 20%) overlapping breeding ranges. We used 20% range overlap as a cut-off because character displacement is only predicted to occur when interactions are sufficiently frequent at the population level⁸. Thus, marginal overlap (e.g. 1%) may be appropriately classified as sympatry

in studies of reproductive isolation [e.g.⁴²], but not in studies of character displacement. It is also important that we do not use too high a threshold (e.g. 50%) as this would remove important cases of relatively recent overlap in young species. We note that almost all pairs of lineages were unambiguously assigned to allopatry (i.e. 0% range overlap) or sympatry (i.e. >20% overlap of the smaller range).

Third, we checked results for accuracy on the basis of published ranges, and locality data in sound archives and museum specimen collections, revising classifications where necessary⁴².

The above method has the benefit of correcting erroneous overlap estimates caused by the fact that digital range polygons are relatively crude representations of global distributions, particularly in the tropics⁴³. However, the revision process is arguably subjective, and raises the issue that our results may be sensitive to a fixed 20% threshold. To explore this more thoroughly, we re-ran analyses with proportional range overlap (generated in stage 1 above) treated as a continuous variable, following recent studies^{9,44}.

Organisation of datasets

Summarizing variation in beaks and songs

To reduce the dimensionality of datasets and remove any potential biases caused by colinearity, we conducted a principal components analysis (PCA) on the correlation matrices of lineage mean values (log-transformed) for the beak and song datasets. We note that using PCA does not alter the Euclidean structure of the data. To minimize variance and type I errors, we used *R* code provided by Revell⁴⁵ to compute PC scores taking into account the expected covariances between species due to phylogenetic relatedness. We note that PCs generated with phylogenetic PCA were highly correlated with those generated using normal PCA (all coefficient correlations >0.8). Beak measurements were reduced to a single component representing beak morphology (PC1_{beak}), which explained 75.8% of the variation (Eigenvalue = 2.23), and with which all three variables had high correlation coefficients (>0.8). For acoustic traits, PCA extracted 14 uncorrelated PCs. The loadings of song and beak characters on the PCs are given in SI Database 1. We quantified divergence as the Euclidean distance between the species centroids of the beak or acoustic space described by the PCs using the 'dist' function in *R*.

Datasets for analyses of trait divergence

To test for character displacement in tarsus length, beak morphology, and song structure we generated three datasets (for sample sizes see SI Table 2):

Dataset 1 compares closest relatives in allopatry and sympatry, including intraspecific lineages. Each lineage was initially included in this analysis twice, once in comparison to its closest relative in sympatry, and once in comparison to its closest relative in allopatry. However, as closest relatives were reciprocal for some lineages, we removed duplicated versions so that each combination of lineages appeared only once (see below). When several allopatric and sympatric comparisons were of equal evolutionary age, we randomly selected one comparison. Three pairs of closest relatives (0.6% of pairs) involved contrasts between different subfamilies, and thus represented outliers in terms of age (>25 Myr old) and ecological niche divergence. We excluded these cases from analyses.

Dataset 2 is the same as dataset 1, but we excluded lineages not yet elevated to species rank, such that data were only included from comparisons between the closest recognised species in allopatry and sympatry.

Dataset 3 is the same as dataset 1, but only included comparisons between the closest lineages in allopatry and sympatry, excluding comparisons between lineages >6 Myr old.

Dataset 4 includes comparisons between all lineages, not just closest relatives, including intraspecific lineages but excluding comparisons between subfamilies. This dataset was constructed by comparing all lineages against each other and then removing duplicate combinations. Duplicate combinations were removed in such a way that each lineage was represented an equal number of times as lineage 1 and as lineage 2.

Dataset 5 is restricted to comparisons between sister species, where sister species are defined as pairs of species-level taxa that are each other's closest relatives, descended from a single common ancestor.

General analytical approach

Analyses of trait divergence using Phylogenetic Linear Mixed Models (PLMMs)

The PLMM approach is a powerful tool for examining ECD and RCD as it can cope with complex datasets, and in particular allows the independent effects of multiple explanatory variables and their interactions to be separated. For example, PLMMs allow us to examine the effects of geographical range overlap on trait divergence while controlling for other potentially confounding variables, such as ecology and correlated evolution among traits. Furthermore,

PLMMs provide a flexible framework for fitting different evolutionary models, and for accounting for non-independence in data arising from shared ancestry and repeated measurement of lineages. Analytical techniques that are designed for repeated measurement data are particularly useful for examining ECD and RCD because they allow individual lineages to be compared with allopatric and sympatric lineages that vary in evolutionary age.

Significance tests, transformations and parameter estimation

We fitted PLMMs using restricted maximum likelihood estimation (REML) in ASReml-R⁴⁶. Response variables were transformed to ensure model residuals were normally distributed and homoscedastic (Euclidean distance in song structure, beak morphology [$PC1_{\text{beak}}$], tarsus length and evolutionary age were square-root transformed). All covariates were mean centred and standardized to unit variance (z -transformed) before analyses. One benefit of this approach is that it alleviates problems of collinearity when quadratic terms are included in our models⁴⁷. The significance of fixed effects were examined using Wald type F -tests with denominator degrees of freedom calculated following Kenward & Roger⁴⁸. We first tested the significance of interactions using full models with all terms included, and then removed higher order interactions to test the main effects in each model. The significance of random effects was tested using log-likelihood ratio tests with all fixed effects and their interactions included in models⁴⁹. Parameter estimates of the effect of allopatry/sympatry on trait divergence presented in supplementary tables are the mean estimates of divergence in allopatry (A) and the difference in sympatry from the allopatric estimate (Diff S). The mean estimate of divergence in sympatry can be calculated as the sum of A and Diff S.

Methods used to account for non-independence in datasets

Our analyses took account of four sources of non-independence:

(1) Non-independence arising through lineages sharing phylogenetic history

We accounted for the effect of shared ancestry on trait divergence by fitting a phylogenetic variance-covariance matrix constructed from the MCC phylogenetic tree as a random effect. As data points were pairwise comparisons between lineages 1 and 2 rather than values for individual species, we connected data points to the phylogenetic variance-covariance matrix via their ancestral node. We also accounted for error in the construction of the phylogenetic tree by including a random effect of the variance in evolutionary age for each pair of lineages which

we estimated from the 1000 posterior trees used to calculate the MCC tree (hereafter referred to as ‘error in evolutionary age’).

(2) Non-independence between lineages

Lineages were represented more than once in each of dataset 1 to 4 (SI Table 2). The non-independence of data points arising from the same species was taken into account by fitting both focal lineage (labeled as Lineage 1 in analysis tables) and the lineage they were compared to (labeled Lineage 2) as random factors. In all analyses, each lineage was represented as the focal and the comparison lineage an equal number of times where possible (see SI Table 2). This was not always the case as it was necessary to remove duplicate combinations, for example when closest relatives were reciprocal for some lineages (datasets 1, 2 and 3), when lineages were excluded due to certain criteria (datasets 3 and 4), and when subfamilies contained different numbers of lineages (dataset 4).

(3) Non-independence of slopes between lineages across evolutionary age

When repeated measurements are taken across time, non-independence not only arises between observations (see above), but can also occur due to subjects (lineages in this case) differing in how they vary over time, i.e. their slopes can vary. We therefore used random regression analyses that allowed the relationship between response variables and evolutionary age to vary across lineages, which accounts for pseudoreplication in slopes over time⁵⁰. We fitted 2x2 unstructured covariance matrices that estimate the lineage intercept, the slope across evolutionary age and the covariance between intercepts and slopes for both lineage 1 and 2. In datasets 1 to 3, where the focal lineage was represented a maximum of two times (SI Table 2), we found that including random regression terms increased the Akaike Information Criteria (AIC) values for all models, and therefore we dropped these terms from the models. However, we present models including random regression terms for dataset 4, where models of all traits had lower AIC values.

(4) Non-independence of errors across evolutionary age within lineages

Repeated measures over time can lead to correlations between residuals within subjects, for instance due to data being recorded at closer time points (temporal autocorrelation). This problem can be modeled using different random effect covariance structures. We examined temporal autocorrelation between residuals within lineages by fitting residual spatial power covariance functions within lineages. This allowed correlated errors to be modeled on

measurements that are made at irregular points in time. We compared models with and without spatial power covariance functions using AIC values and found that for all datasets and all traits, models had lower AIC values without such covariance structures. We therefore used models without spatial power functions.

Interpretation of random effects in models

Random effects were entered into our models to control for the potential sources of non-independence outlined above. The random effect termed ‘error in evolutionary age’ had little effect in all models, confirming that phylogenetic uncertainty does not explain our results. All other random terms were significant in at least one model. For example, the significance of the random term ‘Phylogeny’ indicates that more closely related lineages had more similar phenotypes. Similarly, the significance of the terms ‘Lineage 1’ and ‘Lineage 2’ simply indicates that variance in trait divergence across different lineages was greater than variance in trait divergence involving the same lineage. When the term ‘Lineage 1 (or 2) Evolutionary age slope’ was significant this indicates that variation within species across multiple comparisons was lower than that between lineages over evolutionary time. In all cases, our main results were robust to correction for these effects.

Specific analyses

To test the prediction that trait differences are greater among sympatric versus allopatric lineages, or increase in relation to the extent of geographical range overlap, we conducted the following sets of analyses:

Analysis 1. *Character displacement in closest relatives independent of evolutionary age*

First, we quantified differences between closest relatives in allopatry versus sympatry by analysing divergence in evolutionary age, tarsus length, beak morphology ($PC1_{\text{beak}}$), and song structure. We used separate LMMs for each trait, conducted on dataset 1 with allopatry/sympatry (2-level factor) as a fixed effect, and the identity of lineages 1 and 2 fitted as random factors (SI Table 3).

Analysis 2. *Character displacement in closest relatives controlling for habitat, morphology and evolutionary age*

Analysis 2.1 To determine the effect of evolutionary age and phylogenetic history on patterns detected in *Analysis 1*, we analysed variation in tarsus, beak and song divergence using PLMMs. We fitted allopatry versus sympatry, habitat differences (6-level factor) between lineages, evolutionary age (covariate) and evolutionary age² as fixed effects and the phylogenetic covariance matrix, error in calculating evolutionary age, and the identity of lineages 1 and 2 as random factors (SI Tables 4 to 6). Quadratic terms were fitted to test whether trait divergence reached an asymptote or started to converge with evolutionary age (a negative quadratic term indicates a hump-shaped relationship; a positive quadratic term indicates a cup-shaped relationship). The linear and quadratic terms in our models are expected to vary according to the evolutionary process by which traits evolve. For example, under a Brownian motion (BM) model of evolution trait divergence is expected to increase linearly through time leading to a significant linear term with variance increasing exponentially through time (Extended Data Fig. 10). In contrast, if there are evolutionary constraints on traits, such as with an Ornstein-Uhlenbeck (OU) model of evolution, trait divergence and variance will reach an asymptote over time leading to a significant quadratic term (Extended Data Fig. 10). The linear and quadratic terms of evolutionary age in our models therefore provide information about the process of trait evolution. However, we emphasise that the main objective behind entering linear and quadratic terms of evolutionary age into our PLMMs was not to infer the model of trait evolution (see section 2.2 for treatment of this), but instead to test whether trait divergence over time was different for allopatric and sympatric taxa. We did this by fitting interactions between evolutionary age and allopatry/sympatry that enabled us to estimate separate slopes of trait divergence over time for allopatric and sympatric lineages and test whether these slopes were significantly different. Fitting interactions between the quadratic of evolutionary age and allopatry/sympatry also allowed us to test whether curvature in the slope for sympatric taxa was significantly different from that for allopatric taxa. Importantly, fitting quadratic terms of evolutionary age allows us to test for convergence in traits over time, which is not possible with currently available models such as BM, OU and ACDC.

To assess whether the inclusion of quadratic terms influenced our song results, we fitted a model for song divergence with the terms $\log(\text{evolutionary age})$ and $\text{allopatry} * \log(\text{evolutionary age})$. We found that this had a higher AIC value than the model with quadratic terms for evolutionary age ($\text{AIC } \Delta 2.70$), thus we report results from models containing quadratic terms.

We note that the results of models lacking quadratic terms were very similar, once again showing convergence in song ($F_{1, 26} = 5.56$, $P = 0.02$).

To account for potentially confounding relationships between traits, analyses of beak morphology included differences in tarsus length (covariate) and those of song included both differences in tarsus length and beak morphology (covariate) fitted as fixed effects. Interactions between allopatry/sympatry and all other fixed effects were entered to test if the relationships between habitat, tarsus length, beak morphology and song were affected by geographical range overlap. To account for non-independence in our data, we fitted a phylogenetic relationship matrix, the identity of lineages 1 and 2 (factors) and error in estimating evolutionary age (covariate) as random effects.

We then conducted a series of analyses to explore the sensitivity of the results of Analysis 2.1 to different evolutionary models and other potentially confounding factors.

Analysis 2.2 *Robustness of results to assumptions about the model of trait evolution*

Our PLMMs assume a Brownian motion (BM) model of evolution, which may not be valid when trait divergence is constrained, or rates of divergence are variable over time. We therefore examined whether alternative models of trait evolution better explained variation in tarsus length, beak morphology and song structure. We tested BM models of evolution against: (a) Ornstein-Uhlenbeck (OU) models whereby traits undergo a BM process but evolve towards a central tendency with a strength proportional to parameter, alpha (α)⁵¹; and (b) accelerated/decelerated models of evolution (ACDC) whereby traits diverge under a BM model but rates of evolution accelerate or decelerate over time according to parameter g (Acceleration: $g < 1$. BM: $= g$. Deceleration $g > 1$)^{52,53}. We first examined the correspondence between different methods of estimating models of evolution, second identified best-fit models of evolution in our divergence datasets, and finally assessed the impact of accounting for the best-fit models of evolution on our results.

Analysis 2.2.1 *Correspondence between methods used for estimating evolutionary models*

Phylogenetic generalized least squares (PGLS) and maximum likelihood estimation (ML) are widely used to test different models of evolution. However, these techniques do not allow repeated measures data to be analysed. We therefore examined the correspondence between PGLS (implemented with R packages ‘ape’ and ‘nlme’^{54,55}) and ML (implemented with ‘fitContinuous’ function in R package ‘Geiger’⁵⁶) with a third approach that does allow repeated measures data: PLMM (implemented with ASReml-R) fitted with a phylogenetic

covariance matrix transformed according to specified models of evolution using the ‘transform’ function in ‘Geiger’⁵⁶. We fitted PGLS, ML and PLMM models using raw values of beak morphology, tarsus length and song structure (as defined by PC1 and PC2) mapped on to the MCC tree of 350 lineages, making it possible to assess equivalent models (intercept only) with all three techniques. With each method, we tested the fit of the trait data to three evolutionary models: BM, OU (α ranging from 0 to 5) and ACDC (δ ranging from 0 to 5). To fit ACDC models, we used Bloomberg’s g in the PGLS, and Pagel’s delta (δ) in ML and PLMM. Estimating parameters, such as α in OU models, can be very unstable⁵⁷. Therefore, in our PGLS analyses we estimated values of α (OU) and Bloomberg’s g (ACDC) by fixing α and g at 0.1 increments within the range of 0 to 5 and used AIC values to identify best-fit models. Similarly, in the PLMM analyses we transformed the MCC tree incrementally changing values of α and δ by 0.1 within the range of 0 to 5 and identified best-fit models using AIC values. We found that all three methods identified the same best-fit model of evolution for each trait (SI Table 7). These results reveal that our approach using PLMMs corresponds closely to established techniques for testing evolutionary models, supporting our use of PLMMs for examining different models of evolution in trait divergence data (datasets 1, 4 and 5).

Analysis 2.2.2 *Trait divergence data*

PLMMs (implemented in ASReml-R) were used to determine the best-fit model of trait divergence among sister species, closest relatives only (dataset 1) and all lineages (dataset 4). Following methods described in Analysis 2.2.1, we transformed the MCC tree with values of α and d ranging from 0 to 5 with incremental changes of 0.1 and used AIC values to identify the best-fit model (SI Table 8). In all models, the same fixed and random effects were fitted as those in the main analyses (closest relatives: SI Tables 4 to 6; all lineages: SI Tables 19 to 21). The best-fit model of trait divergence among sister species (dataset 5) was examined using PLMM and PGLS, implemented as in Analysis 2.2.1, with the same fixed effects fitted as in the main analyses. For estimated parameters from these models see section 2.4 (Sister lineages).

Analysis 2.2.3 *Accounting for models of trait evolution*

We found that divergence in ecological traits followed a BM model of evolution, while divergence in song followed an OU model (SI Table 8). Thus, for ecological traits, the assumption of BM evolution in our PLMMs was valid and no further analyses were required. For song, we accounted for the best-fit (OU) process in subsequent PLMMs. This had no effect on the results, whether focusing on closest relatives (SI Table 9) or all lineages (SI Table 21).

One possible interpretation of divergence or convergence is that constraints on evolutionary divergence vary in sympatry versus allopatry. To examine the extent to which our results were explained by this possibility, we used multi-response PLMMs conducted in ASReml-R⁵⁸. First, we estimated best-fit models of evolution in allopatry and sympatry separately by restricting data to allopatric and sympatric comparisons, respectively, and using the PLMM approach described in section 2.2.2. Second, we fitted models with one response variable corresponding to allopatric comparisons and another response variable corresponding to sympatric comparisons. We linked allopatric comparisons to a phylogenetic covariance matrix that was formed from the MCC tree after it was transformed according to the model of evolution that best explained divergence in song in allopatry. We linked a second phylogenetic covariance matrix to sympatric comparisons constructed from the MCC tree following transformation according to the best-fit model of evolution for song divergence among sympatric lineages. Tree transformations were conducted in ‘Geiger’⁵⁶. Exactly the same fixed and random effects as in the main analyses were entered into models. We found that song evolution followed the OU process in both sympatry and allopatry, though variation in the constraint parameter suggested that evolution was slightly more bounded in sympatry (SI Table 10). However, incorporating this factor into our PLMMs did not alter the conclusions of our main analyses (SI Table 10).

Analysis 2.3 *Exclusion of intraspecific lineages*

To investigate the influence of taxonomy, we re-ran models using dataset 2, which only included ovenbird lineages recognised as species (SI Tables 11 to 13).

Analysis 2.4 *Sister lineage analyses*

To investigate whether our results held when focusing on sister lineages only, we ran our PLMMs and PGLSs on a dataset including all true sisters irrespective of their ecological niches ($n = 111$; SI Table 14). When running the PLMMs and PGLSs we accounted for phylogenetic history and the best-fit model of evolution (SI Table 8) using the approach described in section 2.2.2 and including the same fixed effects as in our main analyses. As an additional test, we re-ran exactly the same analysis on sister species (no intraspecific lineages) with conserved beta-niches (occurring in the same microhabitat, altitudinal range and occurring <250 km apart), producing a reduced dataset of 58 pairs of sister species (i.e. most of the dataset used by Pigot & Tobias 2013⁵⁹). The results from PGLS and PLMM were almost identical for these analyses and so for brevity we only present the results of the PLMMs (SI Table 15).

Analysis 2.5 *Exclusion of lineages >6 Myr*

Species interactions are theoretically most powerful during the period after initial divergence, perhaps explaining an apparent tendency for greater trait differences in sympatry during the first 6 Myr after speciation (see Fig. 3). To focus more exclusively on this period, we re-ran models on dataset 3, i.e. only those lineages <6 Myr old ($n = 189$ allopatric comparisons, $n = 83$ sympatric comparisons) (SI Tables 16 to 18).

Analysis 3 *Character displacement across all lineages controlling for habitat, morphology, evolutionary age and the best-fit model of trait evolution*

To examine the evolution of trait divergence across the ovenbird radiation (within subfamilies) we re-ran the models described in section 2.1 using dataset 4 (SI Tables 19 to 21). We accounted for the non-independence of slopes between lineages across evolutionary age by fitting interactions between the identity of lineages 1 and 2 with evolutionary age using 2 x 2 unstructured covariance matrices as random effects. Each covariance matrix estimates the variation explained by the intercept of lineage identity, variation in slopes of lineages across evolutionary age, and the covariance between intercepts and slopes.

Analysis 4 *Influence of range overlap on patterns of character displacement across (a) closest relatives and (b) all lineages, controlling for habitat, morphology, evolutionary age, and best-fit model of trait evolution*

To investigate the sensitivity of our results to using sympatry/allopatry as a dichotomous rather than continuous trait, we re-ran models with the proportion of range overlap as a fixed effect (covariate) instead of our allopatric/sympatric classification (SI Tables 22 to 27; Fig. 4). These analyses only included recognised species because data on degree of range overlap were not available for intraspecific lineages.

Analysis 5 *Verification analyses*

To verify the ability of the PLMM method for testing patterns of character displacement, we carried out a series of analyses to ascertain that our models were performing as expected.

Analysis 5.1 *Permutation tests*

It is possible that our results are influenced by biases in the structure of our datasets and distribution of our response variables. To assess the impact of data structure on our results, we

performed a series of permutation tests whereby we randomly shuffled the response variable in each analysis and re-ran models to obtain parameter estimates for each fixed effect (Extended Data Fig. 6). We repeated this procedure 1000 times and calculated the proportion of permutations where parameter estimates in the main analyses were greater (or less than) the randomly generated parameter estimates (referred to as *P* in Extended Data Fig. 6). We expected that if our results were not influenced by data structure, or by the distribution of the response variables, then the proportion of simulations where parameter estimates from our main analyses differ from that of the permuted data would be similar to the *P*-values presented in our main analyses.

Analysis 5.2 *Trait simulations under different models of evolution*

To test further whether our results were influenced by the structure of datasets when different models of evolution are assumed, we performed a set of simulations. These analyses involved simulating trait data for allopatric and sympatric comparisons across the ovenbird tree, reconstructing datasets 1 and 4 from these simulated data, and re-running the PLMMs described in our main analysis, but using the simulated response variables. We repeated this procedure 1000 times to obtain a distribution of 1000 estimated differences between allopatric and sympatric lineages. We performed these simulations using two different models of evolution to make sure that any interplay between the structure of our datasets and differences in models of evolution did not explain our results. First, we simulated trait data under a BM model of evolution. Second, we simulated trait data under the best-fit model of trait evolution obtained in analysis 2.2.2, which was always an OU process when trait evolution deviated from BM. In the OU analyses, we used the largest alpha value detected for dataset 1 for simulations of closest relatives, and for dataset 4 for simulations of all lineages (analysis 2.2.2, SI Table 8). In all simulations, variances were specified according to variance in trait comparisons in dataset 1 (for closest relatives) or dataset 4 (for all lineages). We calculated the proportion of simulations where parameter estimates in the main analyses were greater (or less than) than the parameter estimates in the simulated datasets (referred to as *P* in Extended Data Fig. 7). We expected that if our results were robust to differences in the model of evolution that the proportion of simulations where the parameter estimates in our main analyses differ from that of the simulated data would be similar to the *P*-values presented in our main analyses.

Analysis 5.3 *Recovering simulated differences between allopatric and sympatric lineages under different models of trait evolution*

The simulations outlined in 5.2 test the robustness of our results to differences in the model of evolution (see also analysis 2.2.3), but do not assess whether PLMMs accurately recover differences in trait divergence between allopatric and sympatric lineages under different models of trait evolution. To test this, we simulated a range of divergences between pairs of lineages under two different evolutionary models: a BM process (Extended Data Fig. 8a), or an OU process (Extended Data Fig. 8b). When an OU process was modeled, we set alpha to 0.15, as this was the strongest constraint parameter detected in our analyses examining the best-fit model of trait evolution on raw trait values (SI Table 7). Simulations were performed using `rTraitCont` function in the R package ‘ape’ and different theta values were specified for allopatric and sympatric comparisons to create a range of trait divergences. We ran each set of simulations 5000 times as this gave a relatively high number of estimates across the entire range of divergences.

2. Supplementary Tables

SI Table 1: Acoustic measures taken from ovenbird songs. Units for temporal characters = seconds; units for spectral characters = hertz (Hz). (1) to (12) are absolute measures automatically extracted from segmented cuts in MATLAB; (13) to (32) are composite measures subsequently calculated from (1) to (12)

Acoustic character (with abbreviation)		Definition
Absolute measures		
1	Song duration (D)*	Interval between the onset of the first note and the offset of the final note
2	Note number (NN)*	Number of notes in the entire song.
3	Song peak frequency (F _{peak})*	Frequency at which peak energy (maximum power) occurs across the entire song, calculated as the maximum of mean power spectral density (PSD) across the song
4	Song maximum song (F _{max})*	Upper frequency bound of entire song, calculated as maximum frequency in the PSD that exceeds 10% max(PSD)
5	Song minimum frequency (F _{min})	Lower frequency bound of entire song, calculated as minimum frequency in the PSD that exceeds 10% max(PSD).
6	Song harmonic structure (Harmonics)	Number of frequency bands exceeding 50% of max frequency (averaged across all notes).
7	Note duration (d _i)	Interval between onset and offset a note (calculated for all notes in the song).
8	Internote interval (int _i)	Interval between offset of a note and the onset of the adjacent note (calculated for all intervals in the song).
9	Note peak time (t _{peak})	Time at which peak energy occurs as a fraction of note duration
10	Note maximum frequency (f _{max})	Upper frequency bound of the note.
11	Note minimum frequency (f _{min})	Lower frequency bound of the note.
12	Note peak frequency (f _{peak})	Frequency at which peak energy (maximum power) occurs across the note.
Composite measures		
13	Overall song pace (Pace)*	Number of notes in the entire song divided by the song duration (NN/D).
14	Song pace in 1 st tercile (Pace 1)	Pace of notes in the first third of the song, i.e. (NN/3)

15	Song pace in 2 nd tercile (Pace 2)	divided by the duration of the first NN/3 notes. Pace of notes in the second third of the song, i.e. (NN/3) divided by the duration of the second NN/3 notes.
16	Song pace in 3 rd tercile (Pace 3)	Pace of notes in the last third of the song, i.e. (NN/3) divided by the duration of the last NN/3 notes.
17	Pace change 1 (Pch1)*	Change in pace between first and second tercile, calculated as P1/P2.
18	Pace change 2 (Pch2)*	Change in pace between second and last tercile, calculated as P2/P3.
19	Song bandwidth (BW)	Spectral range of the entire song, calculated as Fmax minus Fmin.
20	Mean note duration (d_{mean})*	Mean duration of notes, averaged across entire song
21	Variance in note duration (d_{var})*	Variance in note duration across entire song.
22	Mean internote interval (int_{mean})	Mean inter-note interval, averaged across entire song
23	Internote interval variance (int_{var})	Variance in internote interval across entire song
24	Mean note maximum frequency ($f_{\text{max}_{\text{mean}}}$)*	Upper frequency bound of the notes, averaged across the entire song
25	Mean note minimum frequency ($f_{\text{min}_{\text{mean}}}$)*	Lower frequency bound of the notes, averaged across the entire song
26	Mean note peak time ($t_{\text{peak}_{\text{mean}}}$)	Time at which peak energy occurs as a fraction of note duration, averaged across entire song
27	Note peak time variance ($t_{\text{peak}_{\text{var}}}$)	Variance in note peak time across entire song.
28	Mean note peak frequency ($f_{\text{peak}_{\text{mean}}}$)	Note peak frequency averaged across entire song.
29	Note peak frequency variance ($f_{\text{peak}_{\text{var}}}$)*	Variance in note peak frequency across entire song.
30	Note bandwidth (bw)	Spectral range of the note, calculated as fmax minus fmin.
31	Mean note bandwidth (bw_{mean})*	Note bandwidth averaged across entire song.
32	Note bandwidth variance (bw_{var})*	Variance in note bandwidth across entire song.

Note: Asterisks denote measures included in the phylogenetic principal components analysis (PCA; see Organization of datasets - summarising variation in beaks and songs)

SI Table 2: Summary of repeated measurements of lineages and total number of observations in the four datasets used to examine phenotypic divergence in traits.

Dataset	Minimum	Maximum	Median	Total
1	1	2	2	518
2	1	2	1	344
3	1	2	1	272
4	9	126	124	34588
5	1	1	1	111

SI Table 3: Summary of differences in morphology and song between closely related allopatric and sympatric ovenbird lineages

Trait	Parameter		DF	F	P
	Estimate (β) \pm SE				
<i>Evolutionary age</i>					
Sympatry	A	1.89 \pm 0.06	1, 290	286.1	<0.0001
	Diff S	1.18 \pm 0.07			
<i>Tarsus length</i>					
Sympatry	A	1.14 \pm 0.05	1, 302	30.95	<0.0001
	Diff S	0.33 \pm 0.06			
<i>Beak morphology</i>					
Sympatry	A	1.43 \pm 0.06	1, 305	49.65	<0.0001
	Diff S	0.53 \pm 0.07			
<i>Song structure</i>					
Sympatry	A	2.89 \pm 0.04	1, 285	6.90	0.009
	Diff S	0.12 \pm 0.05			

Notes: Output from a phylogenetic linear mixed model (PLMM) using restricted maximum likelihood estimation (REML) implemented in ASReml-R. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S).

SI Table 4: Comparison of tarsus length in closely related sympatric versus allopatric lineages, controlling for habitat and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.34 \pm 0.05	1, 16	38.05	<0.0001
Evolutionary age ²		1, 7	0.00	0.99
Sympatry		1, 14	0.01	0.93
Habitat differences		5, 22	2.21	0.09
Sympatry*Evolutionary age		1, 16	0.26	0.62
Sympatry*Evolutionary age ²		1, 28	2.16	0.15
Sympatry*Habitat differences		5, 23	0.86	0.52
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.20 \pm 0.09	1	17.78	<0.0001
Lineage 1	0.03 \pm 0.03	1	1.09	0.30
Lineage 2	0.07 \pm 0.03	1	7.97	0.005
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.29 \pm 0.04			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the models.

SI Table 5: Comparison of beak morphology in closely related sympatric versus allopatric ovenbird lineages, controlling for habitat, tarsus and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.31 \pm 0.06	1, 35	26.67	<0.0001
Evolutionary age ²		1, 17	2.19	0.16
Sympatry		1, 39	0.33	0.57
Habitat differences		5, 58	2.29	0.06
Tarsus	0.41 \pm 0.04	1, 28	135.40	<0.0001
Sympatry*Evolutionary age		1, 33	1.35	0.25
Sympatry*Evolutionary age ²		1, 60	0.58	0.45
Sympatry*Habitat differences	A: 1 vs 1 Diff S:			
	A: 1 vs 2 Diff S:			
	A: 1 vs 3 Diff S:			
	A: 2 vs 2 Diff S:	5, 47	2.46	0.04
	A: 2 vs 3 Diff S:			
	A: 3 vs 3 Diff S:			
Sympatry*Tarsus		1, 73	0.91	0.34
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.15 \pm 0.08	1	11.01	0.0009
Lineage 1	0.05 \pm 0.04	1	2.50	0.11
Lineage 2	0.01 \pm 0.02	1	0.27	0.60
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.40 \pm 0.05			

Notes: Output from a PLMM using REML implemented in ASReml-R. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S). Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 6: Comparison of song structure in closely related sympatric versus allopatric ovenbird lineages, controlling for habitat, morphology and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.29 \pm 0.05	1, 30	40.03	<0.0001
Evolutionary age ²	-0.12 \pm 0.02	1, 15	28.48	<0.0001
Sympatry	A	3.15 \pm 0.13	1, 33	0.02
	Diff S	-0.13 \pm 0.06		
Habitat differences		5, 62	0.95	0.46
Beak morphology		1, 29	0.01	0.94
Tarsus	0.08 \pm 0.03	1, 29	6.02	0.02
Sympatry*Evolutionary age		1, 28	1.12	0.30
Sympatry*Evolutionary age ²		1, 53	0.83	0.37
Sympatry*Habitat differences		5, 33	0.56	0.73
Sympatry*Beak morphology	A	-0.11 \pm 0.06	1, 57	0.01
	Diff S	0.18 \pm 0.07		
Sympatry*Tarsus		1, 55	0.83	0.37
Random Terms	Variance Component	DF	LRT	P
Phylogeny	0.08 \pm 0.05	1	8.22	0.004
Lineage 1	0.09 \pm 0.02	1	16.96	<0.0001
Lineage 2	0.08 \pm 0.02	1	17.56	<0.0001
Error in evolutionary age	0.001 \pm 0.003	1	0.59	0.89
Residual variance (V_e)	0.15 \pm 0.02			

Notes: Output from a PLMM using REML implemented in ASReml-R. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S). Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 7: Comparison of models of evolution best explaining variation in raw values of tarsus length, beak morphology and song structure (defined by PC1 and PC2), as determined using three different analytical frameworks

Trait	Method	Evolutionary	α
		Model	
Tarsus length	PGLS ³	BM	-
	Max Likelihood ⁴	BM	-
	PLMM ⁵	BM	-
Beak morphology	PGLS	BM	-
	Max Likelihood	BM	-
	PLMM	BM	-
Song PC1	PGLS	OU	0.21
	Max Likelihood	OU	0.22
	PLMM	OU	0.20
Song PC2	PGLS	OU	0.11
	Max Likelihood	OU	0.11
	PLMM	OU	0.10

Notes: Evolutionary models are Ornstein-Uhlenbeck (OU) and Brownian motion (BM); α denotes constraint parameter in OU models. PGLS models were implemented in R-packages ‘ape’ and ‘nlme’; Maximim Likelihood models using ‘fitContinuous’ function in R package ‘Geiger’; and PLMMs in ASReml-R.

SI Table 8: Results of PLMMs identifying models of evolution best explaining variation in phenotypic divergence at three taxonomic scales: sister species, closest relatives and all lineages

Trait	Method	Sister Species	Closest relatives	All lineages
Tarsus length	PLMM	OU (0.21)	BM	BM
	PGLS	OU (0.21)	-	-
Beak morphology	PLMM	OU (0.26)	BM	BM
	PGLS	OU (0.26)	-	-
Song structure	PLMM	OU (1.36)	OU (0.15)	OU (0.10)
	PGLS	OU (1.36)	-	-

SI Table 9: Comparison of song structure in closely related sympatric versus allopatric lineages controlling for habitat, morphology and evolutionary age, and accounting for the best-fit model of trait evolution

Fixed Terms		Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age		0.11 \pm 0.04	1, 14	8.60	0.03
Evolutionary age ²		-0.12 \pm 0.02	1, 13	29.63	<0.0001
Sympatry	A	3.15 \pm 0.07	1, 11	6.33	0.03
	Diff S	-0.14 \pm 0.06			
Habitat differences			5, 17	0.83	0.54
Beak morphology			1, 9	0.005	0.95
Tarsus		0.08 \pm 0.03	1, 9	6.32	0.03
Sympatry*Evolutionary age			1, 11	0.31	0.59
Sympatry*Evolutionary age ²			1, 17	0.61	0.45
Sympatry*Habitat differences			5, 11	0.60	0.41
Sympatry*Beak morphology	A	-0.12 \pm 0.06	1, 17	6.88	0.02
	Diff S	0.18 \pm 0.07			
Sympatry*Tarsus			1, 17	0.92	0.35
Random Terms		Variance Component	DF	LRT	P
Phylogeny		0.15 \pm 0.08	1	4.85	0.03
Lineage 1		0.09 \pm 0.02	1	18.89	<0.0001
Lineage 2		0.09 \pm 0.02	1	24.49	<0.0001
Error in evolutionary age		0.002 \pm 0.003	1	0.99	0.32
Residual variance (V_e)		0.13 \pm 0.02			

Notes: Output from a PLMM using REML implemented in ASReML-R. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S).

Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. Best-fit model of song evolution was an OU process ($\alpha = 0.15$).

SI Table 10: Comparison of song structure in sympatric versus allopatric lineages controlling for habitat, morphology and evolutionary age, and accounting for the best-fit model of song evolution with differing constraint parameters (α) in allopatry versus sympatry

Dataset	Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Close relatives	Allopatry	3.17 \pm 0.06	1, 33	6.62	0.01
	Sympatry	3.03 \pm 0.05			
	Evolutionary age: Allopatry	0.28 \pm 0.05	1, 33	0.002	0.96
	Evolutionary age: Sympatry	0.28 \pm 0.05			
	Evolutionary age ² : Allopatry	-0.12 \pm 0.02	1, 33	0.001	0.98
	Evolutionary age ² : Sympatry	-0.12 \pm 0.02			
All lineages	Allopatry	3.25 \pm 0.06	1, 33981	27.21	<0.0001
	Sympatry	3.20 \pm 0.03			
	Evolutionary age: Allopatry	0.06 \pm 0.02	1, 33981	11.6	0.0006
	Evolutionary age: Sympatry	0.02 \pm 0.01			
	Evolutionary age ² : Allopatry	-0.04 \pm 0.009	1,33981	1.71	0.19
	Evolutionary age ² : Sympatry	-0.03 \pm 0.008			

Notes: Outputs from PLMMs using REML implemented in ASReml-R. For simplicity, only parameter estimates involving the effect of allopatry/sympatry are presented. The best-fit model of song evolution was estimated independently for allopatric and sympatric comparisons and both were found to follow an OU process for closest relatives ($\alpha = 0.30$ in allopatry, 0.40 in sympatry) and all lineages ($\alpha = 0.10$ in allopatry, 0.20 in sympatry).

SI Table 11: Comparison of tarsus length in closely related sympatric versus allopatric lineages, controlling for habitat and evolutionary age, excluding intraspecific lineages

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.29 \pm 0.07	1, 38	18.99	<0.0001
Evolutionary age ²		1, 15	0.01	0.90
Sympatry		1, 29	0.05	0.82
Habitat differences		5, 45	0.84	0.53
Sympatry*Evolutionary age		1, 29	1.95	0.17
Sympatry*Evolutionary age ²	A 0.07 \pm 0.05	1, 20	6.03	0.02
	Diff S -0.17 \pm 0.07			
Sympatry*Habitat differences		5, 32	0.49	0.78
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.13 \pm 0.09	1	6.54	0.01
Lineage 1	0.06 \pm 0.05	1	1.64	0.20
Lineage 2	0.09 \pm 0.04	1	5.69	0.02
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.30 \pm 0.06			

Notes: Output from a PLMM using REML implemented in ASReML-R. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S). Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 12: Comparison of beak morphology in closely related sympatric versus allopatric ovenbird lineages, controlling for habitat, tarsus and evolutionary age, excluding intraspecific lineages

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.28 \pm 0.06	1, 315	19.23	<0.0001
Evolutionary age ²		1, 320	1.66	0.20
Sympatry		1, 320	0.35	0.55
Habitat differences		5, 249	1.54	0.20
Tarsus	0.46 \pm 0.04	1, 323	109.60	<0.0001
Sympatry*Evolutionary age		1, 321	2.37	0.12
Sympatry*Evolutionary age ²		1, 320	0.009	0.92
Sympatry*Habitat differences		5, 319	1.52	0.18
Sympatry*Tarsus		1, 319	1.69	0.20
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.00 \pm 0.00	1	0.00	1.00
Lineage 1	0.00 \pm 0.00	1	0.00	1.00
Lineage 2	0.03 \pm 0.04	1	0.69	0.41
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.53 \pm 0.05			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 13: Comparison of song structure in closely related sympatric versus allopatric ovenbird lineages, controlling for habitat, morphology and evolutionary age, excluding intraspecific lineages

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.27 \pm 0.05	1, 327	30.68	<0.0001
Evolutionary age ²	-0.12 \pm 0.03	1, 316	21.87	<0.0001
Sympatry	A	3.27 \pm 0.07	1, 239	5.08
	Diff S	-0.15 \pm 0.06		
Habitat differences		5, 284	1.58	0.17
Beak morphology		1, 290	1.36	0.91
Tarsus	0.11 \pm 0.04	1, 318	7.99	0.005
Sympatry*Evolutionary age		1, 121	2.21	0.14
Sympatry*Evolutionary age ²		1, 114	3.16	0.08
Sympatry*Habitat differences		5, 127	0.84	0.52
Sympatry*Beak morphology	A	-0.11 \pm 0.07	1, 178	5.06
	Diff S	0.19 \pm 0.08		
Sympatry*Tarsus		1, 171	2.31	0.13
Random Terms	Variance Component	DF	LRT	P
Phylogeny	0.01 \pm 0.02	1	4.21	0.04
Lineage 1	0.07 \pm 0.03	1	5.89	0.02
Lineage 2	0.09 \pm 0.03	1	12.50	0.0004
Error in evolutionary age	0.004 \pm 0.007	1	2.18	0.14
Residual variance (V_e)	0.15 \pm 0.03			

Notes: Output from a PLMM using REML implemented in ASReml-R. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S). Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 14: Comparison of tarsus length, beak morphology and song structure in all 111 true sister species living in sympatry versus allopatry accounting for the best-fit model of trait evolution using phylogenetic generalized least squares (PGLS) and phylogenetic linear mixed models (PLMM)

Analysis	Trait	Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
PGLS	Tarsus	Sympatry		1, 102	1.10	0.30
		Evolutionary age	0.10 \pm 0.06	1, 103	4.47	0.03
		Evolutionary age ²		1, 102	0.01	0.94
		Sympatry*Evolutionary age		1, 102	0.93	0.34
		Sympatry*Evolutionary age ²		1, 101	1.38	0.24
PGLS	Beak	Sympatry		1, 102	0.01	0.93
		Evolutionary age	0.19 \pm 0.07	1, 103	7.38	0.008
		Evolutionary age ²		1, 102	0.26	0.61
		Sympatry*Evolutionary age		1, 101	3.48	0.06
		Sympatry*Evolutionary age ²		1, 100	0.10	0.76
PGLS	Song	Sympatry	-0.36 \pm 0.18	1, 101	4.19	0.04
		Evolutionary age	0.25 \pm 0.07	1, 102	9.81	0.002
		Evolutionary age ²	-0.10 \pm 0.05	1, 102	4.08	0.05
		Sympatry*Evolutionary age	-0.49 \pm 0.17	1, 100	8.06	0.006
		Sympatry*Evolutionary age ²		1, 99	0.001	0.98
PLMM	Tarsus	Sympatry		1, 57	1.00	0.32
		Evolutionary age	0.10 \pm 0.06	1, 96	3.00	0.09
		Evolutionary age ²		1, 84	0.003	0.95
		Sympatry*Evolutionary age		1, 65	0.99	0.32
		Sympatry*Evolutionary age ²		1, 72	1.41	0.24
PLMM	Beak	Sympatry		1, 96	0.001	0.99
		Evolutionary age	0.19 \pm 0.07	1, 103	7.02	0.009
		Evolutionary age ²		1, 99	0.31	0.58
		Sympatry*Evolutionary age		1, 97	2.01	0.16
		Sympatry*Evolutionary age ²		1, 99	0.02	0.91
PLMM	Song	Sympatry	-0.36 \pm 0.18	1, 101	4.19	0.04
		Evolutionary age	0.25 \pm 0.07	1, 102	12.90	0.0005
		Evolutionary age ²	-0.10 \pm 0.05	1, 101	4.61	0.03
		Sympatry*Evolutionary age	-0.49 \pm 0.17	1, 100	8.09	0.005
		Sympatry*Evolutionary age ²		1, 100	0.001	0.98

Notes: Output from three separate phylogenetic generalized least squares (PGLS) models

implemented with R packages 'ape' and 'nlme'. Best-fit model of divergence in tarsus = OU (0.21); beak = OU (0.26); and for song divergence = OU ($\alpha = 1.36$). All models include allopatry/sympatry and habitat differences, model of beak morphology includes differences in tarsus length, model of song includes differences in beak morphology and tarsus length.

SI Table 15: Comparison of tarsus length, beak morphology and song structure in sympatry versus allopatry, restricting the true sister species dataset to those with beta-conserved niches and occurring within 250 km of each other, following Pigot & Tobias⁵⁹ ($n = 58$ sisters).

Trait	Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Tarsus	Sympatry		1, 54	1.43	0.24
	Evolutionary age		1, 54	1.86	0.18
	Evolutionary age ²		1, 54	3.66	0.06
	Sympatry*Evolutionary age		1, 52	0.004	0.99
	Sympatry*Evolutionary age ²	A: -0.07 ± 0.08 Diff S: 0.28 ± 0.13	1, 51	4.31	0.04
Beak	Sympatry ¹	A: 1.12 ± 0.11 Diff S: 0.33 ± 0.18	1, 53	3.43	0.07
	Evolutionary age		1, 53	2.91	0.10
	Evolutionary age ²		1, 53	1.47	0.23
	Sympatry*Evolutionary age		1, 50	3.38	0.07
	Sympatry*Evolutionary age ²		1, 50	0.91	0.34
Song	Sympatry		1, 51	0.07	0.79
	Evolutionary age		1, 52	2.57	0.12
	Evolutionary age ²		1, 50	1.27	0.27
	Sympatry*Evolutionary age		1, 48	3.55	0.07
	Sympatry*Evolutionary age ²		1, 47	0.40	0.53

Notes: Output from a PLMM implemented in ASReml-R. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S). Song model accounts for the OU model of evolution, with constraint parameter (α) = 0.5. Effect of sympatry on beak morphology without tarsus difference in model: $F_{1,54} = 4.47$, $P = 0.03$. A: 1.01 ± 0.14 . Diff S: 0.46 ± 0.2 .

SI Table 16: Comparison of tarsus length in closely related sympatric versus allopatric lineages <6 Myr old, controlling for habitat and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.08 \pm 0.04	1, 45	4.05	0.05
Evolutionary age ²		1, 34	0.20	0.66
Sympatry		1, 64	1.35	0.25
Habitat differences		5, 67	1.10	0.37
Sympatry*Evolutionary age		1, 61	0.48	0.49
Sympatry*Evolutionary age ²		1, 32	2.69	0.11
Sympatry*Habitat differences		5, 42	1.36	0.26
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.08 \pm 0.05	1	13.85	0.0002
Lineage 1	0.00 \pm 0.00	1	0.00	1.00
Lineage 2	0.02 \pm 0.03	1	0.98	0.32
Error in evolutionary age	0.00 \pm 0.00	1	0.03	0.86
Residual variance (V_e)	0.23 \pm 0.03			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 17: Comparison of beak morphology in closely related sympatric versus allopatric ovenbird lineages <6 Myr old, controlling for habitat, tarsus and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.09 \pm 0.04	1, 254	4.55	0.03
Evolutionary age ²		1, 180	0.24	0.62
Sympatry		1, 147	0.008	0.93
Habitat differences		5, 226	1.12	0.35
Tarsus	0.28 \pm 0.04	1, 191	60.91	<0.0001
Sympatry*Evolutionary age		1, 131	0.38	0.54
Sympatry*Evolutionary age ²		1, 189	0.004	0.94
Sympatry*Habitat differences		5, 130	1.35	0.25
Sympatry*Tarsus		1, 106	0.19	0.67
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.00 \pm 0.00	1	0.00	1.00
Lineage 1	0.16 \pm 0.05	1	10.95	0.0009
Lineage 2	0.10 \pm 0.03	1	13.67	0.0002
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.11 \pm 0.04			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 18: Comparison of song structure in closely related sympatric versus allopatric ovenbird lineages <6 Myr old, controlling for habitat, morphology, and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.15 \pm 0.04	1, 259	15.25	0.0001
Evolutionary age ²	-0.07 \pm 0.03	1, 207	4.48	0.04
Sympatry		1, 170	0.35	0.56
Habitat differences		5, 227	0.80	0.55
Beak morphology		1, 258	3.34	0.07
Tarsus		1, 235	2.57	0.11
Sympatry*Evolutionary age		1, 176	0.30	0.58
Sympatry*Evolutionary age ²		1, 220	0.11	0.74
Sympatry*Habitat differences		5, 162	0.55	0.70
Sympatry*Beak morphology		1, 186	0.50	0.48
Sympatry*Tarsus		1, 157	0.29	0.59
Random Terms	Variance Component	DF	LRT	P
Phylogeny	0.00 \pm 0.00	1	0.00	1.00
Lineage 1	0.09 \pm 0.04	1	7.73	0.005
Lineage 2	0.13 \pm 0.03	1	25.99	<0.0001
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.11 \pm 0.04			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model.

SI Table 19: Comparison of tarsus length in all sympatric versus allopatric ovenbird lineages controlling for habitat, and evolutionary age

Fixed Terms		Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age		0.32 \pm 0.07	1, 191	22.75	<0.0001
Evolutionary age ²			1, 189	0.63	0.43
Sympatry			1, 33788	0.009	0.93
Habitat differences	1 vs 1	1.55 \pm 0.61			
	1 vs 2	1.60 \pm 0.61			
	1 vs 3	1.84 \pm 0.61			
	2 vs 2	1.70 \pm 0.61	5, 2897	35.36	<0.0001
	2 vs 3	1.89 \pm 0.61			
	3 vs 3	1.84 \pm 0.61			
Sympatry*Evolutionary age			1, 33778	3.00	0.08
Sympatry*Evolutionary age ²	A	-0.03 \pm 0.03			
	Diff S	-0.03 \pm 0.01	1, 29630	16.05	<0.0001
Sympatry*Habitat differences	A: 1 vs 1	1.57 \pm 0.61			
	Diff S:	0.05 \pm 0.02			
	A: 1 vs 2	1.62 \pm 0.61			
	Diff S:	0.003 \pm 0.03			
	A: 1 vs 3	1.85 \pm 0.61			
	Diff S:	0.11 \pm 0.06	5, 33591	2.59	0.02
	A: 2 vs 2	1.72 \pm 0.62			
	Diff S:	-0.02 \pm 0.04			
	A: 2 vs 3	1.91 \pm 0.61			
	Diff S:	0.01 \pm 0.04			
	A: 3 vs 3	1.88 \pm 0.62			
	Diff S:	-0.16 \pm 0.05			
Random Terms		Variance Component \pm SE	DF	LRT	P
Phylogeny		3.53 \pm 0.43	1	3056.4	<0.0001
Lineage 1 intercept		0.15 \pm 0.01	1	10946.2	<0.0001
Lineage 1 Evolutionary age slope		0.02 \pm 0.002	1	471.4	<0.0001
Covariance between intercept & slope		0.01 \pm 0.004	1	11.3	<0.0001
Lineage 2 intercept		0.15 \pm 0.01	1	10933.8	<0.0001
Lineage 2 Evolutionary age slope		0.02 \pm 0.002	1	438.8	<0.0001
Covariance between intercept & slope		0.01 \pm 0.004	1	9.5	0.002
Error in evolutionary age		0.00 \pm 0.00	1	0.14	0.71
Residual variance (V_e)		0.30 \pm 0.002			

Notes: Output from a PLMM using REML implemented in ASReML-R. Significance of random effects tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. Parameter estimates of effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and mean estimate of divergence in sympatry (Diff S). The assumption of BM model of trait evolution in PLMM is valid as tarsus length evolves under BM in ovenbirds (SI Table 7 and 8).

SI Table 20: Comparison of beak morphology in all sympatric versus allopatric ovenbird lineages controlling for habitat, morphology and evolutionary age

Fixed Terms		Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age		0.34 \pm 0.11	1, 241	9.31	0.003
Evolutionary age ²			1, 220	0.54	0.46
Sympatry	A	2.47 \pm 1.00	1, 33638	6.04	0.01
	Diff S	-0.03 \pm 0.01			
Habitat differences	1 vs 1	2.19 \pm 0.93	5, 2594	14.06	<0.0001
	1 vs 2	2.20 \pm 0.93			
	1 vs 3	1.94 \pm 0.93			
	2 vs 2	2.26 \pm 0.93			
	2 vs 3	2.01 \pm 0.93			
	3 vs 3	1.90 \pm 0.93			
Tarsus		0.25 \pm 0.006	1, 33051	1664.00	<0.0001
Sympatry*Evolutionary age			1, 33934	3.45	0.06
Sympatry* Evolutionary age ²	A	-0.04 \pm 0.05	1, 30382	4.50	0.03
	Diff S	0.02 \pm 0.01			
Sympatry*Habitat differences			5, 33414	1.22	0.29
Sympatry*Tarsus	A	0.24 \pm 0.006	1, 33480	45.14	<0.0001
	Diff S	0.09 \pm 0.01			
Random Terms		Variance Component \pm SE	DF	LRT	P
Phylogeny		9.48 \pm 1.04	1	5021.9	<0.0001
Lineage 1 intercept		0.13 \pm 0.01	1	8037.1	<0.0001
Lineage 1 Evolutionary age slope		0.15 \pm 0.01	1	2812.3	<0.0001
Covariance between intercept & slope		0.05 \pm 0.01	1	36.00	<0.0001
Lineage 2 intercept		0.13 \pm 0.01	1	8105.7	<0.0001
Lineage 2 Evolutionary age slope		0.15 \pm 0.01	1	2775.2	<0.0001
Covariance between intercept & slope		0.06 \pm 0.01	1	39.2	<0.0001
Error in evolutionary age		0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)		0.43 \pm 0.003			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S). The assumption of BM model of trait evolution in PLMM is valid as beak morphology evolves under BM in ovenbirds (SI Table 7 and 8).

SI Table 21: Comparison of song structure in all sympatric versus allopatric ovenbird lineages controlling for habitat, morphology and evolutionary age, and accounting for the best-fit model of trait evolution

Fixed Terms		Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age		0.07 \pm 0.02	1, 183	8.78	0.003
Evolutionary age ²		0.04 \pm 0.01	1, 217	18.76	0.0002
Sympatry	A	3.25 \pm 0.06	1, 33994	27.13	<0.0001
	Diff S	-0.04 \pm 0.007			
Habitat	1 vs 1	3.25 \pm 0.06	5, 3078	30.11	<0.0001
	1 vs 2	3.31 \pm 0.06			
	1 vs 3	3.24 \pm 0.06			
	2 vs 2	3.37 \pm 0.07			
	2 vs 3	3.24 \pm 0.07			
	3 vs 3	3.04 \pm 0.08			
Beak morphology		0.01 \pm 0.003	1, 23818	7.62	0.006
Tarsus			1, 33512	3.06	0.08
Sympatry*Evolutionary age			1, 31092	0.81	0.37
Sympatry*Evolutionary age ²	A	-0.04 \pm 0.01	1, 26077	3.87	0.05
	Diff S	-0.01 \pm 0.05			
Sympatry*Habitat differences			5, 33842	0.85	0.52
Sympatry*Beak morphology			1, 34012	0.65	0.42
Sympatry*Tarsus			1, 33724	0.86	0.77
Random Terms		Variance Component \pm SE	DF	LRT	P
Phylogeny		0.57 \pm 0.08	1	964.60	<0.0001
Lineage 1 intercept		0.09 \pm 0.007	1	14666.75	<0.0001
Lineage 1 Evolutionary age slope		0.002 \pm 0.0003	1	193.73	<0.0001
Covariance between intercept & slope		0.002 \pm 0.001	1	2.50	0.11
Lineage 2 intercept		0.09 \pm 0.007	1	14608.34	<0.0001
Lineage 2 Evolutionary age slope		0.002 \pm 0.003	1	168.52	<0.0001
Covariance between intercept & slope		0.0008 \pm 0.001	1	0.48	0.49
Error in evolutionary age		0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)		0.12 \pm 0.0009			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. Parameter estimates of the effect of sympatry on trait divergence are the mean estimates of divergence in allopatry (A) and the difference between A and the mean estimate of divergence in sympatry (Diff S). Best-fit model of song evolution was an OU process ($\alpha = 0.10$).

SI Table 22: Comparison of tarsus length among closely related ovenbird lineages in relation to extent of range overlap, controlling for habitat and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.23 \pm 0.06	1, 37	14.91	0.0004
Evolutionary age ²		1, 17	0.13	0.72
Range overlap		1, 56	2.94	0.09
Habitat differences		5, 57	0.87	0.51
Range overlap*Evolutionary age		1, 52	0.27	0.60
Range overlap*Evolutionary age ²	-0.19 \pm 0.10	1, 46	4.13	0.05
Range overlap*Habitat differences		5, 76	0.59	0.71
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.08 \pm 0.07	1	5.59	0.02
Lineage 1	0.06 \pm 0.05	1	1.49	0.22
Lineage 2	0.08 \pm 0.04	1	4.65	0.03
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.32 \pm 0.06			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. The assumption of BM model of trait evolution in PLMM is valid as tarsus length evolves under BM in ovenbirds (SI Table 7 and 8).

SI Table 23: Comparison of beak morphology among closely related ovenbird lineages in relation to extent of range overlap, controlling for habitat, tarsus and evolutionary age

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.31 \pm 0.06	1, 328	26.35	< 0.0001
Evolutionary age ²		1, 318	2.51	0.11
Range overlap		1, 327	0.31	0.58
Habitat differences		5, 246	1.59	0.16
Tarsus	0.46 \pm 0.04	1, 323	110.10	< 0.0001
Range overlap*Evolutionary age		1, 319	3.13	0.07
Range overlap*Evolutionary age ²		1, 325	0.31	0.58
Range overlap*Habitat differences		5, 318	0.58	0.78
Range overlap*Tarsus		1, 326	0.01	0.92
Random Terms	Variance Component \pm SE	DF	LRT	P
Phylogeny	0.00 \pm 0.00	1	0.00	1.00
Lineage 1	0.00 \pm 0.00	1	0.00	1.00
Lineage 2	0.05 \pm 0.04	1	0.83	0.36
Error in evolutionary age	0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)	0.52 \pm 0.05			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. The assumption of BM model of trait evolution in PLMM is valid as beak morphology evolves under BM model in ovenbirds (SI Table 7 and 8).

SI Table 24: Comparison of song structure in closely related lineages in relation to extent of range overlap, controlling for habitat, morphology and evolutionary age, and accounting for the best-fit model of trait evolution

Fixed Terms	Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age	0.12 \pm 0.04	1, 132	8.13	0.0005
Evolutionary age ²	-0.12 \pm 0.03	1, 217	22.69	<0.0001
Range overlap	-0.27 \pm 0.09	1, 302	10.04	0.002
Habitat differences		5, 160	1.53	0.18
Beak morphology		1, 284	0.05	0.82
Tarsus	0.12 \pm 0.04	1, 312	9.70	0.002
Range overlap*Evolutionary age		1, 270	0.25	0.62
Range overlap*Evolutionary age ²		1, 305	1.27	0.26
Range overlap*Habitat differences		5, 246	0.93	0.46
Range overlap*Beak morphology		1, 291	0.35	0.55
Range overlap*Tarsus		1, 284	1.12	0.29
Random Terms	Variance Component	DF	LRT	P
Phylogeny	0.02 \pm 0.07	1	0.06	0.81
Lineage 1	0.07 \pm 0.03	1	5.63	0.02
Lineage 2	0.09 \pm 0.03	1	12.01	0.0005
Error in evolutionary age	0.004 \pm 0.007	1	0.00	1.00
Residual variance (V_e)	0.16 \pm 0.03			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. Best-fit model of song evolution with all terms in fitted was an OU process ($\alpha = 0.10$).

SI Table 25: Comparison of tarsus length among all ovenbird lineages in relation to extent of range overlap, controlling for habitat and evolutionary age

Fixed Terms		Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age		0.32 \pm 0.07	1, 191	22.76	<0.0001
Evolutionary age ²			1, 189	0.64	0.42
Range overlap			1, 33775	0.28	0.60
Habitat differences	1 vs 1	1.56 \pm 0.61	5, 2897	35.07	<0.0001
	1 vs 2	1.61 \pm 0.61			
	1 vs 3	1.84 \pm 0.61			
	2 vs 2	1.71 \pm 0.61			
	2 vs 3	1.90 \pm 0.61			
	3 vs 3	1.84 \pm 0.61			
Range overlap*Evolutionary age			1, 33578	3.67	0.06
Range overlap*Evolutionary age ²			1, 31784	4.59	0.03
Range overlap*Habitat differences	1 vs 1	0.006 \pm 0.03	5, 33576	3.30	0.006
	1 vs 2	-0.01 \pm 0.04			
	1 vs 3	0.01 \pm 0.07			
	2 vs 2	-0.02 \pm 0.05			
	2 vs 3	0.17 \pm 0.05			
	3 vs 3	-0.06 \pm 0.07			
Random Terms		Variance Component \pm SE	DF	LRT	P
Phylogeny		3.52 \pm 0.42	1	3080.89	<0.0001
Lineage 1 intercept		0.15 \pm 0.01	1	10954.64	<0.0001
Lineage 1 Evolutionary age slope		0.02 \pm 0.002	1	467.92	<0.0001
Covariance between intercept & slope		0.01 \pm 0.004	1	11.60	0.0006
Lineage 2 intercept		0.15 \pm 0.01	1	10926.38	<0.0001
Lineage 2 Evolutionary age slope		0.02 \pm 0.002	1	440.65	<0.0001
Covariance between intercept & slope		0.01 \pm 0.004	1	9.83	0.002
Error in evolutionary age		0.00 \pm 0.00	1	0.10	0.75
Residual variance (V_e)		0.30 \pm 0.002			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. The assumption of BM model of trait evolution in PLMM is valid as tarsus length evolves under BM in ovenbirds (SI Table 12 and 13).

SI Table 26: Comparison of beak morphology in all ovenbird lineages in relation to extent of range overlap, controlling for habitat, morphology and evolutionary age

Fixed Terms		Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age		0.34 \pm 0.11	1, 241	9.30	0.003
Evolutionary age ²			1, 220	0.54	0.46
Range overlap		-0.05 \pm 0.02	1, 33713	6.42	0.01
Habitat differences	1 vs 1	2.47 \pm 1.00	5, 2596	14.67	<0.0001
	1 vs 2	2.47 \pm 1.00			
	1 vs 3	2.21 \pm 1.00			
	2 vs 2	2.54 \pm 1.00			
	2 vs 3	2.29 \pm 1.00			
	3 vs 3	2.18 \pm 1.00			
Tarsus		0.25 \pm 0.006	1, 33050	1663.00	<0.0001
Range overlap*Evolutionary age			1, 33951	1.56	0.21
Range overlap*Evolutionary age ²		0.04 \pm 0.02	1, 32215	6.12	0.01
Range overlap*Habitat differences	1 vs 1	-0.02 \pm 0.03	5, 33423	2.99	0.01
	1 vs 2	-0.10 \pm 0.05			
	1 vs 3	-0.14 \pm 0.08			
	2 vs 2	-0.17 \pm 0.06			
	2 vs 3	-0.17 \pm 0.06			
	3 vs 3	0.02 \pm 0.08			
Range overlap*Tarsus		0.11 \pm 0.02	1, 33378	39.15	<0.0001
Random Terms		Variance Component \pm SE	DF	LRT	P
Phylogeny		9.52 \pm 1.04	1	5025.28	<0.0001
Lineage 1 intercept		0.13 \pm 0.01	1	8071.24	<0.0001
Lineage 1 Evolutionary age slope		0.15 \pm 0.01	1	2816.34	<0.0001
Covariance between intercept & slope		0.06 \pm 0.01	1	38.98	<0.0001
Lineage 2 intercept		0.13 \pm 0.01	1	8127.38	<0.0001
Lineage 2 Evolutionary age slope		0.15 \pm 0.01	1	2786.34	<0.0001
Covariance between intercept & slope		0.06 \pm 0.01	1	40.45	<0.0001
Error in evolutionary age		0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)		0.43 \pm 0.003			

Notes: Output from a PLMM using REML implemented in ASReml-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. The assumption of BM model of trait evolution in PLMM is valid as beak morphology evolves under BM in ovenbirds (SI Table 12 and 13).

SI Table 27: Comparison of song structure in all ovenbird lineages in relation to extent of range overlap, controlling for habitat, morphology and evolutionary age, and accounting for the best-fit model of trait evolution

Fixed Terms		Parameter Estimate (β) \pm SE	DF	F	P
Evolutionary age		0.02 \pm 0.01	1, 318	4.09	0.04
Evolutionary age ²		-0.03 \pm 0.01	1, 262	16.13	<0.0001
Range overlap		-0.05 \pm 0.01	1, 33962	23.13	<0.0001
Habitat	1 vs 1	3.23 \pm 0.03			
	1 vs 2	3.29 \pm 0.03			
	1 vs 3	3.24 \pm 0.03			
	2 vs 2	3.36 \pm 0.05	5, 2939	30.08	<0.0001
	2 vs 3	3.24 \pm 0.04			
	3 vs 3	3.06 \pm 0.06			
Beak morphology		0.01 \pm 0.003	1, 18815	7.26	0.007
Tarsus			1, 31042	1.48	0.18
Range overlap*Evolutionary age			1, 26997	0.05	0.94
Range overlap*Evolutionary age ²			1, 29694	1.01	0.32
Range overlap*Habitat differences	1 vs 1	-0.02 \pm 0.02			
	1 vs 2	-0.02 \pm 0.03			
	1 vs 3	-0.12 \pm 0.04			
	2 vs 2	0.04 \pm 0.03	5, 33818	2.89	0.01
	2 vs 3	-0.06 \pm 0.03			
	3 vs 3	-0.02 \pm 0.04			
Range overlap*Beak morphology			1, 33663	1.20	0.27
Range overlap*Tarsus			1, 33663	1.31	0.25
Random Terms		Variance Component \pm SE	DF	LRT	P
Phylogeny		1.07 \pm 0.14	1	902.20	<0.0001
Lineage 1 intercept		0.09 \pm 0.007	1	14845.13	<0.0001
Lineage 1 Evolutionary age slope		0.003 \pm 0.0003	1	198.24	<0.0001
Covariance between intercept & slope		0.002 \pm 0.001	1	2.07	0.15
Lineage 2 intercept		0.09 \pm 0.007	1	14811.29	<0.0001
Lineage 2 Evolutionary age slope		0.002 \pm 0.0003	1	169.52	<0.0001
Covariance between intercept & slope		0.0005 \pm 0.001	1	0.22	0.64
Error in evolutionary age		0.00 \pm 0.00	1	0.00	1.00
Residual variance (V_e)		0.12 \pm 0.0009			

Notes: Output from a PLMM using REML implemented in ASReML-R. Significance of random effects was tested using log-likelihood ratio tests (LRT) with all fixed effects and their interactions included in the model. Best-fit model of song evolution was OU process ($\alpha = 0.10$).

3. Supplementary Results and Discussion

Analysis 1 *Character displacement in closest relatives independent of evolutionary age*

Comparing each lineage with its closest relative in sympatry and allopatry, we found that tarsi and beaks were more divergent in sympatry than allopatry (SI Table 3, Fig. 1c,d). Similarly, we found that song structure was more divergent in sympatry than in allopatry (SI Table 3, Fig. 1e). In summary, we found the signature of character displacement in all traits.

Analysis 2.1 *Character displacement in closest relatives controlling for habitat, morphology and evolutionary age*

We found that closest sympatric relatives were more divergent genetically than closest allopatric relatives ($F_{1,305} = 240.53$; $P < 0.0001$; Fig. 1f, Extended Data Fig. 4). We also found that evolutionary age (EA) was greatest between lineages occurring in different habitats (Extended Data Fig. 5), particularly when one lineage occurred in closed habitat (i.e. forest) and the other occurred in open habitat (e.g. grassland). This reflects the slow rate at which ecological niches diverge, i.e. phylogenetic niche conservatism.

When we accounted for the age bias by including EA in our models, the pattern consistent with ECD reported in SI Table 3 disappeared. In other words, models controlling for age detected no difference between divergence in tarsus length (SI Table 4) and beak morphology (SI Table 5) in sympatric versus allopatric lineages. Instead, EA was the strongest predictor of divergence in tarsus length and beak morphology.

Comparing song structure in sympatry versus allopatry in closest relatives, controlling for EA, habitat and ecological trait divergence, revealed no evidence of RCD (SI Table 6). We found that EA^2 explained song divergence between close relatives, with habitat and beak having little effect. The parameter estimate for EA^2 was negative indicating a hump-shaped relationship between age and song divergence: in other words, songs diverge in the early stages of sympatry (i.e. between young lineages) but converge in the later stages (i.e. between older lineages). Throughout the ‘hump-shaped’ relationship, the songs of closely related sympatric lineages were more similar than allopatric lineages. In summary, we found evidence for song convergence in sympatry, a pattern that is not consistent with RCD, but instead provides evidence for agonistic character displacement (ACD)^{4,60}.

Analysis 2.2 *Character displacement in closest relatives, accounting for best-fit model of trait evolution*

The model of evolution best explaining variation in song structure across lineages (SI Table 7), as well as divergence in song structure between lineages (SI Table 8), was an Ornstein-Uhlenbeck (OU) model. In contrast, variation in ecological traits across lineages, as well as divergence between allopatric lineages, was best explained by a Brownian Motion (BM) model (SI Tables 7 and 8). We found no evidence that an accelerated/decelerated (ACDC) model of evolution explained variation in our trait datasets. These results held irrespective of method (PGLS, ML and PLMM). Incorporating the best-fit model of trait evolution into song PLMMs did not change the outcome of our analyses focused on closest relatives (SI Table 9) or all lineages (SI Table 21), confirming that the signature of species interaction was not ecological trait divergence but song convergence.

Analysis 2.3 *Character displacement in closest relatives, excluding intraspecific lineages*

To explore the effects of taxonomy on our results, we re-ran the PLMMs described in (2a) excluding intraspecific lineages. We found that this had no effect on overall patterns of divergence in ecological traits or song, and EA remained the strongest predictor (SI Tables 11 to 13). Once EA had been controlled for, there was no evidence of ECD in tarsus length (SI Table 11) or beak morphology (SI Table 12), and the pattern of character convergence in song structure was retained (SI Table 13).

Analysis 2.4 *Sister lineages analyses*

When we ran our models on ovenbird sister lineages ($n = 111$ pairs), we again found no evidence of ECD in tarsi or beaks, contrasting with significant convergence in song structure (SI Table 14). When we further restricted this dataset, following Pigot & Tobias⁵⁹, to the set of sister species pairs ($n = 58$ pairs) with conserved beta-niches—i.e. occurring within 250 km of each other in similar microhabitats—we found no significant difference in divergence of ecological traits in sympatry versus allopatry (SI Table 15). However, a previous analysis modelling rates of transition from allopatry to sympatry across this dataset revealed that sisters with more divergent beaks achieved sympatry more rapidly⁵⁹, suggesting that a signature of greater divergence in sympatry may be detected when controlling for EA. In accordance with this prediction, a model without tarsus (matching the approach in Pigot & Tobias) found that beak morphology was significantly more divergent in sympatry than allopatry (PLMM: $F_{1,54} =$

4.47, $P = 0.03$; $A: 1.01 \pm 0.14$; $\text{Diff S}: 0.46 \pm 0.2$; SI Table 15). Although this pattern is consistent with ECD, it is not distinguishable from the signature reported by Pigot & Tobias⁵⁹ of delayed sympatry in ecologically similar species, i.e. ecological sorting. This analysis provides a case study of misleading evidence for ECD, and highlights the caution required when inferring underlying processes from patterns of trait variation in sympatry and allopatry.

Analysis 2.5 *Character displacement in closest relatives in the early stages of divergence*

When we ran the models conducted in (2a) only including species that were <6 Myr old, we found that there were no significant differences between allopatric and sympatric species for any trait, nor did we find any significant effects of how trait divergence changed with evolutionary age in sympatry versus allopatry (SI Tables 16 to 18).

Analysis 3 *Character displacement across all lineages controlling for habitat, morphology, evolutionary age and the best-fit model of trait evolution*

To determine whether there was a signature of character displacement over longer timeframes, i.e. when contrasts between older lineages are included in the analyses, we included all pairwise comparisons in the full models. We found that the inclusion of older contrasts in our models had no effect on the pattern of tarsus divergence: there is no evidence of ECD once the strong positive effect of evolutionary age on tarsus length has been taken into account (SI Tables 19). For beak morphology, however, we found a weak but significant pattern of convergence (SI Table 20). We also found that habitat was a significant predictor of divergence in both tarsi and beaks. This effect is best explained, not by species interactions, but by ecological adaptation amongst older sympatric lineages (e.g. driven by comparisons between grassland species with terrestrial lifestyles and forest species with arboreal lifestyles, as these tend to have highly divergent tarsi).

Including older contrasts in song models revealed that age, habitat shifts and correlated evolution with beak morphology explained much of the divergence in song structure over longer timeframes (SI Table 21). In contrast to models restricted to closest relatives, both beak morphology and habitat difference were strong predictors of song divergence. Nonetheless, controlling for these ecological effects, as well as age, we again found evidence for convergent ACD, i.e. songs were significantly more similar in sympatry than allopatry.

Analysis 4 *Influence of range overlap on patterns of character displacement across (a) closest relatives and (b) all lineages, controlling for habitat, morphology, evolutionary age, and best-fit model of trait evolution*

We found that all our results robust to including extent of range overlap instead of allopatry/sympatry (SI Tables 22 to 27). Moreover, this approach provided even stronger support for our conclusion that species interactions promote song convergence whether considering only closest relatives (SI Table 24), or all lineages (SI Table 27).

Analysis 5.1 *Permutation tests*

In analyses on closest relatives and all lineages (Extended Data Fig. 6), we found that permutation P-values were very similar to those obtained using F-tests in the main analyses, confirming that our results could not be explained by biases in the structure of our datasets or distribution of our response variables.

Analysis 5.2 *Trait simulations under different models of evolution*

For all three phenotypic traits, and for both the closest relatives and all lineages datasets, we found that P-values from simulations were qualitatively similar to those in our main analyses: in other words, the P-values shown in Extended Data Fig. 7a,c and e are similar to those given in SI Tables 4 to 6, while those shown in Extended Data Figs. 7b,d and f are similar to those given in Tables 19 to 21. This confirms that the parameter estimates in our main analyses were not confounded by biases inherent in the structure of the data or by varying models of evolution across traits.

Analysis 5.3 *Recovering simulated differences between allopatric and sympatric lineages under different models of trait evolution*

We found that trait differences between closely related pairs of ovenbird lineages estimated by the PLMMs were highly correlated with those simulated under different models of trait evolution (Extended Data Fig. 8). This confirms the ability of PLMMs to detect evolutionary divergence between allopatric and sympatric species under a range of evolutionary models.

Analysis 5.4 *Sister species analyses*

We ascertained that the well-established comparative modeling approach of PGLS produced qualitatively similar results to our main analyses (PLMMs), by comparing results generated from a dataset of 111 true sister species (SI Table 14).

4. Supplementary Notes

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interspecific competition and aggression. *Condor* **71**, 222-239 (1969).

6. Supplementary Code for Statistical Analyses

Key to terms

Z = Z transformation

² = Quadratic

evol_age = evolutionary age

allopatry = 2-level factor classifying allopatric and sympatric comparisons

range_overlap = proportion of range overlap between lineage 1 and 2

habitat_diff = 6-level factor defining habitat differences

tarsus_diff = difference between lineage 1 and 2 in tarsus length

beak_diff = difference between lineage 1 and 2 in principal component 1 of beak morphology

song_diff = Euclidean distance in song structure between lineage 1 and 2

tarsus_diffA = differences in tarsus length between allopatric lineages 1 and 2

tarsus_diffS = differences in tarsus length between sympatric lineages 1 and 2

beak_diffA = differences in principal component 1 of beak morphology between allopatric lineages 1 and 2

beak_diffS = differences in principal component 1 of beak morphology between sympatric lineages 1 and 2

song_diffA = differences in Euclidean distance in song structure between allopatric lineages 1 and 2

song_diffS = differences in Euclidean distance in song structure between sympatric lineages 1 and 2

lineage 1 = identity of lineage 1

lineage 2 = identity of lineage compared to lineage 2

animal = identity of ancestral node of lineage 1 and 2

animalA = identity of ancestral node of lineage 1 and 2 that are allopatric

animalS = identity of ancestral node of lineage 1 and 2 that are sympatric

MCCtree = MCCtree

phylogeny = inverse additive genetic relatedness matrix constructed from the MCCtree with ancestral nodes linked to the phenotypic data

phylogeny2 = inverse additive genetic relatedness matrix constructed from the MCCtree connected to the tips of the tree

phylogeny_error = variance in the genetic distance between lineage 1 and 2 calculating from 1000 posterior samples of the analysis used to generate the MCC tree

α = parameter varied from 0 to 5 at 0.1 increments

g = parameter varied from 0 to 5 at 0.1 increments

δ = parameter varied from 0 to 5 at 0.1 increments

Analysis 1. *Character displacement in closest relatives independent of evolutionary age*

```
Evolutionary_age <- asreml(evol_age ~ allopatry, random=~lineage1+lineage2,
data=dataset1)
```

```
Tarsus <- asreml(tarsus_diff ~ allopatry, random=~lineage1+lineage2, data=dataset1)
```

```
Beak <- asreml(beak_diff ~ allopatry, random=~lineage1+lineage2, data=dataset1)
```

```
Song <- asreml(song_diff ~ allopatry, random=~lineage1+lineage2, data=dataset1)
```

Analysis 2.1. *Character displacement in closest relatives controlling for habitat, morphology and evolutionary age*

```
Tarsus <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset1)
```

```
Beak <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset1)
```

```
Song <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset1)
```

Analysis 2.2. *Exclusion of intraspecific lineages*

```
Tarsus <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset2)
```

```
Beak <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset2)
```

```
Song <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset2)
```

Analysis 2.3. Sister lineage analyses

```
TarsusPGLS<-gls(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
correlation=corMartins(0.21, phylogeny2, fixed=T), data=dataset5)
```

```
phylogenyTtarsus <-transform(MCCtree,model="OU", alpha=0.21)
phylogenyTtarsus<-inverseA(phylogenyTtarsus, nodes="ALL")
phylogenyTtarsus<-sm2asreml(phylogenyTtarsus$Ainv,
phylogenyTtarsus$node.names)
```

```
TarsusPLMM <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(lineage1), ginverse=list(lineage1= phylogenyTtarsus), data=dataset5)
```

```
BeakPGLS<-gls(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, correlation=corMartins(0.26, phylogeny2, fixed=T),
data=dataset5)
```

```
phylogenyTbeak <-transform(MCCtree, model="OU", alpha=0.26)
phylogenyTbeak <-inverseA(phylogenyTbeak, nodes="ALL")
phylogenyTbeak <-sm2asreml(phylogenyTbeak$Ainv, phylogenyTbeak$node.names)
```

```
BeakPLMM <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, random=~giv(lineage1),
ginverse=list(lineage1=phylogenyTbeak), data=dataset5)
```

```
SongPGLS<-gls(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
correlation=corMartins(1.36, phylogeny2, fixed=T), data=dataset5)
```

```
phylogenyTsong <-transform(MCCtree, model="OU", alpha=1.36)
phylogenyTsong <-inverseA(phylogenyTsong, nodes="ALL")
phylogenyTsong <-sm2asreml(phylogenyTsong$Ainv, phylogenyTsong$node.names)
```

```
Song <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(lineage1), ginverse=list(lineage1=phylogenyTsong), data=dataset5)
```

Analysis 2.4.1 Correspondence between methods used for estimating evolutionary models

```
TarsusRawPGLSbm<-<-gls(tarsus_length ~ 1, correlation=corBrownian(1, phylogeny2),  
data= dataset_RawValues)
```

```
TarsusRawPGLSou<-<-gls(tarsus_length ~ 1, correlation=corMartins( $\alpha$ , phylogeny2,  
fixed=T), data= dataset_RawValues)
```

```
TarsusRawPGLSacdc<-<-gls(tarsus_length ~ 1, correlation=corBlomberg( $g$ , phylogeny2,  
fixed=T), data=dataset_RawValues)
```

```
BeakRawPGLSbm<-<-gls(beak_morphology ~ 1, correlation=corBrownian(1,  
phylogeny2), data= dataset_RawValues)
```

```
BeakRawPGLSou<-<-gls(beak_morphology ~ 1, correlation=corMartins( $\alpha$ , phylogeny2,  
fixed=T), data= dataset_RawValues)
```

```
BeakRawPGLSacdc<-<-gls(beak_morphology ~ 1, correlation=corBlomberg( $g$ ,  
phylogeny2, fixed=T), data=dataset_RawValues)
```

```
Song1RawPGLSbm<-<-gls(song_PC1 ~ 1, correlation=corBrownian(1, phylogeny2),  
data= dataset_RawValues)
```

```
Song1RawPGLSou<-<-gls(song_PC1 ~ 1, correlation=corMartins( $\alpha$ , phylogeny2, fixed=T),  
data= dataset_RawValues)
```

```
Song1RawPGLSacdc<-<-gls(song_PC1 ~ 1, correlation=corBlomberg( $g$ , phylogeny2,  
fixed=T), data=dataset_RawValues)
```

```
Song2RawPGLSbm<-<-gls(song_PC2 ~ 1, correlation=corBrownian(1, phylogeny2),  
data= dataset_RawValues)
```

```
Song2RawPGLSou<-<-gls(song_PC2 ~ 1, correlation=corMartins( $\alpha$ , phylogeny2, fixed=T),  
data= dataset_RawValues)
```

```
Song2RawPGLSacdc<-<-gls(song_PC2 ~ 1, correlation=corBlomberg( $g$ , phylogeny2,  
fixed=T), data=dataset_RawValues)
```

```
TarsusRawMLbm<-fitContinuous(phylogeny2, tarsus_length, model=c("BM"))
```

```
TarsusRawMLou<-fitContinuous(phylogeny2, tarsus_length, model=c("OU"))
```

```
TarsusRawMLacdc<-fitContinuous(phylogeny2, tarsus_length, model=c("delta"))
```

```
BeakRawMLbm<-fitContinuous(phylogeny2, beak_morphology, model=c("BM"))
```

```
BeakRawMLou<-fitContinuous(phylogeny2, beak_morphology, model=c("OU"))
```

```
BeakRawMLacdc<-fitContinuous(phylogeny2, beak_morphology, model=c("delta"))
```

```
Song1RawMLbm<-fitContinuous(phylogeny2, song_PC1, model=c("BM"))
```

```
Song1RawMLou<-fitContinuous(phylogeny2, song_PC1, model=c("OU"))  
Song1RawMLacdc<-fitContinuous(phylogeny2, song_PC1, model=c("delta"))  
Song2RawMLbm<-fitContinuous(phylogeny2, song_PC2, model=c("BM"))  
Song2RawMLou<-fitContinuous(phylogeny2, song_PC2, model=c("OU"))  
Song2RawMLacdc<-fitContinuous(phylogeny2, song_PC2, model=c("delta"))  
  
phylogeny2Tou<-transform(MCCTree, model="OU", alpha=  $\alpha$ )  
phylogeny2Tou <-inverseA(phylogeny2Tou, nodes="ALL")  
phylogeny2Tou <-sm2asreml(phylogeny2Tou$Ainv, phylogeny2Tou$node.names)  
  
phylogeny2Tadc<-transform(MCCTree, model="delta", delta=  $\delta$ )  
phylogeny2Tadc <-inverseA(phylogeny2Tadc, nodes="ALL")  
phylogeny2Tadc <-sm2asreml(phylogeny2Tadc$Ainv, phylogeny2Tadc$node.names)  
  
TarsusRawPLMMbm <- asreml(tarsus_length ~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2), data= dataset_RawValues)  
  
TarsusRawPLMMou <- asreml(tarsus_length ~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2Tou), data= dataset_RawValues)  
  
TarsusRawPLMMacdc <- asreml(tarsus_length ~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2Tadc), data= dataset_RawValues)  
  
BeakRawPLMMbm <- asreml(beak_morphology ~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2), data= dataset_RawValues)  
  
BeakRawPLMMou <- asreml(beak_morphology ~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2Tou), data= dataset_RawValues)  
  
BeakRawPLMMacdc <- asreml(beak_morphology ~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2Tadc), data= dataset_RawValues)  
  
Song1RawPLMMbm <- asreml(song_PC1~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2), data= dataset_RawValues)  
  
Song1RawPLMMou <- asreml(song_PC1~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2Tou), data= dataset_RawValues)  
  
Song1RawPLMMacdc <- asreml(song_PC1~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2Tadc), data= dataset_RawValues)  
  
Song2RawPLMMbm <- asreml(song_PC2~ 1, random=~giv(lineage1),  
ginverse=list(lineage1= phylogeny2), data= dataset_RawValues)
```

```
Song2RawPLMMou <- asreml(song_PC2 ~ 1, random=~giv(lineage1),
ginverse=list(lineage1= phylogeny2Tou), data= dataset_RawValues)
```

```
Song2RawPLMMacdc <- asreml(song_PC2 ~ 1, random=~giv(lineage1),
ginverse=list(lineage1= phylogeny2Tacdc), data= dataset_RawValues)
```

Analysis 2.4.2 Trait divergence data

```
phylogenyTou<-transform(MCCTree, model="OU", alpha=  $\alpha$ )
phylogenyTou <-inverseA(phylogenyTou, nodes="ALL")
phylogenyTou <-sm2asreml(phylogenyTou$Ainv, phylogenyTou$node.names)
```

```
phylogenyTacdc<-transform(MCCTree, model="delta", delta=  $\delta$ )
phylogenyTacdc <-inverseA(phylogenyTacdc, nodes="ALL")
phylogenyTacdc <-sm2asreml(phylogenyTacdc$Ainv, phylogenyTacdc$node.names)
```

```
TarsusClosestPLMMbm <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset1)
```

```
TarsusClosestPLMMou <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogenyTou), data=dataset1)
```

```
TarsusClosestPLMMacdc <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogenyTacdc), data=dataset1)
```

```
BeakClosestPLMMbm <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2
+ phylogeny_error, ginverse=list(animal=phylogeny), data=dataset1)
```

```
BeakClosestPLMMou <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2
+ phylogeny_error, ginverse=list(animal=phylogenyTou), data=dataset1)
```

```
BeakClosestPLMMacdc <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2
+ phylogeny_error, ginverse=list(animal=phylogenyTacdc), data=dataset1)
```

```
SongClosestPLMMbm <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
```

```
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset1)
```

```
SongClosestPLMMou <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogenyTou), data=dataset1)
```

```
SongClosestPLMMacdc <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogenyTacdc), data=dataset1)
```

```
TarsusAllPLMMbm <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset4)
```

```
TarsusAllPLMMou <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogenyTou), data=dataset4)
```

```
TarsusAllPLMMacdc <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogenyTacdc), data=dataset4)
```

```
BeakAllPLMMbm <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff
+ Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset4)
```

```
BeakAllPLMMou <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogenyTou), data=dataset4)
```

```
BeakAllPLMMacdc <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff
+ Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogenyTacdc), data=dataset4)
```

```
SongAllPLMMbm <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff
+ Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
```

```
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,  
ginverse=list(animal=phylogeny), data=dataset4)
```

```
SongAllPLMMou <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +  
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +  
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,  
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,  
ginverse=list(animal=phylogenyTou), data=dataset4)
```

```
SongAllPLMMacdc <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff  
+ Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +  
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,  
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,  
ginverse=list(animal=phylogenyTacdc), data=dataset4)
```

```
TarsusSisterPLMMbm <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2), data=dataset5)
```

```
TarsusSisterPLMMou <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2Tou), data=dataset5)
```

```
TarsusSisterPLMMacdc <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2Tacdc), data=dataset5)
```

```
BeakSisterPLMMbm <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2), data=dataset5)
```

```
BeakSisterPLMMou <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2Tou), data=dataset5)
```

```
BeakSisterPLMMacdc <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2Tacdc), data=dataset5)
```

```
SongSisterPLMMbm <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2), data=dataset5)
```

```
SongSisterPLMMou <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +  
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,  
random=~giv(animal), ginverse=list(animal=phylogeny2Tou), data=dataset5)
```

```
SongSisterPLMMacdc <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 +
habitat_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal), ginverse=list(animal=phylogeny2Tacdc), data=dataset5)
```

```
TarsusSisterPGLSbm<-gls(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff
+ allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
correlation=corBrownian(1, phylogeny2), data=dataset5)
```

```
TarsusSisterPGLSou<-gls(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
correlation=corMartins( $\alpha$ , phylogeny2, fixed=T), data=dataset5)
```

```
TarsusSisterPGLSacdc<-gls(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff
+ allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
correlation=corBlomberg( $g$ , phylogeny2, fixed=T), data=dataset5)
```

```
BeakSisterPGLSbm<-gls(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, correlation=corBrownian(1, phylogeny2), data=dataset5)
```

```
BeakSisterPGLSou<-gls(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, correlation=corMartins( $\alpha$ , phylogeny2, fixed=T), data=dataset5)
```

```
BeakSisterPGLSacdc<-gls(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, correlation=corBlomberg( $g$ , phylogeny2, fixed=T), data=dataset5)
```

```
SongSisterPGLSbm<-gls(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
correlation=corBrownian(1, phylogeny2), data=dataset5)
```

```
SongSisterPGLSou<-gls(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
correlation=corMartins( $\alpha$ , phylogeny2, fixed=T), data=dataset5)
```

```
SongSisterPGLSacdc<-gls(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
correlation=corBlomberg( $g$ , phylogeny2, fixed=T), data=dataset5)
```

Analysis 2.4.3 *Accounting for models of trait evolution*

```
phylogenyTouSongClosest<-transform(MCCtree, model="OU", alpha= 0.15)
phylogenyTouSongClosest <-inverseA(phylogenyTouSongClosest, nodes="ALL")
phylogenyTouSongClosest <-sm2asreml(phylogenyTouSongClosest$Ainv,
phylogenyTouSongClosest$node.names)
```

```

phylogenyTouSongAll<-transform(MCCtree, model="OU", alpha= 0.10)
phylogenyTouSongAll <-inverseA(phylogenyTouSongALL, nodes="ALL")
phylogenyTouSongAll <-sm2asreml(phylogenyTouSongAll$Ainv,
phylogenyTouSongAll$node.names)

```

```

SongClosestou <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogenyTouSongClosest), data=dataset1)

```

```

SongAllou <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(animal)+str(~lineage1, lineage1:Zevol_age, us(2):id(lineage1))+
str(~lineage2, lineage2:Zevol_age, us(2):id(lineage2)) + phylogeny_error,
ginverse=list(animal=phylogenyTouSongAll), data=dataset4)

```

```

phylogenyTSongClosestA<- transform(MCCtree, model="OU", alpha= 0.30)
phylogenyTSongClosestA <-inverseA(phylogenyTSongClosestA, nodes="ALL")
phylogenyTSongClosestA <-sm2asreml(phylogenyTSongClosestA$Ainv,
phylogenyTSongClosestA$node.names)

```

```

phylogenyTSongClosestS<- transform(MCCtree, model="OU", alpha= 0.40)
phylogenyTSongClosestS <-inverseA(phylogenyTSongClosestS, nodes="ALL")
phylogenyTSongClosestS <-sm2asreml(phylogenyTSongClosestS$Ainv,
phylogenyTSongClosestS$node.names)

```

```

SongMRClosestStart<- asreml(cbind(song_diffA, song_diffS) ~ trait-1,
random=~us(trait):giv(animalA)+ us(trait):giv(animals) +
us(trait):lineage1+us(trait):lineage2, rcov=~units:indh(trait), control=asreml(Cfixed=T,
ginverse=list(animalsA=phylogenySongClosestA, animalsS= phylogenySongsClosestS),
start.values=T, data=dataset1)

```

```

Gsong<- SongMRClosestStart$gammas.table
Gsong[2:5,2]<-0.000001; Gsong[2:5,3]<-“F”
Gsong[8,2]<-0.000001; Gsong[8,3]<-“F”
Gsong[11,2]<-0.000001; Gsong[11,3]<-“F”

```

```

SongMRClosest<- asreml(cbind(song_diffA, song_diffS) ~ trait:allopatry + trait:evol_age +
trait:evol_age2 + trait:habitat_diff + trait:Ztarsus_diff + trait:Zbeak_diff,
random=~us(trait):giv(animalsA)+ us(trait):giv(animalsS) +
us(trait):lineage1+us(trait):lineage2, rcov=~units:indh(trait), control=asreml(Cfixed=T,
ginverse=list(animalsA=phylogenySongClosestA, animalsS= phylogenySongClosestS),
G.param=Gsong, data=dataset1)

```

```

phylogenyTarsusAllA<- transform(MCCtree, model="OU", alpha= 0.10)

```

```
phylogenyTarsusAllA <-inverseA(phylogenyTarsusAllA, nodes="ALL")
phylogenyTarsusAllA <-sm2asreml(phylogenyTarsusAllA$Ainv,
phylogenyTarsusAllA$node.names)
```

```
phylogenyTarsusAllS<- transform(MCCtree, model="OU", alpha= 0.20)
phylogenyTarsusAllS <-inverseA(phylogenyTarsusAllS, nodes="ALL")
phylogenyTarsusAllS <-sm2asreml(phylogenyTarsusAllS$Ainv,
phylogenyTarsusAllS$node.names)
```

```
SongMRAllStart<- asreml(cbind(song_diffA, song_diffS) ~ trait-1,
random=~us(trait):giv(animalA)+ us(trait):giv(animalS) + str(~trait:lineage1 +
trait:lineage1:Zevol_age, ~us(4):id(lineage1))+ str(~trait:lineage2 +
trait:lineage2:Zevol_age, ~us(4):id(lineage2)), rcov=~units:indh(trait),
control=asreml(Cfixed=T, ginverse=list(animalA=phylogenySongAllA, animalS=
phylogenySongAllS), start.values=T, data=dataset4)
```

```
GsongAll<- SongMRAllStart$gammas.table
GsongAll[2:5,2]<-0.000001; GsongAll[2:5,3]<-“F”
GsongAll[8,2]<-0.000001; GsongAll[8,3]<-“F”
GsongAll[11,2]<-0.000001; GsongAll[11,3]<-“F”
```

```
SongMRAll<- asreml(cbind(song_diffA, song_diffS) ~ trait:allopatry + trait:evol_age +
trait:evol_age2 + trait:habitat_diff + trait:Ztarsus_diff + trait:Zbeak_diff,
random=~us(trait):giv(animalA)+ us(trait):giv(animalS) + str(~trait:lineage1 +
trait:lineage1:Zevol_age, ~us(4):id(lineage1))+ str(~trait:lineage2 +
trait:lineage2:Zevol_age, ~us(4):id(lineage2)), rcov=~units:indh(trait),
control=asreml(Cfixed=T, ginverse=list(animalA=phylogenySongAllA, animalS=
phylogenySongAllS), G.param=GsongAll, data=dataset4)
```

Analysis 2.5 *Exclusion of lineages >6 Myr*

```
Tarsus <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset3)
```

```
Beak <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
allopatry*Ztarsus_diff, random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset3)
```

```
Song <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
ginverse=list(animal=phylogeny), data=dataset3)
```

Analysis 3. *Character displacement across all lineages controlling for habitat, morphology, evolutionary age and the best-fit model of trait evolution*

```
TarsusAll <- asreml(tarsus_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
  allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff,
  random=~giv(animal)+str(~lineage1, lineage1:Zevol_age, us(2):id(lineage1))+
  str(~lineage2, lineage2:Zevol_age, us(2):id(lineage2)) + phylogeny_error,
  ginverse=list(animal=phylogeny), data=dataset4)
```

```
BeakAll <- asreml(beak_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
  Ztarsus_diff + allopatry*Zevol_age + allopatry*Zevol_age2 + allopatry*habitat_diff +
  allopatry*Ztarsus_diff, random=~giv(animal)+str(~lineage1, lineage1:Zevol_age,
  us(2):id(lineage1))+ str(~lineage2, lineage2:Zevol_age, us(2):id(lineage2)) +
  phylogeny_error, ginverse=list(animal=phylogeny), data=dataset4)
```

```
SongAll <- asreml(song_diff ~ allopatry + Zevol_age + Zevol_age2 + habitat_diff +
  Ztarsus_diff + Zbeak_diff + allopatry*Zevol_age + allopatry*Zevol_age2 +
  allopatry*habitat_diff + allopatry*Ztarsus_diff + allopatry*Zbeak_diff,
  random=~giv(animal)+str(~lineage1, lineage1:Zevol_age, us(2):id(lineage1))+
  str(~lineage2, lineage2:Zevol_age, us(2):id(lineage2)) + phylogeny_error,
  ginverse=list(animal=phylogenyTouSongAll), data=dataset4)
```

Analysis 4. *Influence of range overlap on patterns of character displacement across (a) closest relatives and (b) all lineages, controlling for habitat, morphology, evolutionary age, and best-fit model of trait evolution*

```
TarsusRO <- asreml(tarsus_diff ~ range_overlap + Zevol_age + Zevol_age2 + habitat_diff +
  range_overlap*Zevol_age + range_overlap*Zevol_age2 + range_overlap*habitat_diff,
  random=~giv(animal)+lineage1+lineage2+ phylogeny_error,
  ginverse=list(animal=phylogeny), data=dataset1)
```

```
BeakRO <- asreml(beak_diff ~ range_overlap + Zevol_age + Zevol_age2 + habitat_diff +
  Ztarsus_diff + range_overlap*Zevol_age + range_overlap*Zevol_age2 +
  range_overlap*habitat_diff + range_overlap*Ztarsus_diff,
  random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
  ginverse=list(animal=phylogeny), data=dataset1)
```

```
SongRO <- asreml(song_diff ~ range_overlap + Zevol_age + Zevol_age2 + habitat_diff +
  Ztarsus_diff + Zbeak_diff + range_overlap*Zevol_age + range_overlap*Zevol_age2 +
  range_overlap*habitat_diff + range_overlap*Ztarsus_diff + range_overlap*Zbeak_diff,
  random=~giv(animal)+lineage1+lineage2 + phylogeny_error,
  ginverse=list(animal=phylogeny), data=dataset1)
```

```
TarsusAllRO <- asreml(tarsus_diff ~ range_overlap + Zevol_age + Zevol_age2 +
  habitat_diff + range_overlap*Zevol_age + range_overlap*Zevol_age2 +
  range_overlap*habitat_diff, random=~giv(animal)+str(~lineage1, lineage1:Zevol_age,
```

```
us(2):id(lineage1))+ str(~lineage2, lineage2:Zevol_age, us(2):id(lineage2)) +  
phylogeny_error, ginverse=list(animal=phylogeny), data=dataset4)
```

```
BeakAllRO <- asreml(beak_diff ~ range_overlap + Zevol_age + Zevol_age2 + habitat_diff +  
Ztarsus_diff + range_overlap*Zevol_age + range_overlap*Zevol_age2 +  
range_overlap*habitat_diff + range_overlap*Ztarsus_diff,  
random=~giv(animal)+str(~lineage1, lineage1:Zevol_age, us(2):id(lineage1))+  
str(~lineage2, lineage2:Zevol_age, us(2):id(lineage2)) + phylogeny_error,  
ginverse=list(animal=phylogeny), data=dataset4)
```

```
SongAllRO <- asreml(song_diff ~ range_overlap + Zevol_age + Zevol_age2 + habitat_diff +  
Ztarsus_diff + Zbeak_diff + range_overlap*Zevol_age + range_overlap*Zevol_age2 +  
range_overlap*habitat_diff + range_overlap*Ztarsus_diff + range_overlap*Zbeak_diff,  
random=~giv(animal)+str(~lineage1, lineage1:Zevol_age, us(2):id(lineage1))+  
str(~lineage2, lineage2:Zevol_age, us(2):id(lineage2)) + phylogeny_error,  
ginverse=list(animal=phylogenyTouSongAll), data=dataset4)
```