The role of divergent ecological adaptation during allopatric speciation in vertebrates

Sean A. S. Anderson1,2,3* and Jason T. Weir1,2,4

After decades of debate, biologists today largely agree that most speciation events require an allopatric phase (that is, geographic separation), but the role of adaptive ecological divergence during this critical period is still unknown. Here, we show that relatively few allopatric pairs of birds, mammals, or amphibians exhibit trait differences consistent with models of divergent adaptation in each of many ecologically relevant traits. By fitting new evolutionary models to numerous sets of sister-pair trait differences, we find that speciating and recently speciated allopatric taxa seem to overwhelmingly evolve under similar rather than divergent macro-selective pressures. This contradicts the classical view of divergent adaptation as a prominent driver of the early stages of speciation and helps synthesize two historical controversies regarding the ecology and geography of species formation.

We thus create two new mixture models that estimate the proportion of sister pairs in a dataset whose divergence in a given trait has occurred under alternative processes. These are the DA-SO mixture model, in which a proportion (P_DA) of sister pairs diverge under a DA process and the remaining proportion (P_SO) diverge under the SO process, and the SO-BM mixture model (Fig. 2, C to E). [A DA-BM model is also possible but was not used.

1Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada. 2Department of Biological Sciences, University of Toronto at Scarborough, Toronto, ON, Canada. 3Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA. 4Department of Natural History, Royal Ontario Museum, Toronto, ON, Canada.

*Corresponding author. Email: sean.as.anderson@gmail.com

1Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, NC, USA. 2Department of Biological Sciences, University of Toronto at Scarborough, Toronto, ON, Canada. 3Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA. 4Department of Natural History, Royal Ontario Museum, Toronto, ON, Canada.

*Corresponding author. Email: sean.as.anderson@gmail.com

Downloaded from https://www.science.org at University of Toronto on December 15, 2022
Table 1. Support for divergent adaptation in various traits from 15 datasets. Rows are in descending order of the number of allopatric pairs in a dataset. "Number of traits supporting DA-SO" is the number of traits in a dataset for which DA-SO was supported over SO-BM by a minimum of two AICc. "Maximum PDA" is the highest PDA estimate from all traits for which DA-SO was supported in a given dataset and is a key basis for interpreting the role of DA in allopatric divergence. "PCA 2D" refers to two-dimensional Euclidean distances in the PC1-PC2 plane (PCA, principal components analysis). Results for individual analyses are shown in table S1. Sources for trait datasets and trees that were used to calculate divergence times are listed in table S3. Full results with additional parameter estimates are in the supplementary results files (16). Ma, million years; NA, not applicable.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Number of allopatric pairs</th>
<th>Median pair age (Ma)</th>
<th>Traits measured</th>
<th>Number of traits supporting DA-SO/number of traits</th>
<th>Maximum PDA (trait)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birds general</td>
<td>1001</td>
<td>2.8</td>
<td>Morphology PC1-PC3; bill-only PC1-PC3; bill PCA 2D; morphology PCA 2D</td>
<td>5/8</td>
<td>0.133 (bill-only PC1)</td>
</tr>
<tr>
<td>Mammals general</td>
<td>500</td>
<td>2.1</td>
<td>Body mass</td>
<td>0/1</td>
<td>NA</td>
</tr>
<tr>
<td>Birds general</td>
<td>381</td>
<td>4.4</td>
<td>Bill length, width, and depth; hand-wing index; body mass; bill PC1-PC2; bill PCA 2D</td>
<td>6/8</td>
<td>0.145 (bill length)</td>
</tr>
<tr>
<td>Rodents</td>
<td>242</td>
<td>2.6</td>
<td>Appendage lengths; midpoint latitude; six climate variables; morphology PC1-PC3; climate PC1-PC3; morphology PCA 2D; climate PCA 2D</td>
<td>10/25</td>
<td>0.129 (climate PC3)</td>
</tr>
<tr>
<td>Frogs general</td>
<td>146</td>
<td>4.5</td>
<td>Six climate variables; climate PC1 and PC2; climate PCA 2D</td>
<td>5/9</td>
<td>0.147 (annual precipitation)</td>
</tr>
<tr>
<td>New World land birds</td>
<td>129</td>
<td>2.6</td>
<td>Body PC1-PC3; bill PC1-PC3; bill length, width, and depth; wing, tail, and tarsus length</td>
<td>0/12</td>
<td>NA</td>
</tr>
<tr>
<td>New World land birds</td>
<td>111</td>
<td>2.7</td>
<td>Climate PC1-PC3; body mass</td>
<td>2/4</td>
<td>0.321 (climate PC3)</td>
</tr>
<tr>
<td>Emberizoid birds</td>
<td>87</td>
<td>1.8</td>
<td>Bill specialization; bill shape; range area and perimeter; PC1-PC3 of bill geometric morphometrics; bill PCA 2D</td>
<td>3/8</td>
<td>1.00 (PCA 2D)*</td>
</tr>
<tr>
<td>Amazonian birds</td>
<td>86</td>
<td>2.3</td>
<td>Morphology PC1-PC7; song PC1-PC2</td>
<td>1/9</td>
<td>0.041 (song PC1)</td>
</tr>
<tr>
<td>Neotropical ovenbirds (Furnariidae)</td>
<td>69</td>
<td>5.4</td>
<td>Song length and syllable diversity</td>
<td>1/2</td>
<td>0.358 (song length)</td>
</tr>
<tr>
<td>Neotropical ovenbirds (Furnariidae)</td>
<td>37</td>
<td>2.0</td>
<td>Song PC1-PC4; bill PC1; tarsus length; song PCA 2D</td>
<td>0/6</td>
<td>NA</td>
</tr>
<tr>
<td>Salamanders</td>
<td>30</td>
<td>6.4</td>
<td>Eight linear morphometrics; morphology PC1 and PC2; morphology PCA 2D</td>
<td>2/11</td>
<td>0.171 (snout-vent length)</td>
</tr>
<tr>
<td>Plethodontid salamanders</td>
<td>29</td>
<td>6.5</td>
<td>Surface area (SA); volume (V); and SA/V ratio; seven linear morphometrics; seven climate variables; morphology PC1-PC2; Climate PC1-PC3; morphology PCA 2D; climate PCA 2D</td>
<td>1/16</td>
<td>0.072 (mean annual precipitation)</td>
</tr>
<tr>
<td>Plethodontid salamanders</td>
<td>27</td>
<td>5.0</td>
<td>Seven linear morphometrics; morphology PC1 and PC2; morphology PCA 2D</td>
<td>1/10</td>
<td>0.808 (body width)</td>
</tr>
</tbody>
</table>

Total: 38/130

*Support for DA-SO is contingent on an obvious outlier being removed (14).

because of performance testing issues; fig. S1 (14)]. Our main analysis then consisted of fitting the two mixture models to each of the 130 empirical distributions of sister-pair trait differences, which allowed us to generally characterize model support and generate a distribution of PDA estimates. With mixture models, we can address the central question of this paper: If divergent adaptation is generally the predominant process driving allopatric divergence, then (i) the DA-containing model (DA-SO) should be generally well supported over the SO-BM model and (ii) DA-like patterns of trait differences should predominate (i.e., PDA > 50%) in at least some ecologically
relevant traits in each of the 15 sets of sister pairs.

We find instead that only 38 of the 130 analyses strongly support the DA-SO model, and only a minor proportion of sister pairs from each dataset tend to show patterns of divergence consistent with DA in each trait (Fig. 3, Table 1, and table S1). The prevalence of DA was low and varied little across traits and datasets (Fig. 3A); the median $P_{DA}$ from the 38 analyses in which DA-SO was well supported was 9.9% (bolded rows in table S1 show the trait-dataset combinations that support DA-SO). Critically, DA was well supported as the predominant driver of trait divergence (i.e., $P_{DA}$ exceeded 50%) for just one trait each in just 3 of the 15 datasets in our study: a sample of Plethodontid salamanders (for the trait body weight), a sample of New World passerines (for the trait song pitch), and a sample of Emberizoid birds (for the trait bill shape) (Table 1). In other words, in 12 of the 15 groups of sister pairs that we analyzed, including global datasets of birds and mammals, DA was not supported as the prevailing driver of divergence in any of several ecologically relevant traits measured for those taxa (Fig. 3B and table S1). Instead, the SO process was consistently prominent; the median $P_{SO}$ from the best-supported model in each of the 130 analyses was 93.2% (Fig. 3B). Thus, in each dataset, the vast majority of pairs have diverged under similar rather than divergent macro-selective pressures or drift-like processes in most or all ecological traits analyzed. These results are robust to alternative range

Fig. 2. Understanding trait differentiation models. Simulations are shown in (A) to (C), and real data are shown in (D) and (E). “K” denotes parameter count. (A) Replicate evolutionary walks ($n = 15$) of a continuous trait in sister lineages under BM, SO, and DA processes; $\theta_x$ is the trait optimum for lineage $x$. The SO model is agnostic as to whether the optimum shared between sisters differs from that of their common ancestor (as illustrated) or is the same. (B) Points are simulated trait differences for pairs of various ages. Models were fit to these simulated data, and their expectations were plotted. Model parameters determine the expected distribution of trait differences. In (B) to (D), colored lines show the mean and shaded areas show the 95% confidence intervals of this distribution. $D(T)$ is the trait difference at time $T$. (C) DA-SO and SO-BM mixture models fit to simulated mixed datasets. (D) DA-SO and SO-BM mixture models fit to empirical bill-size differences from (32). DA-SO is the better-fit model from AICc (Table S1). Figure S16 shows this style of graph for every dataset. In (B) to (D), colored lines show the mean, and shaded areas show the 95% confidence intervals of this distribution. (E) Model fits to data at a slice in time. Curves are proportion-weighted component densities (left) and the corresponding DA-SO mixture model density (right) expected at 4 million years. Histograms are bill size differences for pairs 3 million to 4.5 million years diverged ($n = 339$ pairs). Ma, million years.
overlap thresholds used for classifying lineages as allopatric (14) (fig. S2).

The consistently low prevalence of the DA process and high prevalence of the SO process are unlikely to be artifacts of model inadequacy or of assumption violations. Simulation-based model performance tests show that estimates of $P_{DA}$ and $P_{SO}$ are accurate over a wide and relevant range of parameter space and dataset sizes (14) (figs. S3 to S5). Moreover, when we intentionally violated model assumptions in our simulations, we were unable to generate errors that falsely recreated the empirical results (14) (figs. S6 to S10). We can also exclude "species sorting" [i.e., a bias in which sister pairs with more pronounced trait differences become sympatric at a higher rate (19)] as a key driver of our results, because simulations show that this process consistently generates a statistical artifact (a negative correlation between trait divergence and sister-pair age) that is largely absent from empirical datasets (14) (figs. S11 to S14). Also, although it is possible that a few of the sister pairs in our datasets were previously sympatric, the common pattern of exaggerated trait differences observed between sympatric close relatives (18, 19) would suggest that unseen sympathy-to- allopatry state transitions would, if anything, tend to inflate rather than suppress support for the DA process. Similarly, although the assumption that trait differences accurately reflect ecological differences is violated when different traits have similar functions [i.e., "many-to-one mapping" (20)], such a violation causes functional divergence to be overestimated rather than underestimated and thus cannot account for the low $P_{DA}$ values that we observed.

Does the ecology of allopatric speciation change with the ecological theater? Estimates of higher speciation rates at higher absolute latitudes (21, 22) have inspired the hypothesis that temperature-zone speciation may be driven to a greater extent by adaptive ecological divergence than is speciation in the tropics (23) because of the greater availability of under-exploited resources (i.e., "ecological opportunity") at temperate latitudes (24). To test this hypothesis, we compiled latitude data from digital range maps for each sister pair in each dataset and created new mixture models that permit the proportion of pairs evolving under a given process (i.e., $P_{DA}$, $P_{SO}$, or $P_{BM}$ in DA-SO or SO-BM models) to vary with latitude (14) (fig. S15). Reanalyzing all sets of trait divergence from 14 of the 15 datasets (122 analyses total; we excluded one dataset because all pairs were Amazonian birds that together covered only a small latitudinal range (14)), we find that the estimated proportion of allopatric sister pairs evolving under a particular evolutionary process is, with few exceptions, latitudinally constant (table S2). Thus, although rates of trait evolution may change across latitudes, the underlying evolutionary process driving allopatric divergence appears to vary little. We speculate that reported estimates of faster evolutionary rates for high-latitude taxa are driven in some cases by "character displacement" [in the sense of (25)] in sympatry (i.e., geographic overlap), and it is the establishment of secondary sympathy rather than allopatric trait divergence that is generally faster at high latitudes (26). This dynamic was implicated for patterns of divergence in avian plumage coloration (27).

We note that ecological adaptation can drive evolution in a number of traits that were not included in our analysis. Adaptive differences in phenotypes such as behavior, cellular attributes, sensory complexes, and life history characteristics are generally not captured in trait datasets. It is therefore possible that adaptive ecological divergence has occurred on undetected trait axes in the sister-pair groups of our study. We also note, however, that most textbook examples of "ecological speciation" in vertebrates exhibit unambiguous adaptive differences in common aspects of adult external morphology (e.g., body size in most taxa, bill shape or size divergence in birds) (2, 28), whereas we find only minor support for divergent adaptation as a prominent driver of divergence in these very same phenotypes and each of many additional traits. If adaptive ecological divergence is a major process during allopatric speciation in these pairs, then it is either much subtler than that observed in vertebrate model systems, there is greater variability in the trait axes on which different related pairs adaptively diverge, or it generally occurs on different and as-yet- unidentified trait axes for reasons that are unclear. The current most parsimonious interpretation is that our results reflect a genuine biological phenomenon: Allopatric divergence is most generally characterized by adaptive evolution to similar selective pressures.

Our study unites two historical controversies in evolution research—the roles of geographic and of ecological divergence in the evolution of new species. Using new models to analyze sister-pair trait differences, we find that adaptive ecological divergence in allopatry appears to be the exception rather than the rule in vertebrates. This result contradicts the classical idea that divergent adaptation initiates the earliest stages of speciation, and it supports an emerging picture in which new species commonly arise despite minimal ecological divergence (8). We suggest that it is notable that many textbook model systems of speciation ecology are sympatric taxa, because their pronounced ecological differences may have primarily evolved during or after the establishment of sympathy. Such differences may then be required more for ecological coexistence than for speciation per se. It is likewise possible that a previously reported correlation between ecological divergence and reproductive isolation in a diverse group of sister taxa (29) was mainly driven by sympatric pairs (sympatric and allopatric pairs were pooled in that analysis). This notion seems plausible because only pre-mating (not post-zygotic) isolation was correlated with ecological divergence in the study, and both ecological disparity and the strength of pre-mating barriers are hypothesized to accelerate in sympathy (through character displacement and "reinforcement" (30), respectively). A key implication of our result is that speciation in allopatry does not generally require lineages to exploit new resources or otherwise adapt to distinct
ecological pressures but relies instead on their prolonged geographic separation. Our findings leave open the possibility that pronounced ecological divergence is generally important after allopatric speciation as lineages expand their ranges and begin to overlap (3, 18).

REFERENCES AND NOTES

11. O. Seehausen

ACKNOWLEDGMENTS

We thank D. Jackson for advice on data standardizations. L. Forsyth, J. Boyko, C. Boccia, and J. Santangelo answered questions about data availability. We thank T. Price, J. Bemmels, V. Luzuiga-Aveiga, E. Mikkelsen, and E. Nikelski for manuscript comments. We also thank the researchers who made their data publicly accessible or shared data when requested. M. Peck (Royal Ontario Museum), P. Sweet (American Museum of Natural History), the Ontario Research Fund Research Excellence, and J.T.W. designed the study. J.T.W. generated New World avian trait data. S.A.S.A. encoded and tested the models, compiled and wrangled published datasets, ran analyses, and wrote the paper with input from J.T.W.

Competing interests: The authors declare no competing interests. Data and materials availability: All data and code for reproducing the main empirical analyses, as well as final results files, are deposited at Zenodo (16). Data on trait divergence in New World avian sister pairs are provided in raw format and analysis-ready format. Data compiled from published sources are provided in the formats in which they were downloaded and in analysis-ready formats. Code for converting downloaded datasets to their analysis-ready formats is provided in deposited files. License information: Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. https://www.science.org/about/science-licenses-journal-article-reuse

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abo7719 Materials and Methods
Figs. S1 to S3
References (S2–S6)
MDAR Reproducibility Checklist

Submitted 28 February 2022; accepted 15 November 2022
10.1126/science.abo7719
The role of divergent ecological adaptation during allopatric speciation in vertebrates
Sean A. S. AndersonJason T. Weir

Science, 378 (6625),

Similar but separate species
Speciation often requires a period of allopatry, when populations are separated long enough to diverge into distinct species. Sister species may occupy different niches, but whether ecological divergence occurs during or after allopatric speciation is poorly understood. Anderson and Weir used trait data on more than 1000 pairs of sister taxa, including birds, mammals, and amphibians, to model trait divergence over time. They found few examples of clear divergent adaptation, with greater support for a model of sister taxa evolving under similar selective pressures toward similar trait optima. —BEL

View the article online
https://www.science.org/doi/10.1126/science.abo7719
Permissions
https://www.science.org/help/reprints-and-permissions