

Article (Discoveries)

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The genomic landscapes of desert birds are structured by contemporary features

Authors: Kaiya Provost^{1,2,3,*}, Stephanie Yun Shue^{4,5}, Meghan Forcellati^{4,6}, Brian Tilston Smith¹

¹ Department of Ornithology, American Museum of Natural History, New York, New York, USA

² Richard Gilder Graduate School, American Museum of Natural History, New York, New York, USA

³ Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, Ohio, USA

⁴ Bergen County Academies, Hackensack, New Jersey, USA

⁵ Biological Sciences, University of California Berkeley, Berkeley, California, USA

⁶ Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York, USA

*Corresponding author: Kaiya L. Provost, provost.27@osu.edu, Department of Evolution, Ecology and Organismal Biology, The Ohio State University. 318 W. 12th Ave. 300 Aronoff Laboratory Columbus, OH 43210, USA

19 Abstract

20 Spatial models show that genetic differentiation can be explained by factors ranging from
21 geographic distance to environmental resistance across the landscape. However, genomes exhibit
22 a landscape of differentiation, which could indicate that multiple factors better explain divergence
23 in different portions of the genome. We test whether the best-predictors of intraspecific
24 differentiation vary across the genome in ten bird species that co-occur in Sonoran and Chihuahuan
25 deserts. Using population-level genomic data, we characterized the genomic landscapes across
26 species and modeled five predictors that represented historical and contemporary mechanisms.
27 The extent of genomic landscapes differed across the ten species, influenced by varying levels of
28 population structuring and admixture between deserts. General dissimilarity matrix modeling
29 indicated that the best-fit models differed from the whole genome and partitions along the genome.
30 The most important predictors of genetic distance were environment and contemporary
31 demography, which each explained 25–38% of observed variation, with paleoclimate and the
32 position of the biogeographic barrier explaining 14–16%, and distance only explaining 9%. In
33 particular, the genome was best explained by the biogeographic barrier in regions where the
34 genome showed high fixation between populations. Similar levels of heterogeneity were observed
35 among species and phenotypic divergence within species. These results illustrate that the genomic
36 landscape of differentiation was influenced by alternative spatial factors operating on different
37 portions of the genome.

38

39 Introduction

40 Levels of nucleotide diversity and the degree of differentiation both vary across genomes
41 (e.g., Ellegren et al., 2012; Li and Ralph 2019). These so-called genomic landscapes are produced
42 by a range of variable processes including ones intrinsic to the genome (meiotic recombination,
43 mutation) and those extrinsic (introgression, selection, and drift). Fluctuating levels of genetic
44 diversity across the genome have been shown to be associated with recombination rate indicating
45 that linked selection reduces variation (e.g., Thom G, Moreira LR, Batista R, Gehara M, Aleixo
46 A, Smith BT, unpublished data, <https://www.biorxiv.org/content/10.1101/2021.12.01.470789v1>).
47 Likewise, speciation genes, mutation rates, and coalescent times are all known to cause variation
48 in differentiation across the genome (Nosil and Schluter 2011, Benzer 1961; Hodgkinson and Eyre-
49 Walker 2011). In contrast to intrinsic processes, extrinsic processes are mediated through
50 interactions with the adaptive and demographic factors operating across space. Despite evidence
51 of the patterns and processes driving a heterogeneous genomic landscape (e.g., Li and Ralph 2019,
52 Wang et al., 2020), studies examining the spatial predictors of genetic differentiation often treat
53 genomic data as homogeneous. Clarifying the relationship between the heterogeneity of the
54 genomic landscape and spatial predictors of differentiation will elucidate how intraspecific
55 variation arises in the complex physical landscape.

56 The spatial processes attributed to population differentiation operate over historical
57 through contemporary time scales. For example, population history is often linked to Pleistocene
58 glacial cycles that shifted and fragmented distributions over the last 2.6 million years. An
59 association of genome-wide structuring linked to population fragmentation can be tested under
60 isolation-by-history (IBH), where genetic distances are modeled against paleo-climatic suitability
61 (Vasconcellos et al., 2019; Moreira et al., 2020). There are also atemporal manifestations of
62 historical isolation, such as isolation-by-barrier (IBB; *sensu* Mayr 1942), which posits that
63 population differentiation is best predicted by a landscape feature, for example a mountain range
64 or river. Over shallower evolutionary scales, non-random mating with individuals in closer

65 geographic proximity can cause genetic differentiation. Geographic distances alone may not be the
66 best predictors of differentiation because adaptation to local climatic conditions causes selection
67 to generate intraspecific differentiation across environmental gradients, which is known as
68 isolation-by-environment (IBE; Wang and Bradburd 2014, Myers et al., 2019, Berg et al., 2015;
69 Zamudio et al., 2016). Because local environmental conditions change rapidly, for example due to
70 species turnover or succession (Phillips 1996, Nuvoloni et al., 2016), associations between
71 differentiation and environment are likely more recent phenomena than historical associations.
72 The increased availability of ecological data for many organisms, such as census data, allows for
73 testing even shallower associations with genetic structuring across the landscape. Contemporary
74 demographic data can be used to test isolation-by-abundance (IBA), where genetic differences are
75 associated with abundance troughs that restrict gene flow (Barton and Hewitt 1981, Hewitt 1989,
76 Barrowclough et al., 2005). Local population size is also known to be a strong driver of genetic
77 structure, especially when compounded with environmental change determining local suitability
78 (Weckworth et al., 2013). While the focus of these models is often on genetic variation, they can
79 also be applied to phenotypic variation (e.g., Moreira et al., 2020). Phenotypic variation is often
80 the product of many loci with little effect that are not always distinguishable from the genome
81 itself. As such, looking directly at phenotype can help reveal whether a particular process is
82 associated with trait variance. Examining the genomic landscape in the context of these alternative
83 spatial models will provide evidence for how factors of varying temporal resolutions influence the
84 peaks and valleys of differentiation. To investigate how landscape features impact genotype and
85 phenotype, we use an exemplar community of co-distributed taxa across the Sonoran and
86 Chihuahuan deserts of the southwestern USA and northern Mexico.

87 Here we characterize the genomic landscapes of birds occurring across the Sonoran and
88 Chihuahuan deserts and test the relative effect of alternative spatial models in predicting patterns
89 of intraspecific differentiation. To do this, we integrate population-level whole-genome
90 resequencing, specimen-based morphometrics, and comparative sampling across ten co-
91 distributed species that occur across the deserts. We hypothesize that the best-predictors of genetic
92 diversity will vary across species and different partitions of the data, reflecting the multiple
93 extrinsic factors that structure variation across the genomic landscape (Supplementary Figure 1).
94 Alternatively, species could show homogeneous patterns either by the same spatial modeling
95 predicting differentiation in windows across the whole genome or by species exhibiting congruent
96 genomic landscapes shaped by the same geographic barrier. We further evaluate whether summary
97 statistics, reflective of alternative evolutionary processes, could explain alternative spatial
98 predictors of genomic landscapes. This comparative framework will provide resolution to the
99 extent at which peaks and valleys of the genomic landscape correspond to historical through
100 contemporary factors.

101 102 **Results**

103 104 *Genomic results*

105 We sequenced the genomes of 221 individuals across 10 focal species of passerine
106 distributed in the Sonoran and Chihuahuan deserts. Based on the amounts of missing data, we
107 created three datasets: a complete dataset, a dataset where up to 75% missing data was allowed,
108 and a dataset where up to 50% missing data was allowed. We found that the three missing data
109 partitions did not vary substantially with respect to coverage or number of SNPs. As such, here we
110 describe the results for the complete dataset (for the 75% and 50% missing data partitions, see

111 Supplementary Information). We recovered sequences with a mean coverage of 2.9 per individual
 112 (range 0.4–8.8), 6–25 million reads per individual, and 5–28 million SNPs per species. Mean
 113 coverage within species ranged from 2.1–4.2 *Phainopepla nitens* the lowest coverage and
 114 *Melozone fusca* having the highest. The average missing data per species ranged from 48–64%.
 115 Across individuals, missing data ranged from 13–93% with a mean of 53% (Table 1).

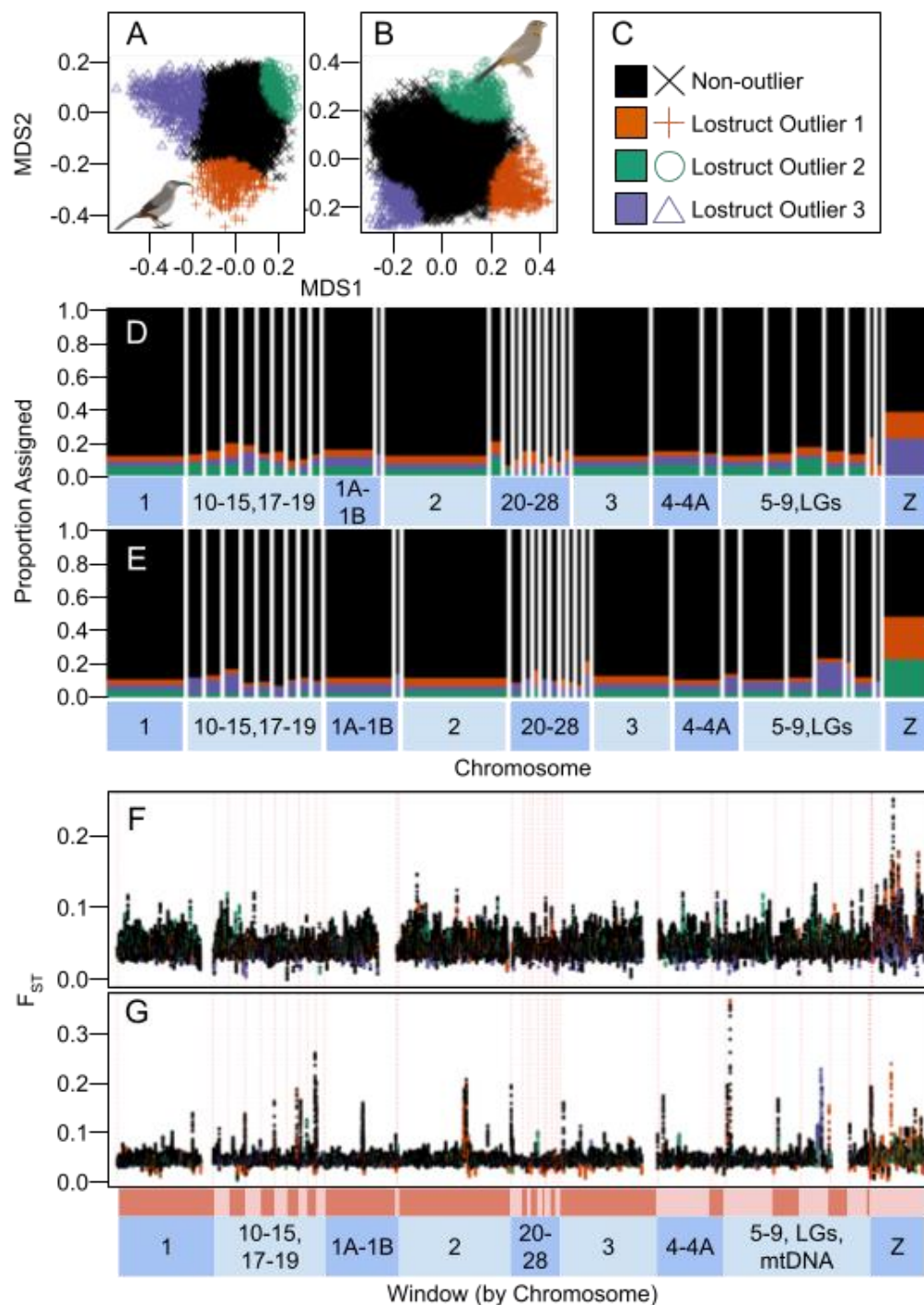
116 We estimated recombination rates using ReLERNN (Adrion et al., 2020). Mean
 117 recombination rates for the entire genome ranged from 8.8–10.6 x 10⁻¹⁰ c/bp (where c is the
 118 probability of a crossover) across species. Correlations between species in mean recombination
 119 across chromosomes range from -0.57 to 0.61 (mean±SD 0.01±0.29). Correlations in mean
 120 recombination at the same genomic positions ranged from -0.31 to 0.36 (mean±SD -0.03±0.17).

121
 122 Table 1: Chromosome-wise values for the recombination rate, F_{ST}, D_{XY}, and proportion of missing data per each
 123 species. Values given as mean±standard deviation (number of chromosomes). These are calculated by weighting all
 124 chromosome means equally; for size-weighted values see Supplementary Table 1. Note that the number of
 125 chromosomes is based off of the pseudo-chromosomes we generated, with a maximum of 36. “Rec”=population
 126 recombination rate, or rho. Values are given for the complete dataset; for the 50% and 75% values, see Supplementary
 127 Table 2.

Species	Rec (x 10 ⁻¹⁰)	F _{ST}	D _{XY}	% Missing Sites
<i>Vireo bellii</i>	9.7±1.2 (33)	0.06±0.09 (35)	0.011 ±0.005 (31)	0.64±0.79 (36)
<i>Amphispiza bilineata</i>	10.0±1.2 (2)	0.02±0.001 (35)	0.018 ±0.005 (20)	0.55±0.43 (36)
<i>Campylorhynchus brunneicapillus</i>	10.4±0.3 (31)	0.03±0.001 (34)	0.011 ±0.008 (31)	0.55±0.02 (36)
<i>Toxostoma crissale</i>	10.5±0.4 (31)	0.04±0.004 (34)	0.01 ±0.006 (31)	0.52±0.41 (36)
<i>Toxostoma curvirostre</i>	10.0±0.5 (34)	0.10±0.023 (34)	0.013 ±0.009 (32)	0.52±0.41 (36)
<i>Auriparus flaviceps</i>	10.2±0.7 (34)	0.05±0.006 (36)	0.015 ±0.007 (35)	0.56±0.47 (36)
<i>Melozone fusca</i>	10.1±0.5 (35)	0.04±0.004 (35)	0.015 ±0.01 (24)	0.51±0.47 (36)
<i>Polioptila melanura</i>	9.7±0.7 (29)	0.03±0.001 (34)	0.014 ±0.01 (23)	0.52±0.43 (36)
<i>Phainopepla nitens</i>	10.0±0.6 (30)	0.02±0.001 (34)	0.012 ±0.007 (28)	0.65±0.01 (36)
<i>Cardinalis sinuatus</i>	9.8±0.6 (36)	0.03±0.005 (36)	0.015 ±0.01 (26)	0.52±0.35 (36)

128
 129 *Lostruct outliers and F_{ST} outliers*

130 We divided the genome into three kinds of partitions. First, we analyzed chromosomes
 131 independently. Second, we identified high F_{ST} outliers and analyzed those. Finally, we performed
 132 a multidimensional scaling (MSDS) analysis the using R package lostruct version 0.0.0.9000 (Li
 133 and Ralph 2019), which subdivided genomes into four partitions, three outliers (LS1, LS2, LS3)
 134 and one non-outlier partition (Figure 1; Supplementary Figure 2). Note that outlier groupings of
 135 the same color are not analogous across taxa. On average across all species 85.3% of labeled values
 136 were non-outliers, and ~4.88% each were LS1, LS2, and LS3.



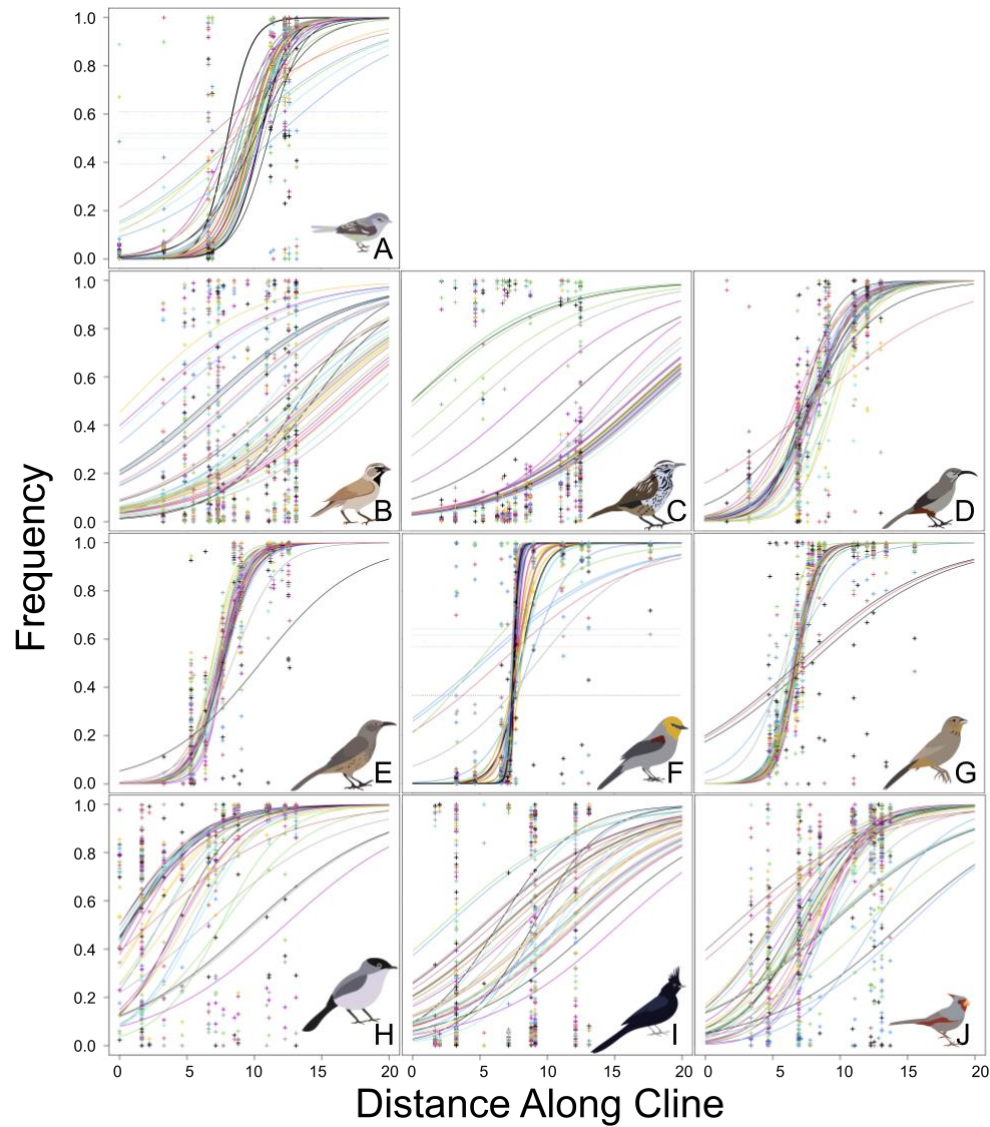
137
 138 Figure 1: Lostruct partitions vary across species and across chromosomes. Two exemplar species pictured, *Toxostoma*
 139 *crissale* (panels A, D, F) and *Melozone fusca* (panels B, E, G). For all 10 species see Supplementary Figure 2. Panels
 140 A and B: Multidimensional scaling coordinates 1 (x-axis) vs 2 (y-axis) for each species, with outlier points highlighted
 141 in orange, green, and purple as different partitions, and non-outlier points in black. Panel C: Legend describing colors
 142 and shapes in panel C, with black X's showing non-outlier partitions, orange crosses showing Lostruct outlier 1, green
 143 circles showing district outlier 2, and purple triangles showing Lostruct outlier 3. Panels D and E: Proportion of
 144 chromosomes assigned to Lostruct outliers and non-outliers in panels D and E. Width of bars approximately
 145 proportional to length of windows assessed in each chromosome. Panels F and G: F_{ST} values for windows across the
 146 genome, colored by Lostruct partition, with windows without Lostruct data in gray. Note that F_{ST} values are not on the
 147 same scale. Chromosomes separated by red lines, with legend at the top.

148 We calculated F_{ST} values across the genome using ANGSD's realSFS function (Meisner
149 and Albrechtsen 2018). F_{ST} outlier analysis for our species across the datasets with complete, 75%,
150 and 50% missing data found largely congruent results (see Supplementary Information for 75%
151 and 50% datasets). The number of high F_{ST} outliers for the complete dataset ranged from 28–758
152 across species (with the total number of windows analyzed per species ranging from 100,733–
153 113,555). The outlier lostruct partitions identified above (LS1, LS2, LS3) vary in the proportion
154 of the F_{ST} outliers examined (for the complete dataset), ranging from 0.0%–3.4% (mean 0.2%) for
155 peaks. Though not significant, there appears to be a trend where species with generally higher F_{ST}
156 have more high F_{ST} outliers identified.

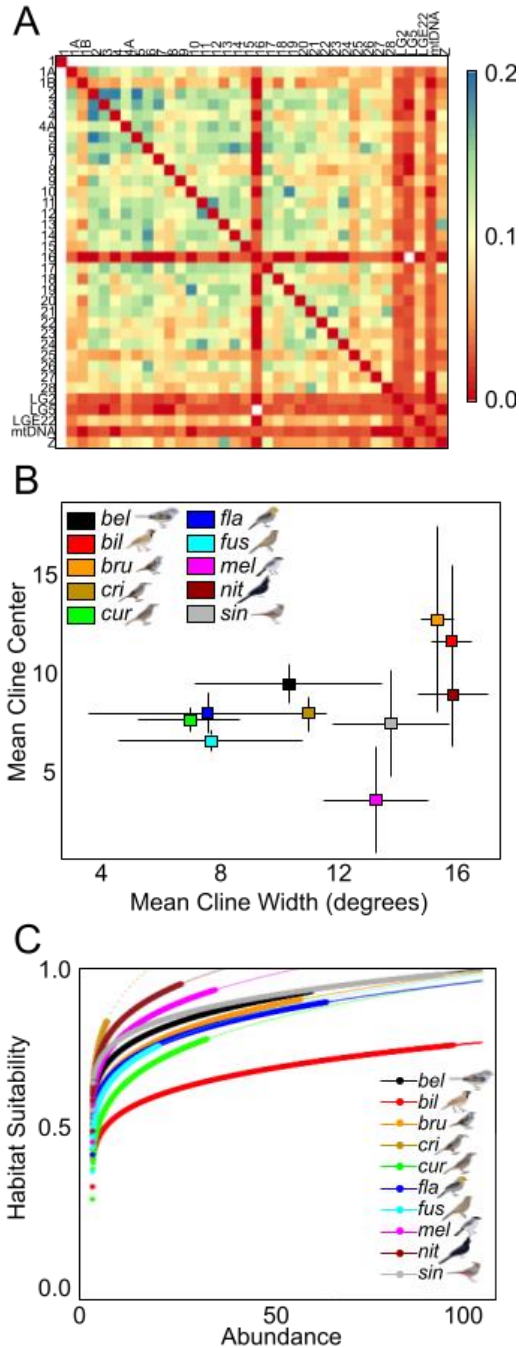
157 158 *Population differentiation*

159 Population differentiation across the Sonoran and Chihuahuan deserts was estimated using
160 PCAngsd in ANGSD (Meisner and Albrechtsen 2018). Species ranged from being highly
161 structured among deserts in four species (*T. curvirostre*, *V. bellii*, *A. flaviceps*, and *P. melanura*),
162 showing a gradient of structuring with admixture in three (*T. crissale*, *M. fusca*, and *Cardinalis*
163 *sinuatus*), or unstructured in the remaining taxa (*A. bilineata*, *C. brunneicapillus*, *P. nitens*;
164 Supplementary Figure 3). F_{ST} values for the species within these three groups varied accordingly:
165 highly structured=0.03–0.10; gradient=0.03–0.04; and unstructured=0.02–0.03. Population
166 differentiation estimated from the chromosomal partitions were generally concordant with
167 genome-level patterns, but smaller chromosomes and/or those with fewer SNPs showed different
168 patterns (Figure 2, Figure 3, Supplementary Figure 4).

169 After estimating population differentiation, we calculated clines of population assignment
170 across the range of each species, examining cline width and cline center. For cline-based analyses,
171 mean cline width ranges from 6.94–15.89° longitude, where the total area encompassed by each
172 species was ~18° longitude (with zero on the cline defined as 116.10°W longitude; Supplementary
173 Table 3; Figure 2; Figure 3; Supplementary Figure 1). Cline width increases as chromosome size
174 decreases ($p=1.4 \times 10^{-6}$, adjusted $R^2=0.06$), though this varies across species (range p 7.7×10^{-7} –0.43,
175 range adjusted R^2 -0.01–0.51). Mean cline center location ranges from 3.58° along the cline
176 (~112.52°W) to 12.70° along the cline (~103.4°W). We found that there were negative correlations
177 between the degree of population structure (measured by F_{ST} ; see Supplementary Information) and
178 both mean cline width and the standard deviation of cline center locations, which is expected based
179 on how clines are calculated. Species with higher F_{ST} between populations had narrower clines
180 and less variation among partitions in the locations of their clines (Supplementary Figure 5).



181
182 Figure 2: Cline width and center location vary across species and across chromosomes. X-axis shows distance (in
183 degrees longitude) along the sampled area. Y-axis shows the projected cline from population assignments of 0 to 1 in
184 each taxon (panel) and each chromosome (colored lines). Hash marks show population assignments for each
185 individual. Species are as follows: A) *Vireo bellii*, B) *Amispiza bilineata*, C) *Campylorhynchus brunneicapillus*, D)
186 *Toxostoma crissale*, E) *Toxostoma curvirostre*, F) *Auriparus flaviceps*, G) *Melozone fusca*, H) *Polioptila melanura*,
187 I) *Phainopepla nitens*, J) *Cardinalis sinuatus*.



188
 189 Figure 3. Species vary in their chromosomal structure, population structure, ecology, and abundance across the
 190 Sonoran and Chihuahuan deserts. A) Standard deviations of Robinson-Foulds distances across species; see
 191 Supplementary Figure 4. Warmer colors indicate lower standard deviations. Chromosomes are arranged in
 192 alphanumeric order. B) Mean cline width in degrees vs. mean cline center across chromosomes for each species; see
 193 Figure 2. Lines from each point show standard deviations. Species names are shortened for legibility (“bel”=*Vireo*
 194 *bellii*, “bil”=*Amphispiza bilineata*, “bru”=*Campylorhynchus brunneicapillus*, “cri”=*Toxostoma crissale*,
 195 “cur”=*Toxostoma curvirostre*, “fla”=*Auriparus flaviceps*, “fus”=*Melospiza fusca*, “mel”=*Poliophtila melanura*,
 196 “nit”=*Phainopepla nitens*, “sin”=*Cardinalis sinuatus*). C) Predicted abundance-habitat suitability relationships for
 197 each species; see Supplementary Figure 6, Supplementary Figure 7, Supplementary Figure 8. Colors indicate
 198 individual species. Points are large for actual abundance metrics for each species; small points show predicted
 199 suitability at non-observed higher abundances. Species names as in Part B.

200 *Morphological variation across the Cochise Filter Barrier*

201 Across the 10 focal species, we measured 294 individuals, including bill, wing, tail, and
202 leg morphology. We collapsed these metrics into a principal components analysis. There were no
203 clear, desert-specific patterns in variation across the Cochise Filter Barrier (N=234), with
204 morphological changes ranging from subtle to significantly different. In our principal components
205 analysis, the first three principal components (PC1, PC2, PC3) explained 74%, 12%, and 6% of
206 the variation in morphology and corresponded approximately to overall body size, bill size/shape,
207 and wing size/shape, respectively (Supplementary Table 4, Supplementary Table 5;
208 Supplementary Figure 9). We found significant differences across the Cochise Filter Barrier in six
209 species in at least one analysis (see Supplementary Information for more details). Between deserts
210 *T. crissale* and *C. sinuatus* differed in body size and bill shape. *Vireo bellii* and *M. fusca* differed
211 in bill shape. *Poliioptila melanura* and *A. flaviceps* differed in body size. No species showed
212 significant differences in wing shape.

213

214 *Climatic suitability and abundance across the Cochise Filter Barrier*

215 Using MaxEnt (Phillips et al., 2006), WorldClim (Hijmans et al., 2005), and other
216 environmental variables (see Methods), we calculated ecological niche models for the present, the
217 mid-Holocene, and the Last Glacial Maximum. During the Last Glacial Maximum, the most
218 suitable areas for all taxa were projected to be further south than the most suitable areas during the
219 present and mid-Holocene. Regions that are predicted to be suitable through all three periods are
220 often reduced compared to current distributions (Supplementary Figure 8; Supplementary Figure
221 10). We calculated abundance for each species using the Breeding Bird Survey (Pardieck et al.,
222 2019). Abundance was correlated with predicted climatic suitability across all taxa, with adjusted
223 R² values of fit lines (log-scaled) ranging from 0.42–0.62 (Figure 3, Supplementary Figure 6,
224 Supplementary Figure 7).

225

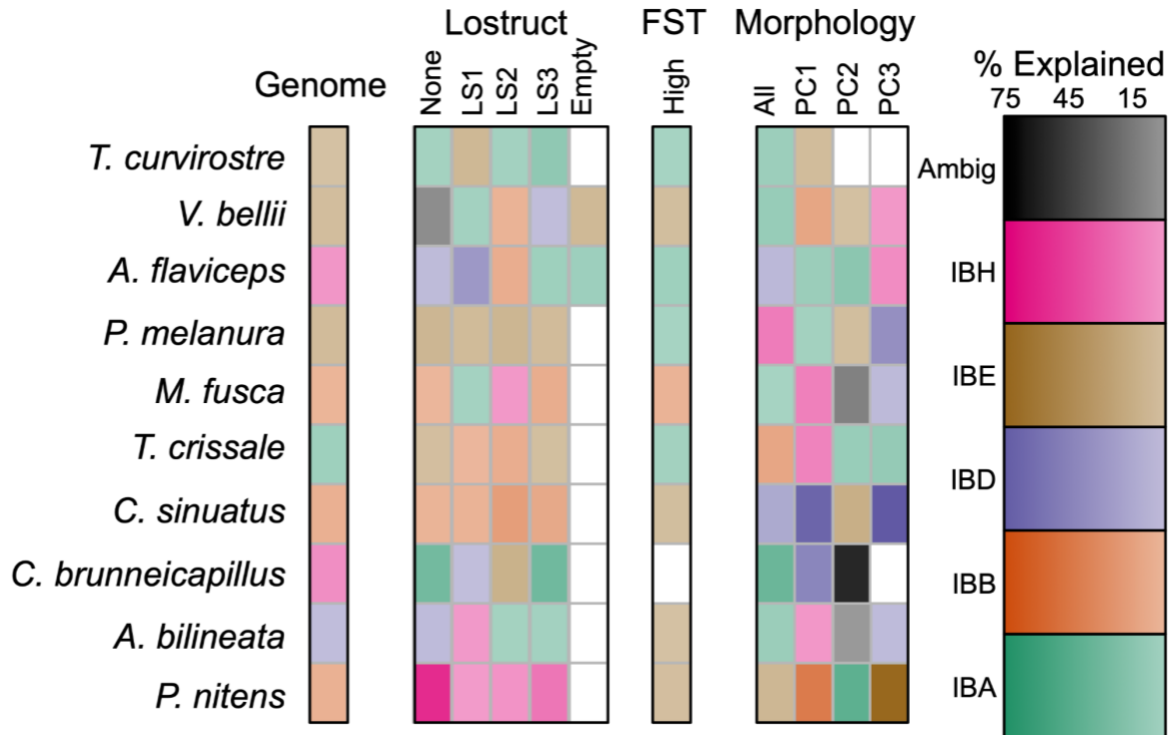
226 *Phenotypic and genotypic datasets are idiosyncratic with respect to landscape features*

227 We chose five metrics of landscape variation (IBA, IBB, IBD, IBE, and IBH) to evaluate
228 against genetic and phenotypic variation within taxa. Differences in variation were attributed to
229 each of these landscape metrics using generalized dissimilarity matrix (GDM) modeling. We
230 evaluated models that were univariate (variation ~ landscape metric), bivariate (variation ~ IBB +
231 landscape metric), and trivariate (variation ~ IBB + IBD + landscape metric); we focus on
232 univariate models. Performance of the GDM models was consistent whether looking at univariate,
233 bivariate, or trivariate data partitions (see Supplementary Information). 2,945/3,030 univariate
234 models converged successfully with an overall 98% convergence. Of the 505 datasets tested,
235 30.0% selected IBE as the best factor explaining variation, 21.3% selected IBB, 18.2% selected
236 IBA, 14.2% selected IBD, 11.5% selected IBH, and the remainder were ambiguous, with multiple
237 models equally explaining variation. Within the ambiguous models, of which there were 23, 82.6%
238 had IBH as one of the best models, 73.9% had IBE as one of the best models, 56.5% had IBA as
239 one of the best models, 23.1% had IBD as one of the best models, and notably, none of them had
240 IBB as one of the best models.

241 Across all of the GDMs performed, percent deviance explained by the best model was
242 variable, ranging from 0.1% to 81.9%. The mean±SD percent deviance explained across all
243 datasets was 16.8%±18.2%. Percent deviance explained for the whole genome was lower on
244 average, ranging from 0.5%–6.9% (mean±SD 3.9%±2.2%). F_{ST} outliers, both high and low, tended
245 to have higher percent deviances explained, ranging from 0.14%–69.9% (mean±SD

246 25.9%±22.4%). Lostruct outliers ranged from 1.0%–54.25% (mean±SD 11.0%±12.6%). Percent
 247 deviance explained had the most extreme range in morphology, from 0.3% to 81.9% (mean±SD
 248 17.5%±20.8%). The percent deviance explained varied across taxa, with means ranging from 7.5%
 249 (*M. fusca*) to 27.9% (*P. nitens*) and standard deviations ranging from 12.1%–24.0%.

250 For the models examining signals across the whole genomes, three species had IBB as the
 251 most important predictor, three had IBE, two had IBH, one had IBA, and one had IBD. (Figure 4;
 252 Supplementary Figure 11). It is notable that all of the genomes identified as having IBE as the best
 253 predictor are taxa that are structured across the Cochise Filter Barrier. Chromosome length does
 254 not significantly predict any differences between models ($p>0.47$, $n=347$).



255
 256 Figure 4: Generalized Dissimilarity Modeling revealed heterogeneous associations between genomic and phenotypic
 257 differentiation and alternative spatial hypothesis. Shown is the GDM model summary for each species and partition.
 258 Species are along the y-axis and arranged from most to least differentiated across the Cochise Filter Barrier. Individual
 259 partitions (genome, F_{ST} high and low outliers, morphology) are along the x-axis. Color indicates the best model. Shade
 260 of color indicates how much support the model has (with darkest shade indicating up to 75% support and lightest
 261 shade indicating 0%). White boxes have no associated data due to failure of models to converge. The alternative
 262 models were as follows: isolation by abundance (IBA), isolation by barrier (IBB), isolation by distance (IBD), isolation
 263 by environment (IBE), and isolation by history (IBH). “Ambig” is shorthand for ambiguous partitions that show a
 264 mixture of models that best explain the data. White boxes represent partitions that failed to converge or did not have
 265 corresponding datasets. For more partitions of data see Supplementary Figure 11.

266
 267 For the lostruct partitions, the three outlier partitions (LS1, LS2, LS3) had 5/30 with IBA
 268 as the best model, 10/30 IBB, 3/30 IBD, 9/30 IBE, and 3/30 IBH. Most species showed at least
 269 some overlap in which model best explained partitions: for example, *A. bilineata*, *T. crissale*, and
 270 *C. sinuatus* all have at least two lostruct partitions best explained by IBB. For the non-outlier
 271 partitions (LS0, and the “empty” partition for *V. bellii* and *A. flaviceps*), these best model chosen
 272 is the same as the best model explaining whole-genome variation in four species (*V. bellii*, *P.*
 273 *melanura*, *C. sinuatus*, *M. fusca*) and that of one of the outlier partitions in all but two species (*V.*

274 *bellii*, *A. bilineata*). Notably, for *P. melanura* IBE explains all three outlier partitions, the genome,
275 and the non-outlier lostruct partitions. Likewise, for *C. sinuatus*, all of these are explained by IBB.

276 All ten species had high-F_{ST} partitions identified (see Supplementary Information for 75%
277 and 50%) across the complete, 75%, and 50% datasets. The genome matched at least one of the
278 high or low partitions in four taxa: *Vireo bellii*, *A. bilineata*, *Toxostoma crissale*, and *Melospiza*
279 *fusca*. With respect to significance, none of the F_{ST} outlier partitions were significantly different
280 (but see Supplementary Information).

281 There was little congruence across the best landscape predictor of morphological data
282 within species. Overall morphological differentiation had the same explanatory variables as PC3
283 for *P. nitens* (IBE), and as PC1 for *C. sinuatus* (IBD). Additionally, some individual PCs did match
284 each other: IBD best explained PC1 and PC3 in *C. brunneicapillus*, IBA best explained PC2 and
285 PC3 in *T. crissale* and PC1 and PC2 in *A. flaviceps*, and for *T. curvirostre*, PC2 and PC3 both
286 showed ambiguous results. Neither overall morphology nor the PCs were significantly different
287 than expected in the univariate dataset (though some were in the bivariate and trivariate datasets;
288 see Supplementary Information).

289 Like overall variation, PC1 (body size) showed an even distribution between all models
290 across the 10 species (i.e., 20% each IBA, IBB, IBD, IBE, and IBH). PC2 (bill shape) was best
291 explained in 30% of species by IBA, 20% by IBE, 10% by IBD, and 40% of the species showed
292 ambiguous results. Lastly, PC3 (wing shape) was best explained in 40% of species by IBD, 20%
293 each by IBA and IBE, 10% IBD, and 10% of species had ambiguous results.

294 295 *Data characteristics of best-fit models*

296 We looked at whether differences in summary statistics could explain our univariate
297 models (IBA, IBB, IBD, IBE, IBH) across taxa (Supplementary Figure 12; Supplementary Figure
298 13; Supplementary Figure 14). The summary statistics we examined were recombination rate,
299 missing data, F_{ST}, D_{XY} calculated using ngsTools (Fumagalli et al., 2014), and the length of the
300 chromosome. The clearest pattern was that datasets with ambiguous results among models had
301 more missing data than all others except IBH models (p<0.0001). IBH results also tended to have
302 more missing data than most other models (p<0.02), but we found that this relationship was not
303 significant when we excluded *P. nitens*, which had both the largest proportion of models explained
304 by IBH and a high proportion of missing data (p>0.70). F_{ST} was significant overall (p<0.04), with
305 IBB models having significantly higher F_{ST} than IBH models. This relationship was no longer
306 significant in bivariate or trivariate models because IBB was not present (see Supplementary
307 Information). D_{XY} was also significant overall (p<0.05), but Tukey's honestly significant
308 difference tests showed that none of the individual comparisons were significant (p>0.06).
309 Recombination rate and chromosome length were not significant for univariate models (p>0.07)
310 though recombination rate was significant for bivariate and trivariate models (see Supplementary
311 Information).

312 313 *Landscape predictors are not influenced by habitat suitability*

314 From the ENMs, we calculated habitat suitability for each species across the deserts.
315 Species with more variable suitability across the contact zone have a higher proportion of IBH as
316 the best model (adjusted-R²=0.54, n=10, p<0.01). As *P. nitens* has both the highest proportion of
317 IBH and the highest variance in suitability, we removed this species in case it was acting as an
318 outlier. After removing this species, the relationship was only nearly significant, but strong

319 (adjusted- $R^2=0.28$, $n=9$, $p<0.09$). Evaluating this relationship with ANOVA tests finds the same
320 results, where no comparisons are significant without *P. nitens*.

321

322 *Significance evaluation of hypotheses of evolution across the Cochise Filter Barrier*

323 Species differ more than expected with respect to what spatial models best explain their
324 genotypes and phenotypes. Best-predictors vary across individual species ($\chi^2=284.0$, $p\sim 0.0$, $df=54$,
325 simulated $p<0.0005$), individual partitions of genotype and phenotype differed ($\chi^2=685.6$, $p\sim 0.0$,
326 $df=324$, simulated $p<0.0005$), and with respect to phylogeographic structure across the Cochise
327 Filter Barrier ($\chi^2=62.9$, $p<6.5\times 10^{-9}$, $df=12$, simulated $p<0.0005$).

328

329 **Discussion**

330 We found that the best-fit spatial model differed across partitions at multiple scales. Our
331 taxa, which varied in levels of genomic diversity, showed evidence that different spatial processes
332 (reflecting historical through contemporary phenomena) had distinct impacts on the genome
333 compared to targeted subsets of the genome. Similar patterns of heterogeneity were observed
334 among species and with their phenotypic datasets. The disparity in predictors of intraspecific
335 differentiation among the whole genome versus windows and between windows extends the view
336 that evolutionary inferences are dependent on which portions of the genome are examined in a
337 spatial framework. The heterogeneity in model fit across partitions was consistent with the
338 expectation that various evolutionary processes contribute to the peaks and valleys of the genomic
339 landscape. By applying this framework across an assemblage of birds that evolved across a
340 common, dynamic region we showed that at the community-scale, predictors of genomic structure
341 remain idiosyncratic, which may reflect taxa at different stages of the evolutionary histories and
342 responses to the biogeographic barrier.

343

344 *Extrinsic drivers of the genomic landscape*

345 Our modeling showed that environmental distance was often a strong predictor of levels of
346 intraspecific differentiation, but this pattern was species- and partition-dependent. Genome-wide
347 patterns of differentiation across the Cochise Filter Barrier are partially shaped by environmental
348 adaptation as observed in non-avian taxa distributed across the barrier (Myers et al., 2019).
349 Environmental adaptation is often recovered in taxa who respond to environmental gradients via
350 altered phenotypes (Branch et al., 2017, Dubec-Messier et al., 2018), genotypes (Berg et al., 2015,
351 Manthey and Moyle 2015), or both (Ribeiro et al., 2019). However, our analyses show there was
352 considerable variation among individual regions in the genome, indicating a more nuanced pattern.
353 The species-specific results we found suggests that individual taxa had unique responses to shared
354 aspects of the landscape. Although the focal taxa are co-distributed, we showed how environmental
355 suitability, their general morphologies, and abundances across space varied among species, which
356 may help explain why best-fit models differed. As such, these species-specific factors may explain
357 isolation-by-environment was the best explanatory variable for many, but not all, of the species
358 we investigated.

359 Individual partitions of the genome also varied with respect to how much environmental
360 variation played a role. At one extreme, environmental variation appears to have little impact on
361 the sex chromosomes. The Z chromosome often showed the barrier (i.e., IBB) as being the most
362 important factor, even in unstructured species such as *Amphispiza bilineata* and *Campylorhynchus*
363 *brunneicapillus*, perhaps because the locus evolves faster than sites under selection for adaptation
364 to local environmental conditions. Sex chromosomes are known to diverge faster than autosomes

365 due to their differences in effective population size (Mank et al., 2010), importance in sexual
366 selection (Kirkpatrick 2017), and the presence of speciation genes (Sæther et al., 2007). Given the
367 lack of evidence for environmental variation predicting spatial genetic differentiation on the Z
368 chromosome, this would suggest that any speciation genes present in these taxa may not be
369 involved in adaptation to the environment.

370 Environment was the most important driver for species with genetic structure. The most
371 intuitive explanation for this was that population structuring in these taxa was facilitated by natural
372 selection to different environments. There was some evidence that this could have happened across
373 other taxa that occur across the Cochise Filter Barrier, as IBE was the best predictor of genome-
374 wide divergence in a community of snakes distributed across the barrier (Myers et al., 2019).
375 However, we must stress that while this explanation was the most intuitive and aligns with
376 predictions, there are numerous processes that can produce IBE (Wang and Bradburd 2014), and
377 it is possible that divergence led to adaptation to these environments secondarily, rather than the
378 reverse, or the patterns are being influenced by some unknown factors that we did not quantify.
379 Nevertheless, at present our results are consistent with the importance of ecologically mediated
380 population differentiation, or isolation-by-environment, in structuring communities across the
381 deserts of North America.

382

383 *Contemporary versus historical predictors of genomic differentiation*

384 Our finding that the best-fit models varied across species was consistent with the
385 expectations that species idiosyncratically respond, over a range of time scales, to the Cochise
386 Filter Barrier. The spatial patterns we examined vary temporally, with Pleistocene environmental
387 changes being a historical process, while geographic distances, abundances, and environmental
388 variation reflecting more contemporary processes. Historical signatures of Pleistocene isolation
389 are commonly recovered patterns for the Cochise Filter Barrier (Provost et al., 2021) and other
390 communities (Shafer et al., 2010; Ralson et al., 2021), but our data showed that isolation in glacial
391 refugia often did not best explain genome-wide differentiation. This could be due to erosion of
392 historical signals as the Cochise Filter Barrier filters taxa and changes contemporary patterns of
393 gene flow. Alternatively, our proxy for IBH (resistance over projected Pleistocene habitat
394 suitability) may be a poor model for actual historical isolation. For example, paleoenvironmental
395 gradients may no longer be as readily detectable. The presence of the barrier alone was a better
396 predictor despite being atemporal.

397 In contrast, current environments best explain three genomes and the majority of partitions
398 for five species (with abundances and geographic distances playing a lesser role), suggesting that
399 phenomena operating on more recent timescales influenced genetic and morphological variation
400 across the landscape. If some of the taxa herein are going through incipient speciation, then these
401 contemporary factors should be most potent. Our identification of species abundances as a
402 relatively important predictor of genetic divergence aligns well with landscape genetic studies that
403 use proxies for the effects of contemporary phenomenon and ecological factors on genetic
404 variation (Burney and Brumfield 2009, Paz et al 2015). For example, urbanization, which
405 fragments and reduces population sizes, is well known to impact rates of gene flow and drift, acting
406 as a strong barrier of gene flow since the 20th century (Miles et al., 2019). Our use of available
407 abundance data across large spatial scales shows a more direct relationship between varying
408 abundances across the landscape with levels of differentiation. Further, while both historical and
409 contemporary processes are influencing taxa across this biogeographic barrier, contemporary
410 patterns are seemingly more influential.

411
412 *Relationship between best-models and window summary-stats*

413 In contrast to the extrinsic drivers of the genomic landscape that we have focused on here,
414 there were no clear associations between partition characteristics and support for a particular
415 model. For example, we found no significant differences in any species between recombination
416 rate across chromosomes and which spatial models were most important on that chromosome. At
417 the phylogeographic-scale, low recombination regions of the genome have been shown to be more
418 likely to reflect population structure (Manthey et al., 2021) and the species tree topology (Thom
419 G, Moreira LR, Batista R, Gehara M, Aleixo A, Smith BT, unpublished data,
420 <https://www.biorxiv.org/content/10.1101/2021.12.01.470789v1>). The avian recombination rate
421 landscape is thought to be conserved across taxa, even though exact genomic locations of
422 divergence across taxa are not (Singhal et al., 2015, Turbek et al., 2021), with our ten focal species
423 ranging in divergence time from ~75 thousand to ~12 million years between taxa (Harris et al.,
424 2018; Kumar et al., 2017; Barker et al., 2015; Mason and Burns 2013; Price et al., 2014; Pasquet
425 et al., 2014; Hooper and Price 2017; Mitchell et al., 2016; Gibb et al., 2015). Correlations in
426 recombination rates at the same genomic position in these species are greater than 0.37 across
427 chromosomes and always positive (Turbek et al., 2021). The ten desert birds we investigated, in
428 contrast, have estimated divergence times ranging from ~10 to ~60 million years between taxa
429 (Kumar et al., 2017; Barker et al., 2015; Mason and Burns 2013), with correlations in
430 recombination rates at the same genomic position that were often smaller in magnitude and
431 negative. This could reflect a real pattern, where the recombination landscapes are only conserved
432 within more closely related species; our closest taxa, the two non-sister *Toxostoma*, do have the
433 highest correlation in recombination rates across windows and are in the top 25% of the
434 distribution in correlations. However, the differences found could have been caused by coverage
435 depth, differences in the recombination rate estimators used, or missing data allowance. In
436 addition, genetic partitions with higher F_{ST} were more likely to show isolation-by-barrier as the
437 best model. These two metrics should be correlated; the former quantifies the degree of
438 differentiation across the Cochise Filter Barrier, and the latter assigns individuals to their
439 respective sides of the Cochise Filter Barrier. In species where there was differentiation, these two
440 measures should describe the same phenomenon. This likely reflects the gradient in differentiation
441 across species in the community. Given the wide variation across taxa, future work must be done
442 to clarify the relationship between genomic architecture and evolutionary signal at multiple
443 phylogenetic scales.

444 We explored the signal in our data by examining multiple ways of partitioning genomic
445 windows, using different thresholds of missing data, and evaluating how data attributes influenced
446 model support. We found that genetic partitions with more missing data were more likely to have
447 ambiguous results. Genetic summary methods like PCA are impacted by missing data, particularly
448 when they are imputed, which can cause individuals with disproportionately high levels of missing
449 data to appear like they are admixed between populations (Yi and Latch 2021). It is likely that the
450 reverse is true, where individuals with disproportionately low levels of missing data should fall
451 out as their own populations more readily. For example, in some of our species (namely *Vireo*
452 *bellii*, *Auriparus flaviceps*, *Polioptila melanura*) the individuals with highest missing data
453 clustered as their own population before detecting any other spatial patterning. We ameliorated
454 this by dropping individuals with too much missing data in some of our datasets. Overall, we did
455 not find qualitative differences in population assignments, but it did generally inflate our fixation
456 values and deflate our genetic diversity values. This is sensible, as reducing the number of

457 individuals should both increase the likelihood of fixation due to sampling error as well as decrease
458 the overall amount of nucleotide diversity.

459

460 *Morphological versus genetic associations*

461 We found that in most taxa, genotypic and phenotypic variation within species, and even
462 different aspects of morphological phenotype within species, were not associated with the same
463 landscape factors. Phenotypes were better explained by abundance, whereas genotypes were better
464 explained by the contemporary environment. Discordance between genetic and phenotypic
465 predictors of spatial variation have been observed in other systems, where phenotypic variation
466 was better explained by the environment (Moreira et al., 2020). This discordance could be due to
467 polygenic traits, where genotype-phenotype associations may be mediated by multiple loci of
468 small effect working in concert, either by changing protein structure or regulation (Yusuf et al.,
469 2020, Knief et al., 2017, Duntsch et al., 2020, Aguillon et al., 2021). However, for some
470 phenotypes like plumage color, single genes of large effect have been implicated which should
471 strengthen correlations between genotype and phenotype, at least for those loci (Sin et al., 2020;
472 Toews et al., 2016). For desert birds in particular, phenotypic variation in metabolism (as well as
473 in microbiomes) has been linked to genes that vary with the environment (Ribero et al., 2019). In
474 our study, as with genetic differentiation, the extent of phenotypic structuring varied across
475 species, with bill and body size being significantly different between deserts in a few taxa, but
476 somewhat surprisingly, environmental variation did not usually explain morphological
477 differences. For example, adaptations in bill morphology are frequently observed, such as in Song
478 Sparrows on the Channel Islands that have higher bill surface area in hotter climates (Gamboa et
479 al., 2021). The lack of a tight correlation between environment and phenotype were likely
480 reflective of the shallowness of the evolutionary divergences and the subtlety of the environmental
481 gradient across deserts. The two *Toxostoma* species in our study have previously shown
482 contrasting patterns with respect to climate on beak morphology: *T. crissale* has larger bills in drier
483 habitats, which may aid in cooling while conserving water, while *T. curvirostre* showed a pattern
484 contrary to thermoregulatory predictions with larger bills in cooler climates (Probst et al., 2021),
485 suggesting even in closely related species climate may not have the same role on morphological
486 variation. Even though phenotypic data partitions often did not have the same explanatory factor
487 with respect to the general dissimilarity modeling, there was a correlation between population
488 structure in the genome (and chromosomes to a lesser extent) and phenotypic variation across these
489 ten birds, in that taxa lacking morphological change also lack genetic variation overall.

490

491 *Conclusion*

492 By quantifying patterns in genotypic and phenotypic variation in communities distributed
493 across a biogeographic barrier, we found that multiple co-occurring processes occur that impact
494 variation within taxa. Although we found that isolation across an environmental gradient was
495 among the most important associations in predicting genetic and phenotypic variation, the best-fit
496 model varied across species and data partitions to reflect these multiple processes. These findings
497 underscore the importance of accounting for heterogeneity in the genome, phenome, and
498 diversification mechanisms acting across time and space to have the most comprehensive picture
499 of spatial structuring in species. This will allow for an assessment of whether best-fit models that
500 are proxies for neutral and adaptive processes are consistent with partitions that are evolving under
501 the same conditions. Without a holistic understanding at each of these levels of organization, as
502 well as the addition of future work that concurrently estimates selection at the organismal and the

503 nucleotide levels, the actual mechanisms that shape communities will remain obscured. Further,
504 while we did not find consistent predictors of phenotypic divergence, it is still an open question
505 whether other measures of phenotypic variation (e.g., behavioral) may better track divergence, or
506 phenotypic divergence does not follow a deterministic pattern along weak environmental
507 gradients. Overall, this work displays the necessity of integrating spatial predictors of population
508 divergence, differentiation across the genomic landscape, and phenotypic variation in
509 understanding the multiple different mechanisms that have produced the population histories we
510 see across contemporary communities of birds in North America.

511

512 **Methods and Materials**

513

514 *Study system*

515 The Sonoran and Chihuahuan deserts contain environmental and landscape variation that
516 make them suitable for testing if any of the five discussed spatial models (IBA, IBB, IBD, IBE,
517 and IBH) structure intraspecific variation in taxa. Across the two deserts and the transition zone
518 between them, there is variation in precipitation, elevation, temperature, and vegetation that could
519 result in local adaptation and isolation-by-environment. (Shreve, 1942; Reynolds et al., 2004).
520 Pleistocene glacial cycles repeatedly separated and connected, such that some taxa experienced
521 dramatic range shifts (Zink 2014, Smith et al., 2011), which could have isolated taxa in each desert.
522 Further, there is a well-studied biogeographic barrier separating the deserts, the Cochise Filter
523 Barrier, which is an environmental disjunction that demarcates the transition between the Sonoran
524 and Chihuahuan deserts of southwestern USA and northern Mexico. The barrier is thought to have
525 begun forming during the Oligo-Miocene and completed during the Plio-Pleistocene (Morafka,
526 1977, Van Devender, 1990; Van Devender et al., 1984, Holmgren et al., 2007, Spencer, 1996) and
527 has formed a community ranging from highly differentiated taxa to unstructured populations
528 (Provost et al., 2021). Demographic troughs caused by spatially varying population abundances
529 could impact the frequency of gene flow across the landscape and the degree of genetic
530 connectivity across the deserts.

531

532 *Genetic sequencing and genome processing*

533 We performed whole-genome-resequencing across 10 species of birds from the Sonoran
534 and Chihuahuan deserts, obtaining genetic samples from new expeditions and loans from natural
535 history museums (*Cardinalis sinuatus*; *Toxostoma crissale*, *Toxostoma curvirostre*; *Amphispiza*
536 *bilineata*, *Melospiza fusca*; *Polioptila melanura*; *Phainopepla nitens*; *Auriparus flaviceps*;
537 *Campylorhynchus brunneicapillus*; *Vireo bellii*; Supplementary Table 6; Supplementary Figure
538 15). These species reflect different songbird morphotypes and ecologies in the deserts (e.g., large-
539 to small-bodied, insectivorous to granivorous, migratory to resident). Three of these species (*V.*
540 *bellii*, *T. curvirostre*, *M. fusca*) have shown evidence of structure across the Cochise Filter Barrier,
541 while an additional three (*P. melanura*, *A. flaviceps*, *C. brunneicapillus*) have shown evidence of
542 no structure (Zink et al., 2001; Rojas-Soto et al., 2007; Teutimez, 2012; Klicka et al., 2016, Smith
543 et al., 2018).

544 Using 221 individuals across our 10 focal species, we sequenced 8–14 individuals in both
545 the Sonoran and Chihuahuan deserts per species for a total of 18–25 samples per species. Library
546 preparation and sequencing was performed by RAPiD Genomics (Gainesville, FL). We mapped
547 raw reads of each species to their phylogenetic closest available reference genomes
548 (Supplementary Table 7): notably, *A. bilineata* and *M. fusca* were mapped to the same genome, as

549 were *C. brunneicapillus*, *T. crissale*, *T. curvirostre*, *P. melanura*, and *P. nitens* (see Supplementary
550 Information). Before mapping, we created pseudo-chromosomal assemblies of these genomes
551 using Satsuma version 3.1.0 (Grabherr et al., 2010) by aligning to the *Taeniopygia guttata* genome
552 (GCF_000151805.1), retaining pseudo-chromosomes with the prefix “PseudoNC”. Hereafter,
553 pseudo-chromosomes will be referred to as chromosomes.

554 We filtered our sequences with FastQ Screen version 0.14.0 (Wingett et al., 2018) to
555 remove contamination by filtering out reads that mapped to PhiX and the following genomes:
556 *Homo sapiens*, *Escherichia coli*, *Enterobacteriophage lambda*, and *Rhodobacter sphaeroides*.
557 From our raw reads, we used a pipeline that produced genotype likelihoods using ANGSD version
558 0.929 (Korneliussen et al., 2014). We converted cleaned FastQ files to BAM using bwa version
559 0.7.15 (Li and Durbin 2009, Li and Durbin 2010) and picard version 2.18.7-SNAPSHOT from the
560 GATK pipeline (McKenna et al., 2010, DePristo et al., 2011, Van der Auwera et al., 2013). Next,
561 we prepared the BAM files to be used in the ANGSD pipeline using samtools version 1.9-37 (Li
562 et al., 2009; Li 2011), bamUtil version 1.0.14 (Jun et al., 2015), and GATK version 3.8-1-0
563 (McKenna et al., 2010). This pipeline creates genotype likelihoods to account for uncertainty for
564 low-coverage sequences.

565 We investigated the impact of missing data on our analyses using three thresholds for
566 retaining sites: a complete dataset, in which all individuals were retained irrespective of missing
567 data; a 75% dataset, in which individuals were only retained if they had less than 75% missing
568 sites; and a 50% dataset, in which individuals were only retained if they had less than 50% missing
569 sites. These different datasets were used for a suite of downstream analyses to assess the sensitivity
570 of the results to individuals with missing data.

571 572 *Evaluating population structure across the Cochise Filter Barrier*

573 We characterized the degree of population structure across the whole genome and in
574 individual chromosomes across the Cochise Filter Barrier in our focal species. First, using
575 PCAngsd in ANGSD (Meisner and Albrechtsen 2018), which assigns individuals to K clusters and
576 estimates admixture proportions for each individual. To evaluate whether there was structure
577 across the Cochise Filter Barrier, we selected K=2 (though we visualized K values from two to
578 three). We performed this for the complete, 75%, and 50% missing data datasets, but found that
579 these values were largely congruent across the datasets, and so we only use the complete dataset
580 for describing population structure (Supplementary Figure 16, Supplementary Figure 17,
581 Supplementary Figure 18). Second, we plotted population assignment changes over space using a
582 cline analysis via the hzar version 0.2-5 R package (Derryberry et al., 2014) and custom scripts
583 (modified from Burbrink et al., 2021). Analyses were conducted in R version 3.6.1 (R Core Team
584 2019). We did this to quantitatively evaluate the differences in population structure across
585 chromosomes and in the genome more broadly. We thus were able to calculate the location and
586 width of clines for the entire genome and each chromosome.

587 Complementing our genome-wide analyses, we ran a local principal components analysis
588 along the genome on the complete dataset using the R package lostruct version 0.0.0.9000 (Li and
589 Ralph 2019). Different chromosomes showed different relationships between individuals (see
590 Supplementary Information). Because of this, we wanted to cluster regions of the genome together
591 that showed similar relationships between individuals in case specific evolutionary processes were
592 causing this pattern. The lostruct method performs principal component analysis on individual
593 windows of the genome, then uses multidimensional scaling (MSDS) to summarize how similar
594 the windows' principal component analyses are when dividing the genome. We extracted three

595 subsets of outliers for each species, which we designated LS1, LS2, and LS3, and compared it to
596 the remainder of the genome, representing non-outliers.

597

598 *Genomic summary statistics*

599 We characterized genetic variation across each species' genome and partitions of the
600 genome by calculating a suite of summary statistics and metrics. To quantify genetic
601 differentiation within each species, we calculated pairwise genetic distances between individuals
602 from VCF files using the bitwise.dist function in poppr R package version 2.9.2 (Kamvar et al.,
603 2014; Kamvar et al., 2015), which served as the genetic distance matrices for our generalized
604 dissimilarity matrix models (see below). The function bitwise.dist calculates the Hamming
605 distance of the DNA (i.e., number of differences between two strings). We scaled this distance
606 such that missing data was assumed to match sites without missing data, but final distances were
607 scaled such that comparisons with more missing data would have inflated distances. Neighbor-
608 joining trees were calculated from these matrices to contrast genealogies across the genome.
609 Genealogies across the genome were visualized by calculating pairwise and normalized Robinson-
610 Foulds (RF) distances between all pairs of trees per species (Robinson and Foulds 1981).
611 Recombination rates (in crossovers per base pair, c/bp) across the genome were estimated using
612 the program ReLERN (Adrion et al., 2020). This program combines simulation with a recurrent
613 neural network to estimate the recombination rate on each chromosome in 100,000 bp windows.
614 We also performed a sliding window D_{XY} analysis using the calcDxy R script included with
615 ngsTools version 1.0.2 (Fumagalli et al., 2014), which gives site-wise D_{XY} values, and then
616 averaged across windows. Windows were overlapping with a size of 100,000 base pairs and offset
617 by 10,000 base pairs. Missing data were calculated using vcftools (Danecek et al., 2011). This was
618 calculated per window, per chromosome, per genome, per site, and per individual.

619 Using ANGSD's realSFS function, we performed a sliding window F_{ST} analysis by
620 converting SAF output from ANGSD to a site frequency spectrum for both desert populations in
621 each species. Detailed settings can be found in the supplementary information. We performed F_{ST}
622 outlier analysis for our species using the calculated F_{ST} values. Z-scores for F_{ST} for each species
623 were calculated using the formula $Z_{F_{ST}} = (\text{observed } F_{ST} - \text{mean } F_{ST}) / \text{SD } F_{ST}$. We split the genome into
624 two different partitions based on these z-scores: F_{ST} peaks, for values of F_{ST} greater than five
625 standard deviations above the mean ($z\text{-score} > 5$) and F_{ST} troughs for values of F_{ST} greater than five
626 standard deviations below the mean ($z\text{-score} < -5$). We only report the F_{ST} peaks in the main
627 manuscript: for F_{ST} troughs, see the supplementary information. We performed this outlier
628 detection for the complete, 75%, and 50% missing datasets.

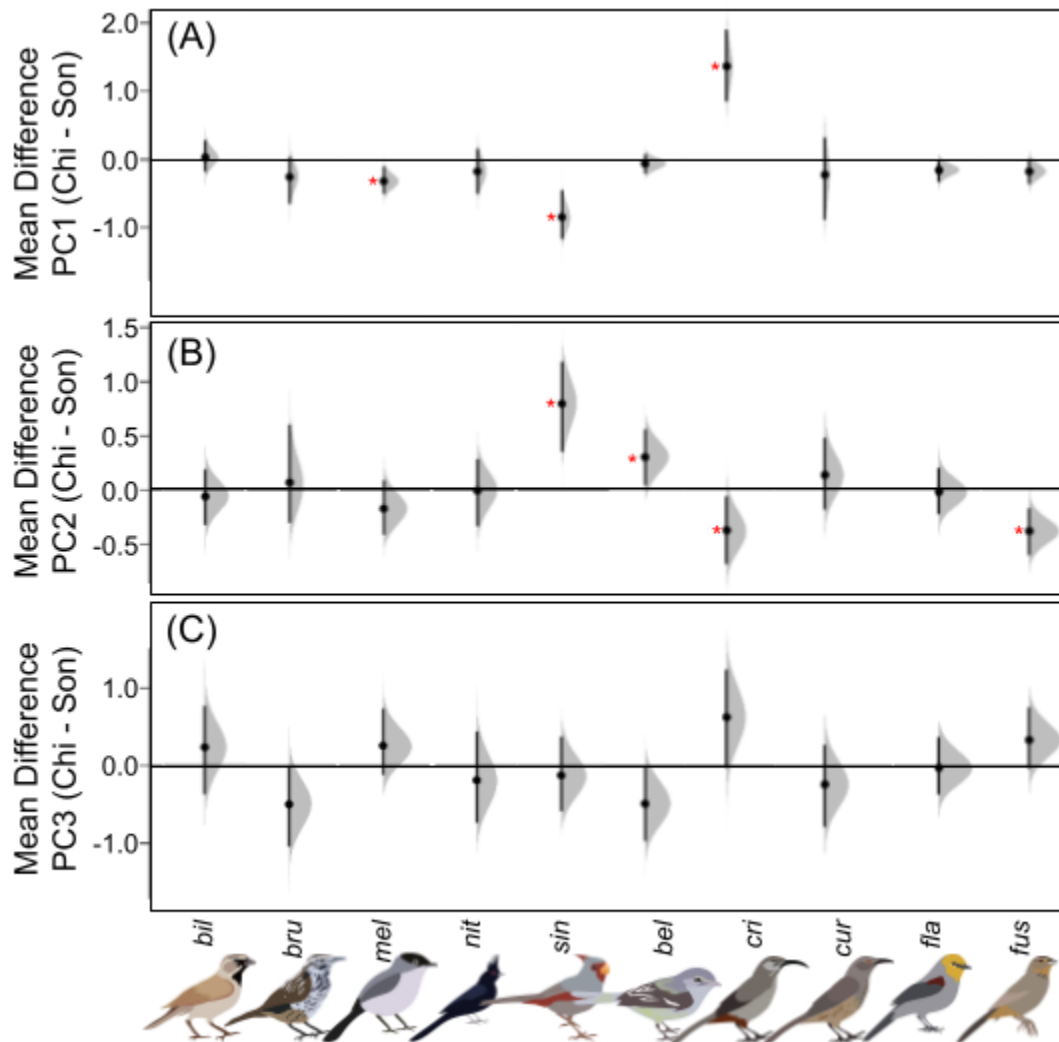
629

630 *Morphological data*

631 We quantified morphological variation in our 10 focal species to assess which of the spatial
632 models best explain morphological variation across the landscape (see *Generalized Dissimilarity*
633 *Matrix Models*). We measured 366 specimens (19–59 per species), excluding known females and
634 known juveniles to account for any variation attributed to sex and age. Of those, 29 were also
635 present in the genomic dataset, with 0–8 individuals per species.

636 We generated seven raw plus seven compound morphological measurements, which we
637 designated as proxies for thermoregulation and dispersal, respectively (see Supplementary
638 Information). We reduced the dimensionality of the 14 morphological measurements using a
639 principal components analysis (PCA). We then calculated four distance matrices between
640 individuals: one Euclidean distance matrix for all morphological variables, where we calculated

641 the euclidean distance between individuals among all raw and calculated measurements; and three
642 euclidean distance matrices for the first three principal components, PC1, PC2, and PC3. We
643 assessed whether there were differences in morphological PCA space between the Sonoran and
644 Chihuahuan Desert populations in each species using DABEST tests in the dabestr package version
645 0.3.0 (Figure 5; Supplementary Figure 19; Supplementary Figure 20; Ho et al., 2019). Note that
646 this method does not give explicit significance values, instead it shows whether expected
647 confidence intervals overlap zero (i.e., no difference between deserts) or not.
648



649
650 Figure 5: Distribution of unpaired mean differences between Sonoran and Chihuahuan desert individuals for each
651 species from DABEST analysis for morphological PC1 (A), PC2 (B), and PC3 (C). Black horizontal line is at zero,
652 black points and vertical lines show mean and confidence intervals for each distribution in gray. Comparisons that do
653 not cross the zero line are considered significant in DABEST tests, indicated with red asterisk. On the X axis are each
654 species with images (scale does not reflect size differences) with species names are shortened for legibility
655 (“bel”=*Vireo bellii*, “bil”=*Amphispiza bilineata*, “bru”=*Campylorhynchus brunneicapillus*, “cri”=*Toxostoma crissale*,
656 “cur”=*Toxostoma curvirostre*, “fla”=*Auriparus flaviceps*, “fus”=*Melospiza fusca*, “mel”=*Poliophtila melanura*,
657 “nit”=*Phainopepla nitens*, “sin”=*Cardinalis sinuatus*).
658

659 *Isolation across the landscape at different temporal resolutions*

660 We calculated IBD matrices by calculating the euclidean geographic distance between the
661 latitude/longitude pair of each specimen in R. We used the WGS84 projection for all data. These
662 variables were somewhat correlated with one another, though less so after accounting for
663 geographic distance (Supplementary Figure 21).

664 To produce data for the IBH model, we calculated environmental resistances in the Last
665 Glacial Maximum (LGM; ~21,000 years ago) for each species. To do this, we created ecological
666 niche models (ENMs) using 19 layers representing contemporary climate (WorldClim; Hijmans
667 et al., 2005) at a resolution of 2.5 arcminutes. We used MaxEnt (Phillips et al., 2006), with
668 ENMeval version 0.3.1 as a wrapper function for model selection (Muscarella et al., 2014).
669 ENMeval optimizes MaxEnt models based on different sets of feature classes and regularization
670 values (see Supplementary Information). The contemporary ENMs (see IBE section below) were
671 then backprojected to the LGM using WorldClim paleoclimate data (Hijmans et al., 2005). We
672 also backprojected to the Mid-Holocene, but contemporary and Mid-Holocene ENMs were highly
673 correlated, so we excluded the Mid-Holocene values from downstream analyses. We then scaled
674 the LGM suitability values to range between 0–1 and calculated resistances across the environment
675 using the least cost path distance method in ResistanceGA version 4.0–14 (Peterman et al., 2014,
676 Peterman 2018). Regions of high resistance are predicted to reflect poor habitat and be costly to
677 traverse through. The ENMs were thresholded to equal sensitivity-specificity values for
678 visualization (Supplementary Figure 22).

679 We approximated IBB by assigning individuals based on their location relative to the
680 Cochise Filter Barrier (see Supplementary Information). For proximity to the Cochise Filter
681 Barrier, we assigned individuals to either Sonoran or Chihuahuan populations either based on the
682 results of the K=2 clustering analysis, if there was structure across longitudes, or according to a
683 cutoff of longitude if there was no structure. We chose 108 °W longitude as our cut off—
684 individuals west of this point were deemed Sonoran, and individuals east of this point were deemed
685 Chihuahuan (but see Provost et al., 2021). In some cases, species with genetic breaks had some
686 uncertainty due to unsampled areas or admixed individuals—we labeled these individuals as being
687 unclear with respect to their desert assignment. Georeferencing on some morphological specimens
688 was poor, but all except two specimens (see Results) were identified at least to county level if not
689 to a specific locality. When localities were given, we georeferenced the specimens to the nearest
690 latitude/longitude. Otherwise, we assigned individuals to the centroid of their state or county.

691 We independently tested IBE by using two datasets: contemporary environmental distance
692 and resistance. For the environmental distances, we used the 19 WorldClim bioclimatic layers (see
693 IBH section). For the latitude/longitude location of each specimen used in both the morphological
694 and genomic analysis, we extracted the values on those WorldClim layers and then calculated the
695 euclidean distances in environmental space between specimens. This gave us an estimate of how
696 different the environments were at each specimen's locality. For the environmental resistances, we
697 created ENMs using the WorldClim layers, then added layers for soil properties, distance to water,
698 terrain features, and vegetation, and occurrence data for the focal species (see Supplementary
699 Information). We then calculated resistances and thresholded as described above.

700 To assess IBA, which had a temporal scale of the last 50 years, we obtained abundance
701 information from the Breeding Bird Survey (Pardieck et al., 2019). This dataset consists of
702 replicated transects where individual birds are counted across the whole of the United States. The
703 methodology for counting is standardized and covers multiple decades of observations, with our
704 dataset comprising data from 1966–2018. We downloaded raw data for all points, then subsetted

705 our data to our ten focal species. We averaged the number of individuals across years (though
706 some points only had a single year). We then interpolated across points using inverse distance
707 weighted interpolation in the spatstat version 2.1-0 package in R (idp=5). The interpolations were
708 converted to rasters with extents and resolutions matching those of the ENMs. We then calculated
709 resistances such that regions of high abundance had low resistance, to generate an abundance
710 distance matrix between individuals.

711

712 *Generalized dissimilarity matrix models*

713 We assessed the relative effect of alternative spatial models on intraspecific variation in
714 our focal species by building generalized dissimilarity matrix models (GDMs). As spatial layers
715 representing our five models, we calculated geographic distances, abundance resistances,
716 environmental distance and resistance, separation by barrier, and paleoenvironmental resistance
717 between all individuals in each species. The models represent different temporal resolutions, with
718 IBH spanning millions to tens of thousands of years ago, IBD spanning thousands to tens of years,
719 IBE spanning hundreds to tens of years, IBA spanning tens to single years, and IBB describing the
720 present-day configuration of the barrier. These predictors served as the input parameters for our
721 GDMs and will be discussed in detail below. With our numerous response matrices (four
722 morphological matrices, three genome matrices for each missing data cutoff, 35 matrices for
723 chromosomes, five matrices for the lostruct partitions, and six matrices for the F_{ST} outliers with
724 missing data cutoffs) and our six predictor matrices (with two for IBE: environmental distance,
725 environmental resistance), we generated generalized dissimilarity matrix models using the gdm
726 package version 1.3.11 in R (Manion et al., 2018). We tested which of IBA, IBB, IBD, IBE, IBH,
727 or a combination best explained the variation in the response matrix (see below). Not all species
728 had all chromosomes sequenced, and not all models converged: we have omitted those data. For
729 each of the 45 response matrices per species, we built a univariate model where the
730 genomic/chromosomal variable was predicted solely by one of the six predictor matrices. We also
731 built models with combinations of two (bivariate) or three variables (trivariate), which we present
732 in the Supplementary Information. Further, we present the GDM results for the chromosomes in
733 the supplementary information. We compared the models based on the highest percent deviance
734 explained.

735 To identify any overarching patterns with respect to which model of landscape evolution
736 best explained genetic diversity (Supplementary Figure 23), we calculated four summary statistics
737 for each chromosome, each lostruct and F_{ST} outlier partition, and the genome as a whole. We tested
738 whether genomic summary statistics on each chromosome (F_{ST} , D_{XY} , missing data, recombination
739 rate) were correlated with explained percent deviance with an analysis of variance (ANOVA) test
740 and a Tukey's honest significant difference test (Chambers et al., 1992, Miller 1981, Yandell 1997)
741 using the stats v. 3.6.1 package in R. We did this for the complete dataset; for 75% and 50%
742 missing data datasets, see Supplementary Information. We also calculated linear models
743 comparing the proportion of each model to species-wide estimates of habitat suitability across the
744 barrier. For all significance tests, we used an alpha value of 0.05 as our significance cutoff.

745 We evaluated whether the best-predictors of genomic landscapes varied across species and
746 across partitions of the data using Chi-squared tests of significance, via the chisq.test function in
747 the stats package in R. For each, the expected distributions assuming no differences between
748 species, partitions, or structure were calculated and compared to the observed distributions. Chi-
749 squared tests were performed both with and without Monte Carlo simulations (N=2000 simulations
750 each repeated 1000 times).

751

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768

769 **Data Availability**

770 These custom functions were deposited into a custom R package, `subspLabelR`, which is
771 available at github.com/kaiyaprovost/subspLabelR, and scripts used to perform these analyses
772 are found at github.com/kaiyaprovost/whole_genome_pipeline. All data used to perform analyses
773 will be available on Dryad upon acceptance.

774

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