Evolution, 2023, **XX(XX)**, 1–13
https://doi.org/10.1093/evolut/qpad031
Advance access publication 1 March 2023
Original Article

Convergence or redundancy: alternative views about the evolutionary genomics of character displacement

Douglas L. Crawford[1], Max C. Thompson[1,2], Trinity Conn[1,3], Madeline Kaufman[1], Trenton Voytko[1], Anna M. Merritt[1], Heather MacKay[1], Tessa Billings[1], Yi Chng[1], Yoel E. Stuart[4], Marjorie F. Oleksiak[1]

[1]Department of Marine Biology and Ecology, RSMAS, University of Miami, Miami, FL, United States
[2]Departments of Psychiatry and Cellular and Molecular Pharmacology, University of California, San Francisco School of Medicine, San Francisco, California, United States
[3]Department of Biology, The Pennsylvania State University, University Park, PA, United States
[4]Department of Biology, Loyola University Chicago, Chicago, IL, United States

Corresponding author: Department of Marine Biology and Ecology, RSMAS, University of Miami, 4600 Rickenbacker Causeway, Miami FL 33149, United States.
Email: dcrawford@rsmas.miami.edu

Abstract

An evolutionary debate contrasts the importance of genetic convergence versus genetic redundancy. In genetic convergence, the same adaptive trait evolves because of similar genetic changes. In genetic redundancy, the adaptive trait evolves using different genetic combinations, and populations might not share the same genetic changes. Here we address this debate by examining single nucleotide polymorphisms (SNPs) associated with the rapid evolution of character displacement in *Anolis carolinensis* populations inhabiting replicate islands with and without a competitor species (1Spp and 2Spp islands, respectively). We identify 215-outliers SNPs that have improbably large F_{ST} values, low nucleotide variation, greater linkage than expected and that are enriched for genes underlying animal movement. The pattern of SNP divergence between 1Spp and 2Spp populations supports both genetic convergence and genetic redundancy for character displacement. In support of genetic convergence: all 215-outliers SNPs are shared among at least three of the five 2Spp island populations, and 23% of outlier SNPS are shared among all five 2Spp island populations. In contrast, in support of genetic redundancy: many outlier SNPs only have meaningful allele frequency differences between 1Spp and 2Spp islands on a few 2Spp islands. That is, on at least one of the 2Spp islands, 77% of outlier SNPs have allele frequencies more similar to those on 1Spp islands than to those on 2Spp islands. Focusing on genetic convergence is scientifically rigorous because it relies on replication. Yet, this focus distracts from the possibility that there are multiple, redundant genetic solutions that enhance the rate and stability of adaptive change.

Keywords: polygenic adaptation, experimental ecology, genetic redundancy, *Anolis*, SNP

Introduction

If we could re-run evolutionary events, would we end up with similar adaptive outcomes? Famously, Gould stated that evolution is *not predictable* (Gould, 1994); instead, phenotypes are constrained by the history of species (Gould & Lewontin, 1979) and would not re-occur if earth's history were restarted and allowed to re-evolve (Gould, 2002). Such stochastic evolution is found in Darwin's finches (Grant & Grant, 2002) and the experimental evolution of *Escherichia coli* over 60,000 generations (Good et al., 2017). Yet, convergent phenotypes are often found among independent taxa: three spine stickleback populations (*Gasterosteus aculeatus*) independently evolved reduced body armor with invasion into freshwater (Hendry et al., 2013; Hohenlohe et al., 2010; Schluter, 2000); *Anolis* species independently evolved common morphology when occupying common niche space among Caribbean islands (Losos, 2011); guppy populations in Trinidad (*Poecilia reticulata*) independently evolved similar life history and coloration when subjected to higher predation (Kemp et al., 2018; Reznick & Bryga, 1996; Reznick et al., 1996); and across a wide geographic range, aquatic fish species from colder environments have independently evolved higher than expected metabolic rates (White et al., 2012). These convergences extend to biochemical traits: *Fundulus* species independently evolve the higher expression of the same three glycolytic enzymes in colder environments (Pierce & Crawford 1997), and diverse bird taxa that routinely encounter high altitudes have independently evolved hemoglobins with greater oxygen affinities (Natarajan et al., 2016).

Based on these and other studies, adaptive evolution can be both idiosyncratic and surprisingly repeatable among closely related taxa (Blount et al., 2018). What is unclear is whether phenotypic convergence is the result of genetic convergence, arising from the same genetic changes. Genetic convergence depends on the genomic architecture of a phenotypic trait. If there is a single gene of large effect, like coat color in mammals, then repeated use of a single gene is common (Manceau et al., 2010; Yeaman, 2022). In contrast, if the genomic architecture is polygenic with genetic redundancy, then genetic convergence is less likely because many different gene combinations can drive adaptive evolution (Barghi et al., 2019, 2020; Yeaman, 2015). This debate is important because redundant polygenic adaptive evolution has the advantage of being rapid, being less sensitive to

Received May 27, 2022; revisions received January 25, 2023; accepted February 28, 2023

migration, and maintaining genetic polymorphisms (Barghi et al., 2020; Ehrlich et al., 2021; Yeaman, 2015). Thus, identifying the genomic architecture underlying rapid evolution is fundamentally important to understand the effects of human-induced environmental change and to inform species conservation strategies (Gilman et al., 2010; Hoffmann & Sgro, 2011; Vandvik et al., 2020).

To address the genetic convergence vs. genetic redundancy debate, we investigate the genomic architecture of character displacement in *Anolis carolinensis* (Stuart et al., 2014). Character displacement is an evolved response among competitors that reduces niche overlap (Brown & Wilson, 1956; Germain et al., 2018; Grant, 1972; Huey & Pianka, 1974; Schluter, 2000; Schluter & Grant, 1984; Stuart & Losos, 2013). This reduction in shared niche space corresponds with increased interspecific phenotypic differences while reducing intraspecific variation (Reynolds et al., 2019). To investigate the genomic architecture of character displacement, we sampled *A. carolinensis* that live on spoil islands in the intracoastal waters along the central coast of eastern Florida (Figure 1). The arrival of *Anolis sagrei*, a competitor, was documented for many of these small islands in 1994. By 2010, approximately 20 generations after *A. sagrei's* arrival, *A. carolinensis* on two species islands (i.e., islands with competitors) showed evolutionary divergence in toe pad morphology associated with an increase in perch height (Stuart et al., 2014). Here, using the individuals sampled in 2010 (Stuart et al., 2014), we sequenced *A. carolinensis* from three islands without competitors (hereafter, 1Spp islands) and five islands with competitors, where *A. carolinensis* co-occurred with *A. sagrei* (hereafter, 2Spp islands, Figure 1, Supplementary Tables S1 and S2). We show that there are 215-outliers single nucleotide polymorphisms (SNPs) where 2Spp islands have small but significant allele frequency differences compared to 1Spp islands. Supporting the effect of natural selection, these outlier SNPs had lower nucleotide variation (pi) and greater LD (linkage disequilibrium) than expected. One perspective of these evolved differences in SNP allele frequencies between 1Spp and 2Spp islands is genetic convergence: all 215-outliers SNPs had similar changes on three out of five 2Spp islands, indicating convergence at the nucleotide level. An alternative perspective is a genetic redundancy: each 2Spp island had substantial allele frequency differences in a unique subset of outlier SNPs. We suggest that both perspectives are correct.

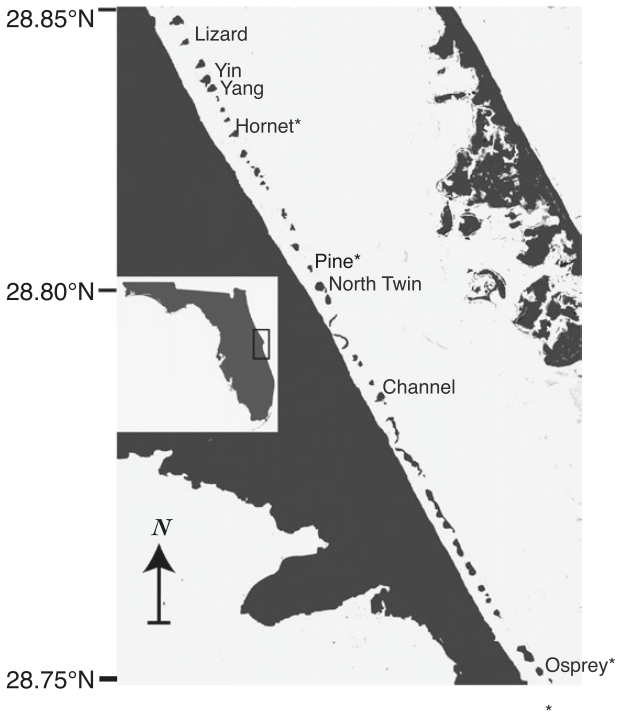

Figure 1. Mosquito Lagoon and experimental islands. Spoil islands in central Florida Intracoastal Waterway created by dredging with latitude on the right axis. Collection islands are named. Islands with * are 1Spp islands having only *A. carolinensis*. Total linear distance among the eight islands is 12.5 km. Each island is ~100 m in diameter.

Materials and methods

Anoles and genomic DNA

Tissue or DNA for 160 *Anolis carolinensis* and 20 *A. sagrei* samples were provided by the Museum of Comparative Zoology at Harvard University (Supplementary Table S2). These samples were collected in 2010 to examine character displacement in native *A. carolinensis* following the introduction of *A. sagrei* onto man-made spoil islands in Mosquito Lagoon, Florida (Stuart et al 2014). One hundred of the samples were genomic DNAs, and 80 samples were tissues (terminal tail clip, Supplementary Table S2).

Genomic DNA was isolated from tail tips using a custom SPRI magnetic bead protocol (Kamath et al., 2020). All DNA samples were gel electrophoresed to ensure high molecular mass and quantified by spectrophotometry and fluorescence using Biotium AccuBlueTM High Sensitivity dsDNA Quantitative Solution according to manufacturer's instructions.

Genotyping-by-sequencing (GBS) libraries were prepared using a modified protocol after Elshire et al (2011). Briefly, high-molecular-weight genomic DNA was aliquoted and digested using the ApeKI restriction enzyme. Digests from each individual sample were uniquely barcoded, pooled, and size selected to yield insert sizes between 300–700 bp (Kemp et al., 2018). Pooled libraries were PCR amplified (15 cycles) using custom primers that extend into the genomic DNA insert by three bases (CTG). Adding three extra-base pairs systematically reduces the number of sequenced GBS tags, enhancing sequencing depth. The final library had a mean size of 424 bp ranging from 188 to 700 bp.

Anolis SNPs

Pooled libraries were sequenced on one lane on an Illumina HiSeq 4000 in a 2 × 150 bp paired-end configuration, yielding approximately 459 million paired-end reads (~138 Gb). The medium Q-Score was 42 with the lower 10% Q-Scores exceeding 32 for all 150 bp. The initial library contained 180 individuals with 8,561,493 polymorphic sites. Twenty individuals were *Anolis sagrei,* and two individuals (Yan 1610 and Yin 1411) clustered with *A. sagrei* and were not used to define *A. carolinesis'* SNPs.

Anolis carolinesis reads were aligned to the *Anolis carolinensis* genome (NCBI RefSeq accession number:/GCF_000090745.1_AnoCar2.0). SNPs for *A. carolinensis* were called using the GBeaSy analysis pipeline Wickland et al 2017 with the following filter settings: minimum read length of 100 bp after barcode and adapter trimming, minimum phred-scaled variant quality of 30 and minimum read depth of 5. SNPs were further filtered by requiring SNPs

to occur in > 50% of individuals, and 66 individuals were removed because they had less than 80% of called SNPs. These filtering steps resulted in 51,155 SNPs among 94 individuals. Final filtering among 94 individuals required all sites to be polymorphic (with fewer individuals, some sites were no longer polymorphic) with a maximum of two alleles (all are biallelic), minimal allele frequency 0.05, and expected heterozygosity (H_e) that does not "exceed" Hardy–Weinberg equilibrium (HWE and a false discovery rate <0.01). SNPs with large H_e that exceeded HWE frequencies were removed (2,280 SNPs). These SNPs with large significant heterozygosity may result from aligning paralogues (different loci), and thus may not represent polymorphisms. No SNPs were removed with low H_e (due to possible demography or other exceptions to HWE). After filtering, 94 individuals yielded 44,120 SNPs. Thus, the final filtered SNP data set was 44K SNPs from 94 individuals (1Spp n = 39 and 2Spp n =54).

Statistical analyses

Eight *A. carolinensis* populations were analyzed: three populations from islands with *A. carolinesis* only (1Spp islands) and five populations from islands where *A. carolinesis* co-exist with *A. sagrei* (2Spp islands, Table 1, Supplementary Table S1). Most analyses pooled the three 1Spp islands and contrasted these with the pooled five 2Spp islands. Minor allele frequency (MiAF), *where the minor* allele is defined across all 94 individuals and thus may be > 0.5 in one or more populations.

Two approaches were used to define SNPs with unusually large allele frequency differences between 1Spp and 2Spp islands: (1) comparison of F_{ST} values to random permutations and (2) a modified FDIST approach to identify outlier SNPs with large and statistically improbable F_{ST} values.

Shared, substantial differences in MiAF were defined by the 95% confidence interval (CI) across the five 2Spp islands for each SNP. Specifically, if the difference between 1Spp and 2Spp MiAF was positive (2Spp has a lower MiAF), then 2Spp's SNP MiAF had to be less than the upper 95% CI for 2Spp islands. Similarly, if 2Spp MiAF was greater than 1Spp MiAF (negative difference), then the 2Spp MiAF had to be larger than 5% CI for 2Spp islands. That is, a substantial difference occurs when the 2Spp MiAF is more similar to 2Spp MiAF than to the other 1Spp MiAF.

Random permutations

F_{ST} values were calculated in VCFTools (version 4.2; Danecek et al., 2011 where the *p*-values per SNP were defined by comparing F_{ST} values to 1,000 random permutations using a custom script (supplemental). Basically, random populations are individuals with all of their SNPs randomly assigned to one of eight islands or to 1Spp vs. 2Spp groups, using the original sample sizes (55 for 2Spp and 39 for 1Spp islands). F_{ST} values were re-calculated for every 1,000 randomizations using VCFTools.

Modified FDIST

To identify outlier SNPs with statistically large F_{ST} values, a modified FDIST (Beaumont & Nichols, 1996) was implemented in Arlequin (Excoffier et al., 2005). This modified approach applies 50,000 coalescent simulations using a hierarchical population structure, in which demes are arranged into *K* groups of d demes and in which migration rates between

Table 1. MiAF of 215 outlier SNPs. (A) MiAF for 1Spp and 2Spp islands, (B) MiAF for 1Spp and 2Spp islands for SNPs with shared substantial differences in five out of five, four out of five, and three out of five 2Spp islands, (C) and (D) the same as (B), but conditioned on whether 2Spp > 1Spp MiAF or vice versa. Starred (*) chi-square significant ($p < .002$) for three convergence categories (5, 4, 3) contingent on if 2Spp > 1Spp MiAF or not. The significant chi-square occurs when there is substantial change in five out of five 2Spp islands depending on the relative 1Spp and 2Spp MiAF. When 2Spp > 1Spp MiAF, there are too few five out of five convergences (3 vs. expected 12), and when 1Spp > 2Spp, there are too many (47 vs. expected 37); $p < .002$.

	1Spp	2Spp	Count	% OF 215
A				
MiAF	0.255	0.134	215	100.0%
MiAF when 2Spp > 1Spp	0.063	0.361	54	25.1%
MiAF when 1Spp > 2Spp	0.319	0.058	161	74.9%
B				
MiAF convergence all, 5 out 5	0.196	0.029	50	23.3%
MiAF convergence 4 out of 5	0.278	0.163	131	60.9%
MiAF convergence 3 out of 5	0.251	0.178	34	15.8%
C When 2Spp > 1Spp				
MiAF convergence all, 5 out 5	0	0.241	3*	1.4%
MiAF convergence 4 out of 5	0.066	0.367	39	18.1%
MiAF convergence 3 out of 5	0.067	0.3709	12	5.6%
D When 1Spp > 2Spp				
MiAF share all, 5 out 5	0.208	0.016	47*	21.9%
MiAF share 4 out of 5	0.368	0.076	92	42.8%
MiAF share 3 out of 5	0.351	0.074	22	10.2%

Note. MiAF = minor allele frequency; SNP = single nucleotide polymorphism.

demes are different within and between groups. Unlike the finite island models, which have led to large frequencies of false positives because populations share different histories (Lotterhos & Whitlock, 2014), the hierarchical island model avoids these false positives by avoiding the assumption of similar ancestry (Excoffier et al., 2009).

Population DAPC and structure

To investigate population structure, we applied discriminant analysis of principal components and Structure analyses. Discriminant analysis of principal components (DAPC; Jombart et al., 2010) in the R-package "adegenet" (ver. 2.0.1) (Jombart, 2008; Jombart & Ahmed, 2011) was used to visualize demographic relationships among islands. Bayesian information criterion was used to identify the most likely number of clusters, and adegenet optimization was used to identify the number of principal components analysis (PCAs) (Jombart et al., 2010). DAPC was run using a wide variety of PCAs: from 3 to 1/3N. Seven PCAs were chosen based on the optimization in DAPC (Jombart et al., 2010). Structure (Pritchard et al., 2000), similar to DAPC, provides the likely number of clusters by applying a Bayesian algorithm. One to eight clusters were used for the Structure admixture model. Each cluster was run with seven replicates, 25,000 burn-in periods, >110,000 replications, and correlated allele frequencies.

For Structure with admixture (Pritchard et al., 2000), the best *K* as suggested by Evanno et al. (2005) was used to align replicate runs. The Evanno approach relies on the rate of change in the log probability of data between successive *K* values as implemented using Structure Harvester (Earl & vonHoldt, 2011). CLUMPP (Porras-Hurtado et al., 2013) was used to align replicate runs. Colors were matched to DAPC colors as closely as possible using Structure Plots v.2 (http://omicsspeaks.com/strplot2/; Ramasamy et al., 2014).

LD: Linkage disequilibrium

TASSEL software (Bradbury et al. 2007; Glaubitz et al. 2014) was used to calculate LDs as D' and the correlation between allele frequencies (R^2) within each "population" (1Spp and 2Spp islands) using a hundred SNP window size (i.e., 100 SNPs, not 100 bp window) for the 44K SNP dataset and a 215 SNP window size (all SNPs) for the 215 SNP data set. Distances among LD pairs were used to partition the data into 300 bp or less, > 300 bp within a chromosome, and interchromosomal. The significances of LDs (D') were calculated relative to random values as defined in TASSEL (Bradbury et al. 2007; Glaubitz et al. 2014). For the 1,000 random LDs, 215 SNPs were chosen from 55 2Spp island individuals with 17K SNPs derived from the 44K SNPs without the SNP-outliers and $H_e > 0.1$. Non-outlier SNPs with $H_e > 0.1$ were chosen to match the genetic variation among outliers: among both 2Spp and 1Spp islands (median $H_e = 0.275$, 2.5% and 97.5 %CI = 0.114 and 0.446); larger H_e increases the frequency of large LD values but does not alter the finding.

Annotations

SNPeff (Cingolani et al., 2012) and PANTHER version 16.0 (released 2020-12-01) (Mi et al., 2012; Thomas, 2003) were used to annotate 44K SNPs (Supplementary Table S4). Identification of SNP's genomic location (intronic, coding, etc., Supplementary Table S5) used SNPeff with *A. carolinensis* genome NCBI RefSeq accession number: / GCF_000090745.1_AnoCar2.0. GO analyses focused on Biological Processes Complete and compared the 215-outliers SNP gene ids (single entry for each annotated gene) to 44K gene ids. Probabilities are based on the Fisher Exact test.

Results

SNPs were identified using genotyping by sequencing (GBS; Elshire et al. 2011) which randomly sampled 0.1% of the *A. carolinensis* genome. We identified 44,120 SNPs in 94 individuals (1Spp $n = 39$ and 2Spp $n = 55$), after requiring that each SNP was present in 50% of individuals and that each individual had a least 80% of SNPs. Additionally, we required that each SNP has at least 5% MiAFs (calculated across all 94 individuals) with at least 5 reads per allele. We choose 5% MiAFs so that each minor allele occurred in more than four individuals; this, plus the minimum of five reads, helped ensure that SNPs were not sequencing errors.

Population structure and demography

Among 1Spp and 2Spp islands, pairwise F_{ST} values calculated using all 44,120 SNPs were small; most were significant (26 out of 28 pairs) and were unrelated to 1Spp versus 2Spp island status (Supplementary Figure S1, Supplementary Table S3). Moreover, geographic distance was unrelated to island-pairwise F_{ST} values (Supplementary Figure S1), even though distances between island pairs ranged from 30 m between Ying and Yang to 12.5 km between Osprey and Lizard (Figure 1). Similarly, the relative number of migrants per generation (N_em) was unrelated to distance (Supplementary Figure S1). Notably, the median N_em was 3.4 (range among pairs of islands was from 1.6 to 13.5 migrants per generation). These migration rates are large enough to prevent neutral divergence among islands (Slatkin, 1994).

To corroborate these F_{ST} results without predefining populations, we used all 44,120 SNPs and applied two clustering algorithms: Structure (Pritchard et al., 2000) and discriminant analysis of principal components (DAPCs; Jombart et al., 2010; Figure 2). Both Structure and DAPC cluster individuals by shared allele frequencies to define common ancestry. The Structure analysis with the best support was for three groups ($K = 3$). At $K = 3$, neither 1Spp nor 2Spp island populations shared a common ancestor. Instead, each of the three clades shared individuals from both 1Spp and 2Spp islands. DAPC analysis agrees with these Structure analyses, finding that all 2Spp island individuals clustered with individuals from one or more 1Spp islands. Choosing *K*s with different group numbers did not alter these findings (Figure 2). Thus, we conclude that regardless of the *K* values, the results for Structure and DAPC are similar to the pairwise F_{ST} values: genetic structure in *A. carolinensis* is unrelated to 1Spp vs. 2Spp status or geographic distance (Figure 2). Thus, demographic processes should not confound the detection of adaptive genetic differences (Casillas & Barbadilla, 2017; Lotterhos & Whitlock, 2014).

Outlier SNPs

To detect individual SNPs most likely evolving by natural selection in response to competition, we used two approaches. First, we identified SNPs with large and improbable F_{ST} values that differentiated 1Spp from 2Spp islands (Supplementary Table S4) by pooling the three 1Spp island samples and contrasting these to the pooled samples from the five 2Spp islands (Figure 3). The significance of these observed F_{ST} values was

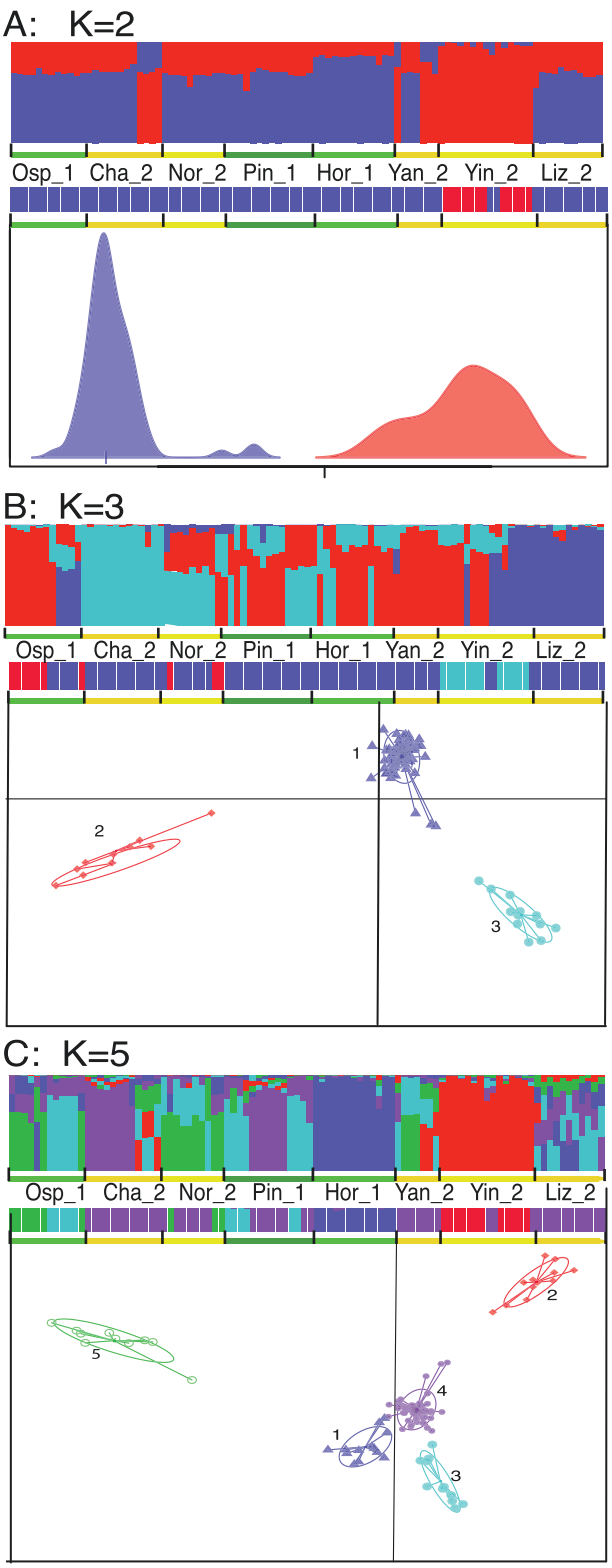

Figure 2. Structure and discriminant analysis of principal component (DAPC) plots for different assumed number of groups (*K*). (A) *K* = 2, (B) *K* = 3, and (C) *K* = 5. For each panel the top is Structure plots with admixture and are color coded similar to DAPC. Underneath the Structure plots are color bars showing the 94 individuals color coded to match the populations identified by DAPC in the lower plot. For Structure plot and color bar, islands are listed from south to north, with gold line indicating 2Spp islands, and green lines indicating 1Spp islands (having only the native *A. carolinensis*). For DAPC, the optimal number of PC = 7, as defined using the optimization criterion. Structure was run seven times for each *K* of 2–8. CLUMPP was used to align replicate runs. For Structure, the best number of groups is *K* = 3 as defined by the rate of change in the log probability. DAPC did not identify *K* with a meaningful minimum Bayesian information criterion (BIC) (minima were *K* = 1 or 80).

determined by comparing them to 1,000 random permutations of the 44K SNPs (total of 44 × 10^6 random F_{ST} values), where individuals were randomly assigned to a population while maintaining the same sample sizes as the observed populations. Relative to random permutations, 1,737 SNPs had large, improbable F_{ST} values ($p \leq .002$; Figure 3).

The second approach was a modification of FDIST (Beaumont & Nichols, 1996) to define outlier SNPs. This approach compares a single SNP's F_{ST} value to genome-wide F_{ST} distributions by contrasting it to all SNPs with similar heterozygosity. The likelihood of an SNP's F_{ST} value is calculated from 50,000 coalescent simulations in which there is no assumption that migration rates are equal among populations (Excoffier et al., 2005). Comparing F_{ST} values between pooled 1Spp and pooled 2Spp islands revealed 254 outlier SNPs (p-values between 0.01 and 10^{-27}; Supplementary Figure S2B and C). All 254 outlier SNPs were also significant ($p < .002$) in the random permutations used in the first approach. Of these 254 SNPs, 215-outliers SNPs were exclusive to 1Spp vs. 2Spp island comparisons and were not significant within 1Spp comparisons or within 2Spp comparisons. These 215-outlier SNPs are distributed across the genome (Figure 4) and have a minimum F_{ST} value of 0.16 (average 0.222, maximum 0.45).

We next asked, how likely is it that there will be 215 SNPs with F_{ST} values of at least 0.16 within a set of 44K SNPs due to chance? That is, within each of the 1,000 random sets of 44K SNPs, how often are there SNPs with F_{ST} values > 0.16, the minimum F_{ST} value for the 215-outliers (Supplementary Figure S2A)? The average number of SNPs with F_{ST} values >0.16 among each of the 1,000 random 44K SNP sets was only 6.5 (s.e. = 0.26, range 0–158), and 999 of the 1,000 random sets had fewer than 70 SNPs with F_{ST} values > 0.16. Thus, F_{ST} values > 0.16 rarely occur randomly (Figure 3), and as many as 215 SNPs with F_{ST} values > 0.16 were never seen among the randomized 44K SNP sets (Supplementary Figure S2A). Thus, this conservative set of 215-outliers SNPs is most likely evolving by natural selection and is responsible for the character displacement in *A. carolinensis*.

Pi, LD, and GO for the 215-outliers

If 215-outliers SNPs are rapidly evolving by natural selection, some selection scenarios predict reduced nucleotide variation (i.e., pi) around these SNPs and higher allele frequency correlations among them (i.e., LD) (Barghi et al., 2020).

We calculated pi, the average number of pairwise nucleotide differences per site (Nei & Li, 1979) across 300bp. Pi for the 215-outlier SNPs among 2Spp islands is 0.23% and, as predicted, is significantly less than pi of 0.27% on 1Spp islands ($p < .0001$ Kolmogorov–Smirnov, Supplementary Figure S4). Yet, the mean pi for the 215 outliers is significantly greater than pi for the non-outliers on the 2Spp islands (pi = 0.15%) and for the 1,000 random sets of 215 SNPs for 2Spp islands ($p < .0001$ Kolmogorov–Smirnov). Using a window of 1,000 bp did not alter these findings because there are few SNPs that are 300–10^5 bp apart (Supplementary Figure S3).

Significant LD among the 215-outliers SNPs occur in 42 SNPs forming 59 significant LD pairs (Supplementary Figures S5 and S6). For these 42 SNPs, the frequency of significant LD

is the same for 1Spp and 2Spp islands because all outlier SNP pairs are in LD within 300 bp or 1,000 bp. However, compared to non-outlier SNPs in LD on 2Spp or 1Spp islands, outlier SNPs have nearly twice as many significant LD pairs (100% of the outliers with significant LD vs. 53% for non-outliers, $p < .001$). Compared to 1,000 random sets of 215 SNPs on 2Spp islands, outlier SNPs again have nearly twice as many significant LD pairs (100% for 215-outliers vs. 55% for random sets, $p < .001$; Supplementary Figure S5). Importantly, not all 44K SNPs were used for determining random LDs; instead, the random LDs only used 17K SNPs with similar H_e to the observed 215-outliers. Thus, the smaller LDs among random pairs of SNPs are not due to differences in allele frequencies.

Finally, we investigated the enrichment of the 215-outliers SNPs relative to the 44K SNPS for genomic regions (e.g., exons vs. introns or in the transcribed 3′ UTR; Supplementary Table S5). Two of the 215-outliers SNPs are non-synonymous changes, but the relative frequency of non-synonymous polymorphisms is no larger than that found in all 44K SNPs. The only genomic region significantly different between the 215-outliers and the remaining 44K SNPs was the frequency of 3' UTR SNPs: 2.1% of 215-outliers vs. 0.7% of 44K were 3' UTRs ($p < .012$) (Supplementary Table S5). Among significant GO terms (Supplementary Table S6), there is approximately sevenfold enrichment for genes associated with animal locomotive behavior and walking behavior ($p < .05$) relative to expectation based on 44K SNPs. This is consistent with a shift in *A. carolinensis*' perching behavior in the presence of *A. sagrei*.

Genomic architecture of character displacement: Polygenic, standing genetic variation, and convergence vs. redundant SNPs

We asked three questions concerning genomic architecture: (1) is character displacement polygenic, (2) do the derived outlier SNP alleles on 2Spp islands arise from standing genetic variation, and (3) what evidence exists for genetic convergence versus genetic redundancy?

First, is the evolution of character displacement polygenic, involving many genes across the genome? The 215-outliers SNPs in *A. carolinensis* are distributed across the genome (Figure 4). Of these 44K SNPs, 47% are associated with expressed genes, which is similar to the proportion of genic regions in the whole *A. carolinensis* genome. Both these data indicate an unbiased sampling of the genome. Importantly, these 215-outliers SNPs were discovered by sequencing only 0.1% of the *A. carolinensis* genome. Thus, across the entire genome, there are potentially many more outlier SNPs, indicating that the response by *A. carolinensis* to competition is polygenic.

Second, does adaptation arise from standing genetic variation? If we assume that 1Spp islands represent the ancestral, pre-competition state, then derived adaptive SNP alleles would arise from these 1Spp populations. On 1Spp islands, the average MiAF (where the minor allele is defined across

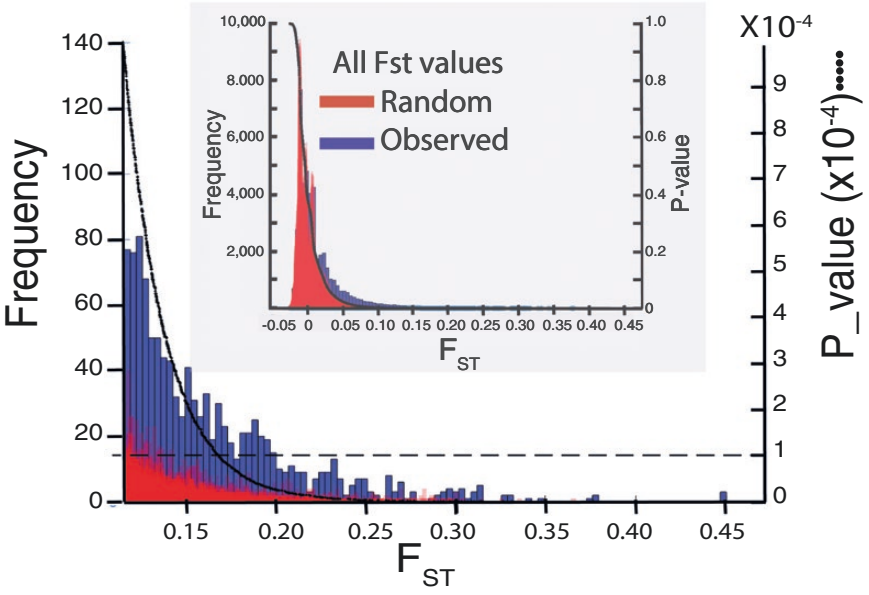

Figure 3. Observed and random F_{ST} values. Frequency of F_{ST} values > 0.10 with *p*-values (right Y-axis) of the observed F_{ST} values as dotted curve (< 10^{-3}). Blue histogram shows observed; red histogram shows 44 × 10^6 random permutations. Inset: all F_{ST} values between pooled 1Spp and pooled 2Spp islands with *p*-values (right Y-axis).

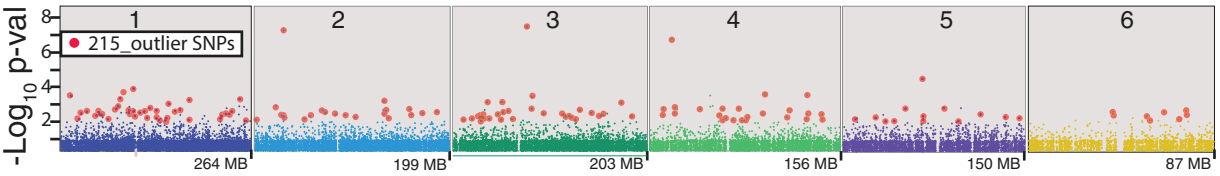

Figure 4. Distribution of 215-outliers single nucleotide polymorphisms (SNPs) across the six chromosomes. Outlier *p*-values, as negative $\log_{10}$ (e.g., 2 = 10^{-2}, or 1%) for the *Anolis carolinensis* genome's six chromosomes. The seven large linkage groups and undefined scaffolds are not shown. Red spheres are the 215-outliers SNPs. Y-axis shows the negative $\log_{10}$ *p*-values for the F_{ST} values from FDIST.

all 94 individuals and thus may be > 0.5 in one or more populations) for the 215-outliers SNP was 0.26, and 191 of these outlier SNPs have heterozygosity (H_e) that exceeds 0.1 with MiAF > 0.05 (Figure 5A). These allele frequencies and resulting H_e are large and indicative of evolution from standing genetic variation. Additionally, the 215-outliers MiAF are significantly larger than the 44K non-outlier MiAF: for both 1Spp and 2Spp islands, the MiAF for 215-outliers SNPs (median 1Spp = 0.23 and 2Spp = 0.09) is significantly greater than 44K SNP MiAF (median = 0.033 and 0.034). These data indicate that most outlier MiAF on 1Spp islands are not rare and exceed the MiAF for non-outliers, indicating that divergence between 1Spp and 2Spp islands arose from standing genetic variation, not new mutations or rare polymorphisms.

Third, what was the relative evidence for genetic convergence and genetic redundancy in response to the competition? Convergence is demonstrated by outlier MiAF being similar among 2Spp islands and outside of the range of 1Spp MiAF. Visually, the shared bright colors (red or blue; vs. white) in Figure 5B indicate SNPs with similar MiAF on 2Spp islands that are different from MiAF on 1Spp islands. This is more clearly seen in Figure 5C which shows 10 arbitrary outlier SNPs with MiAFs for each island: many of the colored circles representing each 2Spp island's MiAF are outside the range of all 1Spp islands' MiAF. We can quantify convergence on 2Spp island by counting the number of outlier SNPs where a 2Spp island MiAF is outside the range of 1Spp island MiAF and ask on how many islands this has occurred (Figure 5D). Figure 5D shows that 144 of the 215 (67%) outlier SNPs are outside the 1Spp MiAF range on all five 2Spp islands and nearly all outlier SNPs (213, 99%) are outside the range of 1Spp island MiAF for three or more 2Spp islands. This convergence is also seen by correlating change in MiAF among 2Spp islands: the average R^2 for MiAF among pairs of 2Spp islands is 68% (range of 59%–70%; Supplementary Figure S8) and all R^2 are significant and positive.

Other evidence supports redundancy. For example, we can determine the frequency of 2Spp island SNPs where there is a shared, substantial difference in MiAF relative 1Spp MiAF and how often they occur on all five, four, or three 2Spp islands (Table 1). A shared, substantial difference has two criteria: (1) shared: the outlier SNPs' MiAF are within the 2Spp MiAF 95% CI, and (2) substantially different: outside the range of 1Spp MiAF. Figure 5E shows that only 50 (23%) of 215-outliers SNPs have shared, substantial MiAF differences on all five 2Spp islands and thus, 165 outlier SNPs (77%) lack a shared, substantial difference on one or more 2Spp islands. That is, on one or more 2Spp islands, a majority of the 215-outlier SNPs (77%) have more similar MiAF to 1Spps islands than to 2Spp islands. All 2Spp islands have a similar number of 215-outlliers SNPs with MiAF more similar to 1Spp islands: among each 2Spp island the average number of SNPs with MiAF more similar to 1Spp island is 26 (range 23–28). Thus, each island has its own unique set of 215-outlier SNPs that is substantially different from 1Spp islands. There are significantly more shared SNP (chi-square 13.1, $p < .001$) across all five 2Spp islands when there is a reduction in MiAF on 2Spp islands (47 with an expected 37.4 when 1Spp > 2Spp MiAF) and too few when 2Spp island MiAF is greater than 1Spp MiAF (only 3 with expected 12.5; Table 1). Closer inspection of MiAF (Supplementary Table S4) shows that 42 of the 50 SNPs shared among all five 2Spp islands have 2Spp MiAF that are equal to zero. That is, of the 50 SNPs that share a substantial difference across all five 2spp islands, there is an enrichment for the loss of the minor allele on 2Spp islands.

Discussion

On small islands in Mosquito Lagoon, Florida, between 1995 and 2010 *A. carolinensis* rapidly evolved character displacement in response to competition with *A. sagrei*, evolving larger toe pads in association with a shift to higher perch height (Stuart et al., 2014). Nearly a decade later in 2019, a survey of these same islands confirmed that perch height was positively correlated with competitor presence and competitor density (Kamath et al., 2020; Stuart et al., 2014), indicating that competition was driving change in habitat use and subsequent morphological evolution. To investigate the genomic architecture driving this adaptive character displacement, we sequenced ~0.1% of the *A. carolinensis* genome, revealing 44K SNPS of which 215 SNPs were statistical outliers with significant allele frequency differences between 1Spp and 2Spp islands.

We propose that the 215-outliers are evolving by natural selection because (1) these 215-outliers SNPs have F_{ST} values that are significantly larger than the F_{ST} values among other SNPs in genome-wide comparisons (Figure 3, Supplementary Figure S2), (2) a large number of outliers is highly improbable, (3) pi for these 215-outliers are smaller on 2Spp islands than on 1Spp islands (Supplementary Figure S5), (4) the 215-outliers have more significant LD than expected by chance (Supplementary Figure S6), and (5) on at least three of the five 2Spp islands, all 215-outliers have a shared substantial difference in allele frequencies from 1Spp island populations.

The 215-outliers occur between 1Spp and 2Spp islands where the demographic structure is unrelated to 1Spp and 2Spp status (Figure 2). The lack of demographic structure and the high migration rates among islands (Figure 2, Supplementary Figure S1, Supplementary Table S3) mean that neutral processes are unlikely to confound the outlier tests (Casillas & Barbadilla, 2017; Lotterhos & Whitlock, 2014). That is, because 1Spp and 2Spp islands share a common gene pool (Figure 2), it is less likely that any SNP will have a large F_{ST} value. Additionally, the high false positive rates associated with some outlier tests (Lotterhos & Whitlock, 2014) are minimized here because the coalescence analysis avoids the assumptions of similar ancestry or equal migration among populations (Excoffier et al., 2009). Furthermore, the large number of outliers (i.e., 215) was never observed among 1,000 random sets of 44K SNPs; all but one random SNP set having < 70 outliers.

We cannot be sure that all 215-outliers are specifically associated with the adaptive evolution of character displacement. First, not all 215-outlier SNPs are independent: 42 of these SNPs are in LD with distances ranging from a few base pairs to tens of millions of base pairs or between chromosomes (Supplementary Figure S5). Thus, a few of the 215-outliers may not be evolving independently because they are physically linked to other outliers. Second, while among random sets of 44K SNPs, there are many fewer than the 215-outliers, some of these SNPs from random populations are the outlier, which means that random populations can create significant outliers. Thus, it is likely that some of the 215-outliers are false positives. However, each of the 215-outlier SNPs has shared substantial differences in MiAF from 1Spp islands

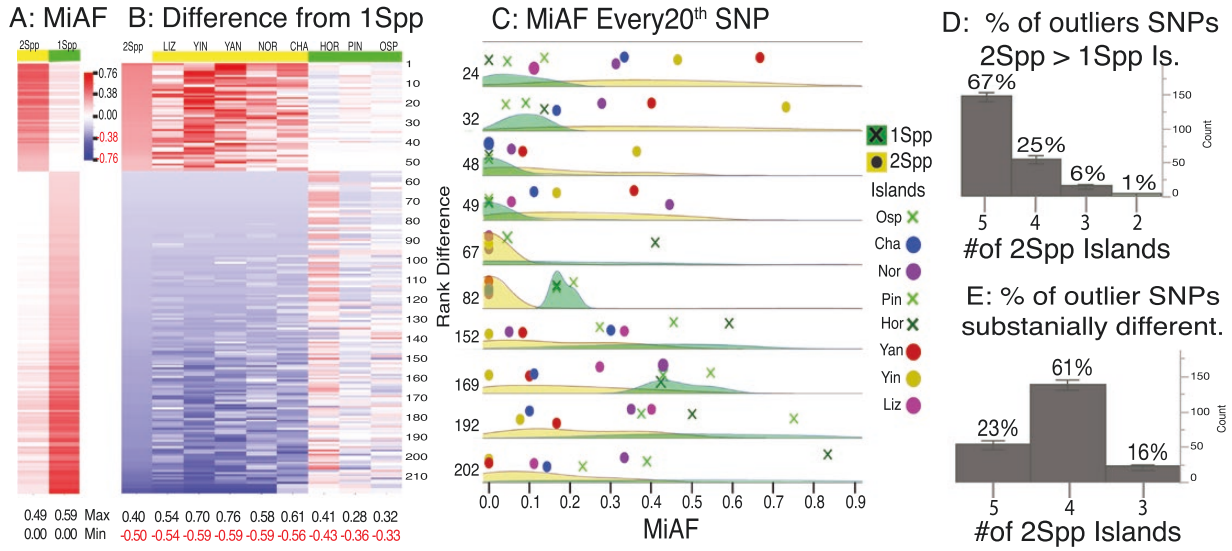

Figure 5. Minor allele frequency (MiAF) for the 215-outliers single nucleotide polymorphisms (SNPs). (A) MiAF heatmap across five pooled 2Spp islands and the three pooled 1Spp islands. Rows are 215-outliers SNPs. (B) Differences in MiAF from 1Spp islands average. Columns display the MiAF differences between 1Spp islands average vs. 2Spp islands average (first column) or vs. each individual island. At the top of each row is the island name (2Spp = gold; 1Spp = green). SNPs are in the same order for (A) and (B) and are listed from largest to smallest difference between pooled 2Spp vs. 1Spp islands. Values for (A) and (B) heatmap colors range from −0.76 to +0.76. (C) MiAF for ten arbitrary outlier SNPs (every 20th SNP based on chromosomal position) listed in rank order of the difference between 2Spp and 1Spp MiAFs (rank order is unrelated to position). 1Spp islands are green kernel densities with green "X" for each of the three 1Spp islands. 2Spp islands are gold kernel densities with color spots for each of the five 2Spp islands. (D) Histogram of frequency of outlier SNPs found on how many 2 Spp islands (out of five possible) that are outside the range of 1Spp island MiAF. "5" indicates that 67% of outlier SNPs MiAF on all five 2Spp islands are > 1Spp MiAF. (E) Histogram of frequency of outlier SNPs on 2Spp islands that are substantially different from 1Spp MiAF. Specifically, 2Spp islands MiAF are within the 95% confidence limits of 2Spp island MiAF and outside the range of 1Spp island MiAF. "5" indicates that 23% of outlier MiAF are substantially different on all five 2Spp islands.

on three or more islands, and no island has a greater share of these SNPs. Overall, our data indicate that random, neutral, or demographic processes are unlikely to be driving the improbably large F_{ST} values among all 215-outliers SNPs, and thus, it is more parsimonious to suggest that a majority of the 215-outliers SNPs are evolving by natural selection.

The conclusion that the 215-outliers are evolving by natural selection is further supported by the observed reduction in nucleotide diversity (pi) between 2Spp and 1Spp islands and the larger-than-expected LDs. Pi and LD are altered by selective sweeps, where selection for an allele will decrease pi and increase LD with the largest effects occurring with rare alleles (Beaumont & Nichols, 1996; Charlesworth, 2010; Pritchard & Przeworski, 2001). As predicted, the pi surrounding the 215-outliers on 2Spp islands is significantly smaller than it is on 1Spp islands (Barton et al., 2017; Pennings & Hermisson, 2006; Przeworski, 2002; Przeworski et al., 2005). Yet, pi values for these 215-outliers SNPs are larger than for non-outliers on 2Spp islands. Additionally, as expected there are nearly twice as many significant LD pairs on 2Spp islands compared to non-outliers or to 1,000 random sets of 215 SNPs (Supplementary Figure S5). There is also an expectation that the derived loci relative to the ancestor will have greater LD (Voight et al., 2006). Yet, for the 215-outliers SNPs, there is no difference in the frequencies of LDs within the 1Spp and 2Spp islands. These data on pi and LD, therefore, meet some expectations for evolution by natural selection suggesting a more complex scenario, which is discussed below.

Selective sweeps are most effective in decreasing pi and increasing LDs for alleles with low MiAF, (Beaumont & Nichols, 1996; Charlesworth, 2010; Pritchard & Przeworski, 2001), yet, alleles with large MiAF (or large H_e) are more effective for adaptive change (Falconer & Mackay, 1996; Simons et al., 2018). Here, the 215 outliers are derived from 1Spp islands where the MiAF is large, and these SNPs have a large H_e. Thus, on 2Spp islands, we suggest most of the 215-outliers are caused by directional selection acting on SNPs with large ancestral MiAF in the 1Spp populations. This generates 2Spp outliers with smaller pi than on 1Spp islands (as expected) but with larger pi than for 2Spp non-outliers. For LDs, the larger LDs among 215-outliers than among random or non-outliers support the supposition that these outliers are affected by natural selection. Yet, LDs were similar for 1Spp and 2Spp islands. An explanation for these LD patterns is that relative to the other 44K non-outlier SNPs, the 215-outlier SNPs are effecting a phenotypic change and thus, more likely to have functional constraints. This would enhance background selection and increase LDs in both populations and result in larger LDs than randomly expected (Beaumont & Nichols, 1996; Charlesworth, 2010; Pritchard & Przeworski, 2001). Overall, then, the large improbable F_{ST} values, the smaller pi on 2Spp islands than on 1Spp islands, and the larger LD relative to random expectation are indicative of natural selection.

Genomic architecture

Character displacement in *Anolis carolinensis* is polygenic, relying on many more than the 215-outliers discovered by sequencing 0.1% of the genome. This supposition assumes that the sequences used to identify the 44K SNPs are not biased to coding regions but are a representative sample of the non-repetitive genome. Support for a representative sample is shown by the distribution of SNPs across the entire *A. carolinensis* genome (Figure 4) and the fact that the frequency of the SNP's genomic regions (e.g., intergenic) is similar to the frequency in the whole genome (Supplementary Table S5). Only one type of genomic region differs between the 44K and

215 outliers: the outliers have a threefold significant overrepresentation by 3' UTRs, suggesting that adaptation relied on RNA expression pathways (transcription, splicing, stability, etc.).

The inferred genomic architecture also provides an explanation for rapid evolution of character displacement. Rapid evolution is more likely if derived alleles arise from standing genetic variation (Höllinger et al., 2019; Przeworski, 2002; Przeworski et al., 2005). On 1Spp islands, 89% of 215-outlier SNPs are frequent, with a minimum H_e of 0.1 and a MiAF of > 0.05 (this MiAF differs from the 5% minimum allele frequency used to filter SNPs across all eight populations). Additionally, the MiAF for all 215-outlier SNPs on 1Spp islands is significantly higher than the MiAF for the other 44K SNPs (median 0.23 vs. 0.03, $p < .001$). If we assume the ancestral state is represented by 1Spp island populations, then large starting MiAF for the 215-outliers suggests evolution from standing genetic variation and not from rare alleles or recent mutations.

In summary, character displacement evolved from standing genetic variation primarily from non-coding genetic variants and potentially involves 1,000-fold more outlier SNPs than the 215-outliers defined here.

Convergence and redundancy

There are two perspectives on the evolution of character displacement among the five 2Spp islands: shared genetic convergence and idiosyncratic genetic redundancy.

One evolutionary perspective is convergent or parallel evolution (Conte et al., 2012; Waters & McCulloch, 2021). Convergence is when the same adaptation occurs in independent populations or species. Adaptation often favors convergent phenotypic traits (Hendry et al., 2013; Hohenlohe et al., 2010; Natarajan et al., 2016; Pierce & Crawford, 1997; Schluter, 2000). Yet, here we are asking about genetic convergence: the shared nucleotide variation associated with an adaptive phenotype. For our purposes, genetic convergence is a substantial difference in outlier allele frequencies between 2Spp and 1Spp islands shared among 2Spp islands; that is, the 2Spp MiAF is outside of the range of 1Spp's MiAF and within the 2Spp's 95% CI. Our data on genetic convergence during character displacement are evidenced by the 50 outlier SNPs (23%) that have a shared substantial difference on all five 2Spp islands (Figure 5E), and the fact that all of the 215-outlier SNPs had a shared substantial difference on at least three of the five 2Spp islands.

The 23% of outlier SNP with genetic convergence shown across all five 2Spp islands is not dissimilar to other reports of genetic convergence (Conte et al., 2012; Ferris et al., 2021; Hohenlohe et al., 2010; Stern, 2013). A review of convergent evolution among eukaryotes including vertebrates and arthropods found a mean 32% convergence probability of sharing the same gene (Conte et al., 2012). For example, threespine stickleback populations adapting to similar ecosystems share 37% of the same genomic windows (Rennison et al., 2019) (though not necessarily the same SNPs). For the killifish *Fundulus heteroclitus*, a rapid adaptive response to pollution involved some of the same genes across four replicate populations but not the same site-specific polymorphisms (Reid et al. 2016). Similarly, in response to independent environmental clines, wild mouse populations have similar genetic changes in 16% of genes (Ferris et al. 2021). In one of the best-understood cases, the ability of adult humans to drink milk involves the same locus across all human populations, yet the SNPs and their effects differ among human populations (Segurel & Bon, 2017; Tishkoff et al., 2007). These examples and the synthesis by Conte et al. (2012) suggest that genetic convergence for the same gene or genetic region is not unusual. The data presented here suggest that genetic convergence using the same SNP also occurs when populations share a common genetic background. That is, when we re-run adaptive evolution on five separate islands united by migration, the same SNP often has similar adaptive changes.

The second perspective is genetic redundancy where there are many more adaptive alleles than needed to achieve an adaptive phenotype (Barghi et al., 2020; Nowak et al., 1997; Yeaman, 2015, 2022). With an abundance of adaptive alleles, many different combinations of alleles can produce an adaptive phenotype and evolving populations can have a unique set of adaptive loci (Barghi et al., 2019, 2020; Yeaman, 2015). Two other important aspects of redundancy are that (1) with many potential combinations, adaptive alleles will not go to fixation, which maintains polymorphism, and (2) migration has less impact on mitigating adaptive divergence (Barghi et al., 2020; Yeaman, 2015). Yet, evolution with redundancy creates a scientific challenge to identify adaptive alleles because there will be inconsistency in the genes associated with adaptation among populations (Barghi et al., 2019; Ehrlich et al., 2021; Yeaman, 2015) as well as temporal inconsistency as the alleles affecting adaptation turnover (Yeaman, 2022).

Evidence for genetic redundancy in *Anolis* character displacement emerges when an outlier SNP's MiAF on a 2Spp island is more similar to the 1Spp MiAF than it is to the MiAF of the other 2Spp islands. For example, SNPs #24, #152, and #202 (Figure 5C) have MiAFs within the range of 1Spp MiAF. Across the 215-outliers SNPs, 33% show this pattern (Figure 5D). Moreover, we stated that convergence was evident because across all five 2Spp islands, 50 SNPs (23%) had a shared, substantial difference from 1Spp MiAF. Yet, this also means that on one or more 2Spp islands, 77% of the 215-outliers SNPs are not substantially different from 1Spp islands (Figure 5E). Interestingly, these different changes among the five 2Spp islands occur even though migration is significant. This redundancy is not driven by one or a few unusual 2Spp islands; instead, each 2Spp island has a similar number of outlier SNPs that lack a substantial difference from 1Spp islands. Thus, each 2Spp island uses a unique subset of the 215-outlier SNPs associated with adaptation. This is the hallmark of redundancy: populations utilizing different genetic combinations to achieve an adaptation.

We argued that 215-outlier SNPs are evolving by natural selection, yet we cannot be sure that all 215-outliers are specifically associated with the adaptive evolution of character displacement. A common solution to this uncertainty is to only examine the most extreme outliers. We identified the ten SNPs with the largest change in MiAF for each 2Spp island relative to 1Spp MiAFs. On average a 2Spp island only shares 3.6 of these top 10 SNPs (range 2–5 out of ten SNPs) with any other 2Spp island. For any pair of 2Spp islands, the maximum number shared is three. Thus, 70% of outliers with the largest allele frequency changes are not shared among all 2Spp islands. Among the top 10 SNPs with the most extreme differences, the largest difference in MiAF occurs on Yang Island where the MiAF is 0.76 larger than the average 1Spp MiAF. This is nearly an 80% increase in allele frequency for the derived allele on this 2Spp island from the ancestral

allele on the 1Spp islands. Yet, on the other four 2Spp islands, 26%–56% of individuals are homozygotes for the ancestral allele for this extreme SNP, i.e., many to most individuals lack this derived allele on the other 2Spp islands. Thus, even when examining the most extreme evolved difference among 2Spp and 1Spp islands, there is a lack of convergence—the outlier SNP is not substantially increased in all populations—again suggesting genetic redundancy during replicated adaptation.

Our observations add to the growing number of examples of rapid evolution via polygenic, redundant changes (Barghi et al., 2019, 2020; Crawford et al., 2020; Ehrlich et al., 2021; Librado & Rozas, 2016; Margres et al., 2017; Perrier & Charmantier, 2019; Rennison et al., 2019). Importantly, with many independently derived variants affecting adaptation, redundancy may be one of the more important explanations for why there is so much standing genetic variation (Lewontin, 1997).

Caveats concerning redundancy

A concern with the genetic convergence shown here is the potential lack of evolutionary independence among islands. Specifically, the derived alleles arise from a common genetic background but the changes on 2Spp islands may not be independent. That is, since alleles are shared through migration, these islands lack sufficient independence. Yet, the high migration and the lack of demography that separates 1Spp from 2spp islands would also reduce the differences in allele frequency between these two types of islands. That is, with no demographic separating 1Spp and 2Spps islands, migration from 1Spp islands should reduce the effectiveness of natural selection (Slatkin, 1994). And evolution would have to act differently on each 2Spp island to drive the SNPs-specific difference in 215-outliers. Thus, for the 215-outliers, the shared substantial difference between all 2Spp islands and 1Spp islands is indicative of convergence from a shared genetic background.

Second, we may be underestimating the extent of genetic redundancy because we excluded 39 outlier SNPs that were significant outliers within an ecological island type (within 1Spp or 2Spp islands). We excluded these 39 SNP to remove SNPs that might be evolving to island-specific conditions and not due to competition. While this is a conservative approach, it does remove potentially redundant SNPs. Our findings were also biased away from redundancy by pooling 1Spp and 2Spp islands to calculate F_{ST} values, which would miss a large change in allele frequency on a single 2Spp island.

Finally, we might also be overestimating redundancy. First, we assumed that the only meaningful ecological difference among islands was the presence or absence of the competitor, *A. sagrei*. If islands vary ecologically and favor different local adaptations, then we might see unique SNP sets on each island (e.g., Ehrlich et al., 2021). However, each 215-outlier SNP lacked significant F_{ST} values within either 1Spp islands or 2Spp islands. Second, by not sequencing the whole genome it is possible that there are undiscovered loci of major effect with fixed differences between 1Spp and 2Spp island populations. Third, it is possible that adaptation on 2Spp islands is ongoing and that a more consistent pattern of allele frequency changes will appear. However, a 2019 study on some of these islands found little additional evolution in toe morphology on 2Spp islands (Kamath et al., 2020). Thus, while the allele combinations responsible for the adaptive evolution observed in 2010 may continue to evolve, they were sufficient to achieve a stable phenotype. Fourth, adaptive evolution is best detected by repeatability, but redundancy is the absence of repeatability. There is no solution to this concern: inconsistency in a gene's influence on adaptive evolution could reflect redundancy or, alternatively, nothing biologically important has been detected.

Conclusion

Genetic convergence and genetic redundancy are not mutually exclusive. Character displacement in *A. carolinensis* has attributes of both genetic convergence (all 215-outliers SNPs are substantially different on at least three of five 2Spp islands) and genetic redundancy (77% of outlier SNPs are not shared among all five 2Spp islands). This is likely because behavioral and morphological responses to competition are complex and driven by polygenic adaption. Polygenic adaptation with genetic redundancy means that many genes affect a phenotype, and there are a diverse number of genotype-to-phenotype mappings. While complex adaptation lacks repeatability, and is often ignored, it has the advantageous attributes of acting rapidly on standing genetic variation, being less sensitive to homogenizing migration, and maintaining genetic polymorphisms (Barton et al., 2017; Pritchard & Di Rienzo, 2010; Sella & Barton, 2019; Wittmann et al., 2017; Yeaman, 2015). More broadly, these data suggest that polygenic traits with redundancies and large-standing genetic variation should be able to respond to anthropogenic climate change that alters community structure and ecological interactions.

Supplementary material

Supplementary material is available online at *Evolution* (https://academic.oup.com/evolut/qpad031).

Data availability

The complete sequence data are available at NCBI Bioproject PRJNA833453, which includes all 94 individuals used here, plus *Anolis sagrei* samples, and individuals excluded because of low coverage. Sequences are named as "Spp_Island_Status_MCZ#_sex" where "Spp" is Ac or As (*A. carolinensis* or *A. sagrei*, respectively) and islands are as defined in Figure 1 and Supplementary Tables S1 and S2. MCZ # is the Museum of Comparative Zoology, Harvard, identification number. A more useable data set is the VCF file for the 44K SNPs in the 94 individuals used here, and these curated data are available in Dryad.

Dryad data

All curated data, including VCF for all 94 individuals and 44,120 SNPs, primary analyses (F_{ST}, H_e, MAF…), and tables are available in Dryad (https://datadryad.org/stash/share/aHnTommLunFup2qjv71x1Kt8QGORIShPF7xR0h-kypI). These include: (1) **94_44K_ALL_V.vcf**: a VCF file of all 44K SNPs in 94 *A. carolinensis* used in the analyses presented here; (2) **Supplemental_215_outlier_details.txt:** a tab-delimited file of 215-outliers SNPs, with chromosomal position, annotation, H_O, F_{ST}, randomization values, *p*-values, H_e, and minor and major allele frequencies; (3) **Supplemental 44K_SNPs_details.txt:** a tab-delimited file of all 44,120 SNPs, with chromosomal position, annotation, H_O, F_{ST}, randomization

values, *p*-values, H_e, and minor and major allele frequencies; and (4) **Supplemental_islands_descripiton.txt:** a tab-delimited file with Island name, eco-type (1Spp vs. 2Spp), latitude and longitude, and sample size per island. **Supplemental_Sample_description.txt:** a tab-delimited file of individual samples used from the Museum of Comparative Zoology, Harvard University with catalog numbers, abbreviations, sex, and tissue.

Author contributions

Conceptualization: D.L.C., M.F.O., and Y.E.S. Methodologies: M.F.O. Investigation: M.C.T., T.C., M.K., T.V., A.I., H.M., T.B., Y.C., D.L.C., and M.F.O. Visualization: M.C.T., T.C., D.L.C., and M.F.O. Funding acquisition: D.L.C. and M.F.O. Project administration: D.L.C. and M.F.O. Writing—original draft: M.C.T., T.C., M.K., T.V., A.I., H.M., T.B., Y.C., D.L.C., and M.F.O. Writing—review and editing: D.L.C., Y.E.S., and M.F.O.

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

This research was initiated as a research-intensive undergraduate class made possible by the support of the University of Miami RSMAS undergraduate program. *Anolis* samples were provided by the Museum of Comparative Zoology at Harvard University. We are grateful for the thoughtful comments from R. B. Huey, J. Losos, and P. Hohenlohe. This research was supported by funds from the National Science Foundation Division of Integrative Organismal Systems 1556396 (M.F.O.), 1754437 (D.L.C.), and previous support for *Anolis* sampling and study of character displacement: National Science Foundation Divisions of Environmental Biology 1110521 (Y.E.S. and J. Losos).

References

Barghi, N., Hermisson, J., & Schlotterer, C. (2020). Polygenic adaptation: A unifying framework to understand positive selection. *Nature Reviews Genetics*, 21(12), 769–781. https://doi.org/10.1038/s41576-020-0250-z

Barghi, N., Tobler, R., Nolte, V., Jaksic, A. M., Mallard, F., Otte, K. A., Dolezal, M., Taus, T., Kofler, R., & Schlotterer, C. (2019). Genetic redundancy fuels polygenic adaptation in Drosophila. *PLoS Biology*, 17(2), e3000128. https://doi.org/10.1371/journal.pbio.3000128

Barton, N. H., Etheridge, A. M., & Veber, A. (2017). The infinitesimal model: Definition, derivation, and implications. *Theoretical Population Biology*, 118, 50–73. https://doi.org/10.1016/j.tpb.2017.06.001

Beaumont, M. A., & Nichols, R. A. (1996). Evaluating loci for use in the genetic analysis of population structure. *Proceedings of the Royal Society B: Biological Sciences*, 263, 1619–1626.

Blount, Z. D., Lenski, R. E., & Losos, J. B. (2018). Contingency and determinism in evolution: Replaying life's tape. *Science*, 362, eaam5979.

Bradbury, P. J., Zhang, Z., Kroon, D. E., Casstevens, T. M., Ramdoss, Y., & Buckler, E. S. (2007). TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics*, 23(19), 2633–2635. https://doi.org/10.1093/bioinformatics/btm308

Brown, W. L., & Wilson, E. O. (1956). Character displacement. *Systematic Zoology*, 5(2), 49. https://doi.org/10.2307/2411924

Casillas, S., & Barbadilla, A. (2017). Molecular population genetics. *Genetics*, 205(3), 1003–1035. https://doi.org/10.1534/genetics.116.196493

Charlesworth, B. (2010). Molecular population genomics: A short history. *Genetics Research*, 92(5–6), 397–411. https://doi.org/10.1017/S0016672310000522

Cingolani, P., Platts, A., Wang le, L., Coon, M., Nguyen, T., Wang, L., Land, S. J., Lu, X., & Ruden, D. M. (2012). A program for annotating and predicting the effects of single nucleotide polymorphisms, SnpEff: SNPs in the genome of *Drosophila melanogaster* strain w1118; iso-2; iso-3. *Fly (Austin)*, 6, 80–92.

Conte, G. L., Arnegard, M. E., Peichel, C. L., & Schluter, D. (2012). The probability of genetic parallelism and convergence in natural populations. *Proceedings of the Royal Society B: Biological Sciences*, 279(1749), 5039–5047. https://doi.org/10.1098/rspb.2012.2146

Crawford, D. L., Schulte, P. M., Whitehead, A., & Oleksiak, M. F. (2020). Evolutionary physiology and genomics in the highly adaptable killifish (*Fundulus heteroclitus*). *Comprehensive Physiology*, 10(2), 637–671. https://doi.org/10.1002/cphy.c190004

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S. T., McVean, G., & Durbin, R.; 1000 Genomes Project Analysis Group1000 Genomes Project Analysis Group (2011). The variant call format and VCFtools. *Bioinformatics*, 27(15), 2156–2158. https://doi.org/10.1093/bioinformatics/btr330

Earl, D. A., & vonHoldt, B. M. (2011). Structure harvester: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, 4(2), 359–361. https://doi.org/10.1007/s12686-011-9548-7

Ehrlich, M. A., Wagner, D. N., Oleksiak, M. F., & Crawford, D. L. (2021). Polygenic selection within a single generation leads to subtle divergence among ecological niches. *Genome Biology and Evolution*, 13(2), evaa257. https://doi.org/10.1093/gbe/evaa257

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS One*, 6(5), e19379. https://doi.org/10.1371/journal.pone.0019379

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, 14(8), 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Excoffier, L., Hofer, T., & Foll, M. (2009). Detecting loci under selection in a hierarchically structured population. *Heredity*, 103(4), 285–298. https://doi.org/10.1038/hdy.2009.74

Excoffier, L., Laval, G., & Schneider, S. (2005). Arlequin (version 3.0): An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics*, 1, 47–50.

Falconer, D. S., & T. F. C. Mackay. (1996). *Introduction to quantitative genetics*. Pearson.

Ferris, K. G., Chavez, A. S., Suzuki, T. A., Beckman, E. J., Phifer-Rixey, M., Bi, K., & Nachman, M. W. (2021). The genomics of rapid climatic adaptation and parallel evolution in North American house mice. *PLoS Genetics*, 17(4), e1009495. https://doi.org/10.1371/journal.pgen.1009495

Germain, R. M., Williams, J. L., Schluter, D., & Angert, A. L. (2018). Moving character displacement beyond characters using contemporary coexistence theory. *Trends in Ecology and Evolution*, 33(2), 74–84. https://doi.org/10.1016/j.tree.2017.11.002

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology and Evolution*, 25(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Glaubitz, J. C., Casstevens, T. M., Lu, F., Harriman, J., Elshire, R. J., Sun, Q., & Buckler, E. S. (2014). TASSEL-GBS: A high capacity genotyping by sequencing analysis pipeline. *PLoS One*, 9(2), e90346. https://doi.org/10.1371/journal.pone.0090346

Good, B. H., McDonald, M. J., Barrick, J. E., Lenski, R. E., & Desai, M. M. (2017). The dynamics of molecular evolution over 60,000 generations. *Nature*, 551(7678), 45–50. https://doi.org/10.1038/nature24287

Gould, S. J. (1994). The evolution of life on the earth. *Scientific American*, 271(4), 84–91. https://doi.org/10.1038/scientificamerican1094-84

Gould, S. J. (2002). *The structure of evolutionary theory*. Harvard University Press.
Gould, S. J., & Lewontin, R. C. (1979). Spandrels of San-Marco and the Panglossian paradigm—A critique of the adaptationist program. *Proceedings of the Royal Society B: Biological Sciences*, 205, 581–598.
Grant, P. R. (1972). Convergent and divergent character displacement. *Biological Journal of the Linnean Society*, 4(1), 39–68. https://doi.org/10.1111/j.1095-8312.1972.tb00690.x
Grant, P. R., & Grant, B. R. (2002). Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, 296(5568), 707–711. https://doi.org/10.1126/science.1070315
Hendry, A. P., Peichel, C. L., Matthews, B., Boughman, J. W., & Nosil, P. (2013). Stickleback research: The now and the next. *Evolutionary Ecology Research*, 15, 111–141.
Hoffmann, A. A., & Sgro, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, 470(7335), 479–485. https://doi.org/10.1038/nature09670
Hohenlohe, P. A., Bassham, S., Etter, P. D., Stiffler, N., Johnson, E. A., & Cresko, W. A. (2010). Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *PLoS Genetics*, 6(2), e1000862. https://doi.org/10.1371/journal.pgen.1000862
Höllinger, I., Pennings, P. S., & Hermisson, J. (2019). Polygenic adaptation: From sweeps to subtle frequency shifts. *PLoS Genetics*, 15(3), e1008035. https://doi.org/10.1371/journal.pgen.1008035
Huey, R. B., & Pianka, E. R. (1974). Ecological character displacement in a Lizard. *American Zoologist*, 14, 1127–1136.
Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24(11), 1403–1405. https://doi.org/10.1093/bioinformatics/btn129
Jombart, T., & Ahmed, I. (2011). adegenet 1.3-1: New tools for the analysis of genome-wide SNP data. *Bioinformatics*, 27, 3070–3071.
Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genetics*, 11, 94. https://doi.org/10.1186/1471-2156-11-94
Kamath, A., Herrmann, N. C., Gotanda, K. M., Shim, K. C., LaFond, J., Cottone, G., Falkner, H., Campbell, T. S., & Stuart, Y. E. (2020). Character displacement in the midst of background evolution in island populations of Anolis lizards: A spatiotemporal perspective. *Evolution*, 74(10), 2250–2264. https://doi.org/10.1111/evo.14079
Kemp, D. J., Batistic, F. K., & Reznick, D. N. (2018). Predictable adaptive trajectories of sexual coloration in the wild: Evidence from replicate experimental guppy populations. *Evolution*, 72(11), 2462–2477. https://doi.org/10.1111/evo.13564
Lewontin, R. C. 1997. The paradox of variation. In M. Ridley (Ed.), *Evolution* (pp. 79–88). Oxford University Press.
Librado, P., & Rozas, J. (2016). Weak polygenic selection drives the rapid adaptation of the chemosensory system: Lessons from the upstream regions of the major gene families. *Genome Biology and Evolution*, 8(8), 2493–2504. https://doi.org/10.1093/gbe/evw191
Losos, J. B. (2011). Convergence, adaptation, and constraint. *Evolution*, 65(7), 1827–1840. https://doi.org/10.1111/j.1558-5646.2011.01289.x
Lotterhos, K. E., & Whitlock, M. C. (2014). Evaluation of demographic history and neutral parameterization on the performance of FST outlier tests. *Molecular Ecology*, 23(9), 2178–2192. https://doi.org/10.1111/mec.12725
Manceau, M., Domingues, V. S., Linnen, C. R., Rosenblum, E. B., & Hoekstra, H. E. (2010). Convergence in pigmentation at multiple levels: Mutations, genes and function. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1552), 2439–2450. https://doi.org/10.1098/rstb.2010.0104
Margres, M. J., Wray, K. P., Hassinger, A. T. B., Ward, M. J., McGivern, J. J., Moriarty Lemmon, E., Lemmon, A. R., & Rokyta, D. R. (2017). Quantity, not quality: Rapid adaptation in a polygenic trait proceeded exclusively through expression differentiation. *Molecular Biology and Evolution*, 34(12), 3099–3110. https://doi.org/10.1093/molbev/msx231
Mi, H., Muruganujan, A., & Thomas, P. D. (2012). PANTHER in 2013: Modeling the evolution of gene function, and other gene attributes, in the context of phylogenetic trees. *Nucleic Acids Research*, 41(D1), D377–D386. https://doi.org/10.1093/nar/gks1118
Natarajan, C., Hoffmann, F. G., Weber, R. E., Fago, A., Witt, C. C., & Storz, J. F. (2016). Predictable convergence in hemoglobin function has unpredictable molecular underpinnings. *Science*, 354(6310), 336–339. https://doi.org/10.1126/science.aaf9070
Nei, M., & Li, W. H. (1979). Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences*, 76(10), 5269–5273. https://doi.org/10.1073/pnas.76.10.5269
Nowak, M. A., Boerlijst, M. C., Cooke, J., & Smith, J. M. (1997). Evolution of genetic redundancy. *Nature*, 388(6638), 167–171. https://doi.org/10.1038/40618
Pennings, P. S., & Hermisson, J. (2006). Soft sweeps II—Molecular population genetics of adaptation from recurrent mutation or migration. *Molecular Biology and Evolution*, 23(5), 1076–1084. https://doi.org/10.1093/molbev/msj117
Perrier, C., & Charmantier, A. (2019). On the importance of time scales when studying adaptive evolution. *Evolution Letters*, 3(3), 240–247. https://doi.org/10.1002/evl3.86
Pierce, V. A., & Crawford, D. L. (1997). Phylogenetic analysis of glycolytic enzyme expression. *Science*, 276(5310), 256–259. https://doi.org/10.1126/science.276.5310.256
Porras-Hurtado, L., Ruiz, Y., Santos, C., Phillips, C., Carracedo, A., & Lareu, M. V. (2013). An overview of STRUCTURE: Applications, parameter settings, and supporting software. *Frontiers in Genetics*, 4, 98. https://doi.org/10.3389/fgene.2013.00098
Pritchard, J. K., & Di Rienzo, A. (2010). Adaptation—Not by sweeps alone. *Nature Reviews Genetics*, 11(10), 665–667. https://doi.org/10.1038/nrg2880
Pritchard, J. K., & Przeworski, M. (2001). Linkage disequilibrium in humans: Models and data. *American Journal of Human Genetics*, 69(1), 1–14. https://doi.org/10.1086/321275
Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155(2), 945–959. https://doi.org/10.1093/genetics/155.2.945
Przeworski, M. (2002). The signature of positive selection at randomly chosen loci. *Genetics*, 160(3), 1179–1189. https://doi.org/10.1093/genetics/160.3.1179
Przeworski, M., Coop, G., & Wall, J. D. (2005). The signature of positive selection on standing genetic variation. *Evolution*, 59(11), 2312–2323.
Ramasamy, R., Ramasamy, S., Bindroo, B., & Naik, V. (2014). STRUCTURE PLOT: A program for drawing elegant STRUCTURE bar plots in user friendly interface. *SpringerPlus*, 3, 431.
Reid, N. M., Proestou, D. A., Clark, B. W., Warren, W. C., Colbourne, J. K., Shaw, J. R., Karchner, S. I., Hahn, M. E., Nacci, D., Oleksiak, M. F., Crawford, D. L., & Whitehead, A. (2016). The genomic landscape of rapid repeated evolutionary adaptation to toxic pollution in wild fish. *Science*, 354(6317), 1305–1308. https://doi.org/10.1126/science.aah4993
Rennison, D. J., Stuart, Y. E., Bolnick, D. I., & Peichel, C. L. (2019). Ecological factors and morphological traits are associated with repeated genomic differentiation between lake and stream stickleback. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(1777), 20180241. https://doi.org/10.1098/rstb.2018.0241
Reynolds, R. G., Kolbe, J. J., Glor, R. E., Lopez-Darias, M., Gomez Pourroy, C. V., Harrison, A. S., Queiroz, K. de, Revell, L. J., & Losos, J. B. (2019). Phylogeographic and phenotypic outcomes of brown anole colonization across the Caribbean provide insight into the beginning stages of an adaptive radiation. *Journal of Evolutionary Biology*, 33, 468–494.
Reznick, D. N., & Bryga, H. A. (1996). Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). V. Genetic basis of parallelism in life histories. *The American Naturalist*, 147(3), 339–359. https://doi.org/10.1086/285855

Reznick, D. N., Rodd, F. H., & Cardenas, M. (1996). Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). IV. Parallelism in life-history phenotypes. *The American Naturalist*, 147(3), 319–338. https://doi.org/10.1086/285854

Schluter, D. (2000). Ecological character displacement in adaptive radiation. *American Naturalist*, 156(S4), S4–S16. https://doi.org/10.1086/303412

Schluter, D., & Grant, P. R. (1984). Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution*, 38(4), 856–869. https://doi.org/10.1111/j.1558-5646.1984.tb00357.x

Segurel, L., & Bon, C. (2017). On the evolution of lactase persistence in humans. *Annual Review of Genomics and Human Genetics*, 18, 297–319. https://doi.org/10.1146/annurev-genom-091416-035340

Sella, G., & Barton, N. H. (2019). Thinking about the evolution of complex traits in the era of genome-wide association studies. *Annual Review of Genomics and Human Genetics*, 20, 461–493. https://doi.org/10.1146/annurev-genom-083115-022316

Simons, Y. B., Bullaughey, K., Hudson, R. R., & Sella, G. (2018). A population genetic interpretation of GWAS findings for human quantitative traits. *PLoS Biology*, 16(3), e2002985. https://doi.org/10.1371/journal.pbio.2002985

Slatkin, M. 1994. Gene flow and population structure. In L. A. Real (Ed.), *Ecological Genetics* (pp. 3–17). Princeton University Press.

Stern, D. L. (2013). The genetic causes of convergent evolution. *Nature Reviews Genetics*, 14(11), 751–764. https://doi.org/10.1038/nrg3483

Stuart, Y. E., Campbell, T. S., Hohenlohe, P. A., Reynolds, R. G., Revell, L. J., & Losos, J. B. (2014). Rapid evolution of a native species following invasion by a congener. *Science*, 346(6208), 463–466. https://doi.org/10.1126/science.1257008

Stuart, Y. E., & Losos, J. B. (2013). Ecological character displacement: Glass half full or half empty? *Trends in Ecology and Evolution*, 28(7), 402–408. https://doi.org/10.1016/j.tree.2013.02.014

Thomas, P. D., Campbell, M. J., Kejariwal, A., Mi, H., Karlak, B., Daverman, R., Diemer, K., Muruganujan, A., & Narechania, A. (2003). PANTHER: A library of protein families and subfamilies indexed by function. *Genome Research*, 13(9), 2129–2141. https://doi.org/10.1101/gr.772403

Tishkoff, S. A., Reed, F. A., Ranciaro, A., Voight, B. F., Babbitt, C. C., Silverman, J. S., Powell, K., Mortensen, H. M., Hirbo, J. B., Osman, M., Ibrahim, M., Omar, S. A., Lema, G., Nyambo, T. B., Ghori, J., Bumpstead, S., Pritchard, J. K., Wray, G. A., & Deloukas, P. (2007). Convergent adaptation of human lactase persistence in Africa and Europe. *Nature Genetics*, 39(1), 31–40. https://doi.org/10.1038/ng1946

Vandvik, V., Skarpaas, O., Klanderud, K., Telford, R. J., Halbritter, A. H., & Goldberg, D. E. (2020). Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 117(37), 22858–22865. https://doi.org/10.1073/pnas.2003377117

Voight, B. F., Kudaravalli, S., Wen, X., & Pritchard, J. K. (2006). A map of recent positive selection in the human genome. *PLoS Biology*, 4(3), e72. https://doi.org/10.1371/journal.pbio.0040072

Waters, J. M., & McCulloch, G. A. (2021). Reinventing the wheel? Reassessing the roles of gene flow, sorting and convergence in repeated evolution. *Molecular Ecology*, 30(17), 4162–4172. https://doi.org/10.1111/mec.16018

White, C. R., Alton, L. A., & Frappell, P. B. (2012). Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. *Proceedings Biological Sciences*, 279(1734), 1740–1747. https://doi.org/10.1098/rspb.2011.2060

Wickland, D. P., Battu, G., Hudson, K. A., Diers, B. W., & Hudson, M. E. (2017). A comparison of genotyping-by-sequencing analysis methods on low-coverage crop datasets shows advantages of a new workflow, GB-eaSy. *BMC Bioinformatics*, 18(1), 586. https://doi.org/10.1186/s12859-017-2000-6

Wittmann, M. J., Bergland, A. O., Feldman, M. W., Schmidt, P. S., & Petrov, D. A. (2017). Seasonally fluctuating selection can maintain polymorphism at many loci via segregation lift. *Proceedings of the National Academy of Sciences of the United States of America*, 114(46), E9932–E9941. https://doi.org/10.1073/pnas.1702994114

Yeaman, S. (2015). Local adaptation by alleles of small effect. *American Naturalist*, 186(Suppl 1), S74–S89. https://doi.org/10.1086/682405

Yeaman, S. (2022). Evolution of polygenic traits under global vs local adaptation. *Genetics*, 220, iyab134.