Quantifying the degree of gene reuse during local adaptation

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Abstract

Several factors influence the degree of gene reuse during repeated adaptation, offering insights into how evolution is constrained at the genomic level. Although numerous studies have identified signatures of genomic repeatability in adaptive evolution, there is a lack of synthesis regarding the statistical tests used to quantify gene reuse across lineages. In this review, we survey published studies to (i) compile a comprehensive list of statistical indices available for quantifying gene reuse during adaptation and (ii) compare patterns of the degree of gene reuse across 120 taxa and four trait categories. Our analysis reveals that currently gene reuse studies are biased in focal species and traits commonly studied. Importantly, relatively few genomic loci contribute to repeatability and this variability is context dependent. By summarizing currently available indices to quantify gene reuse, we propose a straightforward methodological framework for designing studies that quantify gene reuse during repeated adaptation. While this review advances our understanding of the degree of gene reuse, we emphasize the need for broader and more inclusive research to uncover the factors driving variability in gene reuse during adaptive evolution.

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ABSTRACT

Several factors influence the degree of gene reuse during repeated adaptation, offering insights into how evolution is constrained at the genomic level. Although numerous studies have identified signatures of genomic repeatability in adaptive evolution, there is a lack of synthesis regarding the statistical tests used to quantify gene reuse across lineages. In this review, we survey published studies to (i) compile a comprehensive list of statistical indices available for quantifying gene reuse during adaptation and (ii) compare patterns of the degree of gene reuse across 120 taxa and four trait categories. Our analysis reveals that currently gene reuse studies are biased in focal species and traits commonly studied. Importantly, relatively few genomic loci contribute to repeatability and this variability is context dependent. By summarizing currently available indices to quantify gene reuse, we propose a straightforward methodological framework for designing studies that quantify gene reuse during repeated adaptation. While this review advances our understanding of the degree of gene reuse, we emphasize the need for broader and more inclusive research to uncover the factors driving variability in gene reuse during adaptive evolution.

In nature, different lineages often adapt to similar environmental pressures by reusing the same genes, though not necessarily the same mutations—a phenomenon termed as **repeated adaptation** (Arendt and Reznick 2008; Conte et al. 2012; Martin and Orgogozo 2013; Bohutínská and Peichel 2024). Also referred to as replicated, parallel, or convergent adaptation (Arendt and Reznick 2008), this process emphasizes the reuse of genes (hereafter referred to as **"gene reuse"**) across lineages (see definition in (Bohutínská and Peichel 2024) facing comparable environmental conditions (Martin and Orgogozo 2013). Also identified as genetic parallelism (Rosenblum, Parent, and Brandt 2014), significant progress has been made in understanding the factors influencing the probability of gene reuse during repeated phenotypic evolution. However, there remains a gap in our knowledge about the factors governing the degree of gene reuse or extent of genomic repeatability. Identifying these factors is crucial to elucidate how genomic constraints shape evolutionary processes and affect the predictability of adaptation (Speed and Arbuckle 2017; Yeaman et al. 2018; Pearless and Freed 2024). By exploring the variability in the degree of gene reuse underlying repeated evolution of different traits across various taxa, we can better understand the rules determining repeatable patterns of evolution across the diversity of life.

Reverse genetic methods can be used to investigate gene reuse across different lineages facing similar environmental challenges by using a genome scan approach to identify candidate genes in populations subjected to contrasting environmental conditions (Bomblies and Peichel 2022; Bohutínská and Peichel 2024). Additionally, experimental evolution studies have successfully revealed the nature of parallel evolution in microbial systems (Speed and Arbuckle 2017). In this review, we leverage published studies to discuss the key factors influencing degree of gene reuse, examine current indices used to quantify genomic parallelism, survey current literature to identify patterns of variation in degree of gene reuse, and propose a conceptual framework to guide future research. Through this synthesis, we aim to provide a comprehensive foundation for advancing the study of genomic basis of repeated adaptation, offering insights into both its variability and broader implications for evolutionary predictability.

Factors affecting the probability and degree of gene reuse underlying repeated adaptation

The probability of parallelism—the likelihood of parallel genetic changes occurring at the molecular level—is shaped by a variety of biological and ecological factors. In the most preliminary model, which used extreme value theory, Orr (2005) explored the probability of fixation of the same mutation in two independent populations and found the probability of parallelism at the nucleotide level is greater under a model including natural selection compared with a purely neutral model (Orr 2005). Since then, several studies have identified various factors which can affect the probability of genetic parallelism (see (Rosenblum, Parent, and Brandt 2014) for review of studies). In population genetics, three factors - the mutation rate of the locus, the probability that mutations at the locus are net beneficial and the average magnitude of the fitness change caused by these mutational effects, are factors that predict if a mutation will contribute to parallel evolution (Stern 2013).

Indeed theoretical studies have shown that the predictability of parallel evolution in natural populations is influenced by factors like standing genetic variation (SGV) and gene flow (Elmer and Meyer 2011; Conte et al. 2012; Ralph and Coop 2015; Hoban et al. 2016; Bomblies and Peichel 2022). Beneficial alleles present in SGV or transferred via gene flow before selection events can elevate the likelihood of parallel evolution, as supported by modeling studies. For instance, Lee and Coop (2017) highlighted the role of shared selective sweeps under strong, recent selection pressures (Lee and Coop 2017), while MacPherson and Nuismer (2017) demonstrated that the probability of parallel genetic evolution increases with stronger selection and larger effective population sizes, particularly for genes with significant phenotypic effects (MacPherson and Nuismer 2017). Similarly, Chevin *et al.* (2010) showed that mutation heterogeneity across loci favors parallel evolution, especially when pleiotropy is low or variance in pleiotropy and fitness effects is high (Chevin, Martin, and Lenormand 2010). Gene reuse is more probable when populations originate from a shared ancestor compared to when they arise from distinct, divergent ancestors which has been now established using several empirical studies (Conte et al. 2012; Bohutínská and Peichel 2024).

The factors limiting the probability of genetic parallelism can in theory also cause variability in the degree of gene reuse. The probability of gene reuse depends on the beneficial nature of a mutation such that the mutation should increase net fitness where the deleterious effects are minimal. Thus, it can be predicted that the mutations that cause large phenotypic effects, such as many null mutations, may not be favored by natural selection because pleiotropic effects on traits have antagonistic effects on fitness (Stern 2013). But this inference of magnitude gets at the fitness effect of mutations not the extent of reuse of mutations. Moreover, the probability of gene reuse can be decoupled from the degree of gene reuse where similar factors such as SGV or completely different factors can affect degree of gene reuse. Indeed, divergence time between lineages is a key determinant, with gene reuse decreasing as divergence increases. However, a comprehensive review of all possible factors which can drive this variability is lacking and requires a timely assessment.

How do we quantify gene reuse currently?

Both non-parametric and parametric statistical tests have been used to quantify the degree of gene reuse during repeated adaptation. An important distinction when using these indices is in their consideration of the genetic architecture of the trait which has been essentially missing until now. Borrowing from ecological studies (Connor and Simberloff 1979), similarity indices have been extended to identify repeated phenotypic evolution with the caveat that these indices are often not rooted in probability-based frameworks. These indices essentially indicate if the observed number of genes underlying repeatability exceed null expectations. The conclusions about the causes of the degree of gene reuse is made after the significance testing. We highlight a few such indices below.

Bailey, Rodrigue, and Kassen (2015) studied parallel evolution in bacterial populations and used **Jaccard similarity indices** (*J*) to estimate the probability of genetic parallelism where *J* describes that likelihood that the same gene is mutated in two independent lineages (Bailey, Rodrigue, and Kassen 2015). They compared degree of parallelism across different biological hierarchical levels by comparing gene overlap between lineages. Their results showed that degree of parallelism followed a decreasing order with the highest J index value associated with fitness and lowest to phenotype.

The **hypergeometric test** is frequently applied to calculate similarity in ecological contexts (Connor and Simberloff 1979), but its extension to genomic datasets presents additional complexity. To address this, Plaisier et al. (2010) introduced a modified version of this test called the Rank–Rank Hypergeometric Overlap (RRHO), a threshold-free algorithm. RRHO evaluates gene set overlap in differential expression datasets by iteratively comparing two gene lists ranked by their differential expression levels across profiling experiments, calculating the statistical significance of overlapping genes at each step (Plaisier et al. 2010). Subsequent studies have adapted this approach to assess genic overlap among lineages, thereby quantifying gene reuse in response to environmental changes. For instance, Cheng et al. (2021) employed pairwise hypergeometric tests using the R function `dhyper` to show that East Asian songbirds exhibit parallel functional responses to extreme elevation, despite relying on different genes (Cheng et al. 2021). Their results revealed that on average, any two pairs of bird lineages shared 10.9 candidate genes, with no single gene found in all comparisons. Similarly, Wang et al. applied comparable methods to uncover substantial evidence of parallel adaptation at the SNP, gene, and pathway levels in four highland maize populations (Wang et al. 2021).

Wilcoxon-signed rank tests can also be used to quantify similarity of genes between lineages. Yeaman et al. (2016) used the **null-W** method to detect repeated gene reuse in cases of convergent adaptation to environmental variables in two distantly related species, lodgepole pine and interior spruce (Yeaman et al. 2016). Briefly, they used a Wilcoxon-signed rank test to compare ρ^2 values of non-top-candidate genes and top-candidate orthologs to a background set of 10,000 SNPs. Null distributions of W statistics were transformed into Z-scores and empirical p-values were calculated by comparing these scores to the null distribution. This approach accounts for the role of linkage disequilibrium in creating regions with high association signals by chance. They quantified similarities in the signatures of association underlying convergent adaptation by comparing the strength of association for SNPs within top-candidate orthologs to a null distribution derived from non-top-candidate orthologs. Their analysis suggested that around 10-18% of locally adapted genes were evolving convergently.

Chaturvedi et al. (2018) utilized an **X-fold enrichment** metric to evaluate and quantify the excess overlap of SNPs associated with host plant use in Melissa blue butterflies (Chaturvedi et al. 2018). The reported X-fold enrichment values served as indicators of predictability in the context of parallel genetic changes underlying host use in multiple lineages. For instance, an X-fold enrichment of 2.0 implies that twice as many SNPs are associated with host plant use in repeated colonization events as would be expected by chance. This result indicates that patterns of genomic change can be anticipated at twice the rate of random expectations. While most SNPs were strongly associated with host use in none or only one lineage, the study identified an approximate twofold excess of SNPs associated with host use across both lineages. Chaturvedi et al. (2023) applied the same X-fold enrichment metric to explore repeated gene reuse during adaptation to climatic variables in eight species of *Timema* stick insects. Their findings underscored the collective influence of shared ecological factors and genomic backgrounds on the degree of genomic parallelism (Chaturvedi et al. 2022). Their analysis revealed a two- to fourfold excess of genomic parallelism for various climate variables across species. Furthermore, the results demonstrated a predictable decline in genomic parallelism with greater divergence times between species (also see (Rêgo et al. 2020) for experimental evolution application).

While these indices are useful, they cannot always differentiate between the level of repeatability and the proportion of genes available for adaptation by considering the genomic architecture of the trait in question. Yeaman et al. (2018) introduced the **C-score** index, a novel metric to quantify constraints driving the observed levels of repeated adaptation (Yeaman et al. 2018). The C-scores are derived from the hypergeometric distribution and allows for simultaneous analysis across multiple lineages. Their test produces three indices C_{hyper}, C_{chisq} (collectively called C-scores) and $P_{a,lik}$. Here the C-scores quantify the probability of repeatability given the level of contraints (constraint is used here to indicate the number of loci available for repeatability). $P_{a,lik}$ quantifies the proportion of genes available for adaptation. Thus, if multiple genes are contributing to a trait, the $P_{a,lik}$ index will be high and the C-scores will be low due to low level of constraints. Conversely, if only a single large effect gene is contributing to a trait and is being repeated, the $P_{a,lik}$ index will be low and the C-scores will be high due to high level of constraints. In this way, the three indices together enable comparisons across species and trait types and provides a framework to estimate the effective proportion of adaptation-capable genes within a genome. This builds on models which identify the mode of convergent evolution wherein standing genetic variation or gene flow before the selection episode could lead to different probabilities of genetic changes.

Finally, Yeaman, and Whitlock (2023) developed **PicMin**, a statistical approach which estimates the significance of repeated molecular evolution for individual genes by leveraging genome scan results (Booker, Yeaman, and Whitlock 2023). Importantly, the model is adaptable to any number of lineages, with its statistical power increasing as more lineages exhibit signals of repeated adaptation at a given gene. When applying PicMin to compare two lineages, the p-value for each gene is calculated as the cumulative probability density for the larger of the two **p-values**. The expected number of false positives is determined by considering the number of orthologs being compared. The number of genes showing signals of repeated adaptation can then be estimated by subtracting the expected false positives from the total number of genes with a p-value below a given threshold. A binomial test is subsequently used to determine the significance of the excess number of genes relative to the null expectation.

Together these indices present a solid start towards recognizing a standard set of methods to cross-validate the observed degree of gene reuse in repeated adaptation studies.

Quantitative Comparison of Degree of Gene Reuse from published studies

To objectively investigate the degree of gene reuse underlying repeated adaptation, we conducted a quantitative review of published studies spanning diverse taxa and traits. Our goal was to visualize patterns of variability and assess the consistency of genome-wide parallelism across lineages while ensuring studies shared comparable sequencing methodologies, analytical frameworks, and study designs. We briefly describe our methods here, please refer to supplementary methods for details. We also discuss the major details of our analyses here but have provided additional details from the studies in the supplementary table which can be used by readers for future work.

Literature Search Criteria and Data Collection

Using comprehensive literature search criteria, we compiled data from 104 studies investigating repeated genomic adaptation across two or more lineages. These studies included mostly studies using reverse-genetics approach to identify genomic regions associated with repeated adaptation. We also included studies from microbial systems which included experimental evolution to include microbial taxa in our list of species. From these studies, we extracted key information including the trait category, types of genomic loci analyzed, the total number of loci tested, and the proportion of loci shared across lineages (among others, see Supplementary methods). Traits were categorized as morphological, physiological, life-history, or behavioral, resulting in 97 unique traits (see Supplementary Table 1). We identified the types of loci used to test for parallel adaptation, which included single nucleotide variants (SNVs), quantitative trait loci (QTLs), mutations, structural variants (SVs), genes or orthologues, and differentially expressed genes (DEGs). For studies with variation in the number of loci associated with a trait across lineages, we used an average to approximate the number of loci. Additionally, we noted whether studies applied formal significance testing to check if the observed number of parallel or repeated loci were more than expected under random chance. Genome size for each focal species was recorded from the original manuscript or NCBI-SRA. Lastly, we summarized patterns of variation in shared loci based on species or phylum, trait category, genomic locus type, and genome size.

What does the data tell us about studies on genomic basis of repeated adaptation?

Our final dataset spanned 13 phyla and approximately 97 unique species (Figure 2). *Chordata* was the most represented phylum, particularly fishes (N = 42), followed by *Tracheophyta* (N = 17) and *Arthropoda* (N = 17). Across all four trait categories, physiological traits dominated (N = 86), while behavioral traits were the least represented (N = 6) (Figure 3A). Only 20 out of 107 studies focused on oligogenic traits, whereas most studies investigated traits with polygenic genetic architectures and most of our selected studies were focused on multi-locus traits which was essential for our comparison (Figure 3A).

Most studies in our dataset utilized SNVs to identify parallel genomic changes (N = 56, Figure 2). To address genome coverage limitations, many studies employed a window-based approach or aggregated SNVs to the gene level, treating "genes" as the loci for comparison. We observed that genome size significantly influenced the number of shared loci across lineages, with clear variation linked to taxonomic classification (Figure 3B, $R^2 = 0.016$; *p-value* = <0.005).

We summarized how many genetic variants contribute to repeatability across studies by calculating the proportion of trait-associated loci identified as "shared loci" within each study. On average, 15.85% of SNVs were shared in SNV-based datasets (N = 28 studies), 14% of genes in gene-based datasets (N = 21), 17.6% of mutations in mutation-based datasets (N = 10), 22% of QTLs in QTL-based datasets (N = 5), and only 0.64% of differentially expressed genes in expression-based datasets (N = 5). However, this comparison was limited due to inconsistencies in how gene reuse numbers were reported across studies. To address this, we selected 20 SNP-based and 14 gene-based studies where comparisons were clearly defined. Among these, we found that, on average, only 13.2% of total SNVs in a dataset were trait-associated, of which 20.3% were shared across lineages. In contrast, 89.5% of total genes were trait-associated, but only 14% were shared. This analysis highlights that relatively few genomic loci contribute to repeatability, with gene reuse being least detected in gene expression studies.

Several methods were employed to identify outlier loci, including genotype-by-environment association analyses, F_{st} outlier tests, parametric and non-parametric tests, QTL analyses, and linear mixed models. Several statistical tests were applied to identify if the observed number of shared loci were more than expected under chance. These included Jaccard Similarity Index (*J*) (5 studies), Hyper-Geometric tests (5 studies), False Discovery Rate (FDR) statistics and Fisher Exact Test (12 studies), and permutation tests or X-fold enrichment tests or Null-W (12 studies) (Supplementary Table 1).

Based on an analysis of 104 published studies spanning 120 taxa, three key themes emerged about the current state of studies on gene reuse during adaptation (Figure 2). First**,** most studies focus on specific traits, predominantly morphological or life-history traits. Behavioral traits are grossly underrepresented. This can be fixed as we have made considerable advances in studying the genetics of behavioral traits (Hoekstra and Robinson 2022). Second, measures of degree of gene reuse vary widely across species, traits, evolutionary scales, and genetic levels, including loci and chromosomal rearrangements. Importantly, relatively few genomic loci contribute to repeatability which could support the idea that only major genes contribute to adaptation due to constraints of genetic architecture. Third, the methodologies to quantify gene reuse are many and a more standardized framework could be useful for making more meaningful comparisons about degree of gene reuse across several scales and levels. Currently, non-parametric tests still dominate quantification of gene reuse. However, these approaches can be problematic and can identify false positives due to linkage disequilibrium or overlooked features of genomic data. Permutation-based approaches can overcome these limitations and can address the need for additional cross-validation in genotype-environment association studies (Yeaman et al. 2018; Chaturvedi et al. 2022).

Conclusion

In the 18th century, Laplace's demon symbolized the idea of perfect knowledge, capable of predicting the universe's every detail across time. Similarly, in evolution, understanding predictability is key to uncovering whether the challenges faced by diverse species can be resolved by a limited set of reliable, reusable solutions. While we may never achieve complete knowledge, patterns of predictable evolutionary change offer hope. Our review highlights the high variability in the degree of gene reuse during adaptation and shows that this variability is context dependent. We emphasize the need for broader taxonomic and trait representation, suggest relevant indices, as well as standardized frameworks for quantifying gene reuse. Though we may not yet fully understand gene reuse, the groundwork is firmly in place to refine analyses and advance our understanding of its role in evolution.

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AUTHORS' CONTRIBUTIONS

SC conceptualized the project. LVD searched for literature and created the final dataset of published studies. LVD and GS summarized information from papers to create Supplementary Table 1. GS summarized patterns from the table and created the figures. SC prepared the manuscript with input from LVD and GS. All authors reviewed and provided comments on the manuscript.

COMPETING INTERESTS

The authors have no competing interests.

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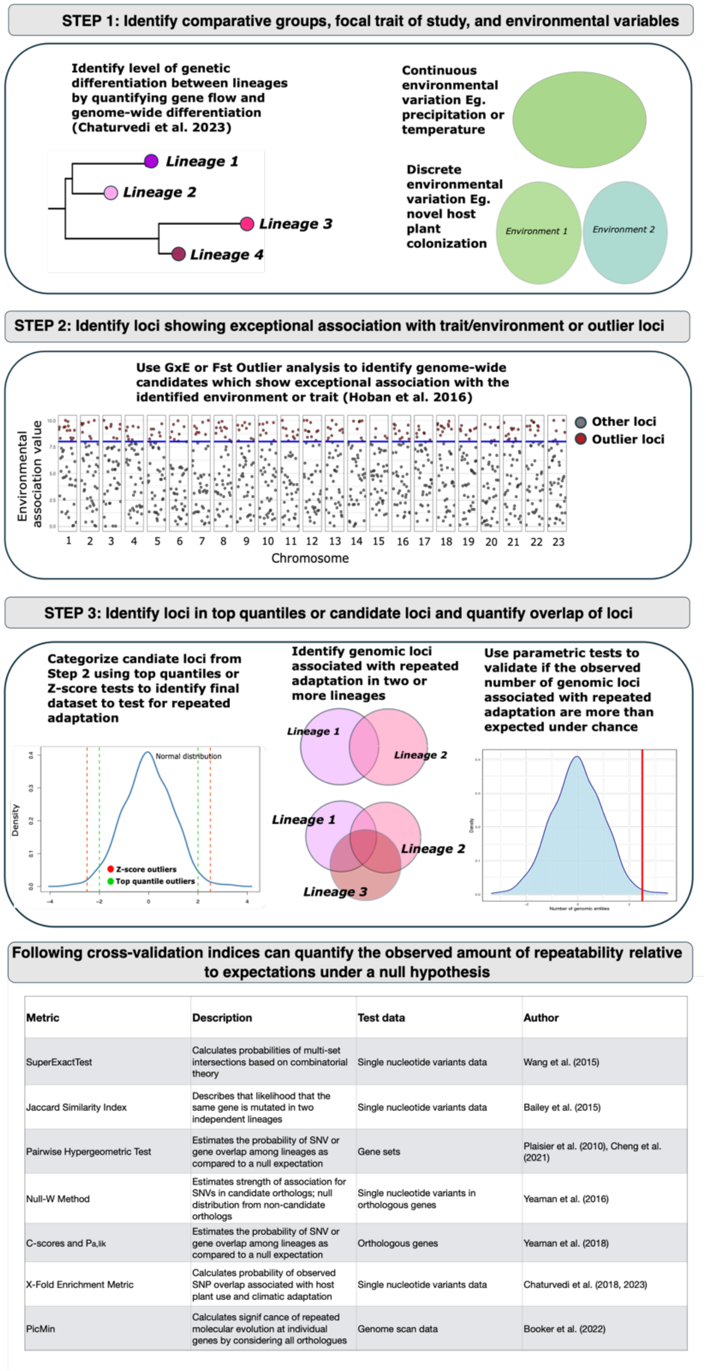
FIGURES

Figure 1 [BOX 1]: A standardized framework to design studies focused on quantifying gene reuse during repeated adaptation using reverse genetics approaches. Researchers can follow the following three step procedure to design studies which can aim to quantify degree of gene reuse during repeated adaptation. This protocol is based on using reverse-genetics approach to study natural populations but can be extended to experimental evolution studies. Here we define lineages genetically distinguishable unit that can encompass populations, species, or even different kingdoms, representing a branch in the tree of life. In step 2, each point represents a genomic locus (see categories in Supplementary Table 1).



STEP 1: Identify comparative groups, focal trait of study, and environmental variables

Identify level of genetic differentiation between lineages by quantifying gene flow and genome-wide differentiation (Chaturvedi et al. 2023)

Continuous environmental variation Eg. precipitation or temperature

Discrete environmental variation Eg. novel host plant colonization

STEP 2: Identify loci showing exceptional association with trait/environment or outlier loci

Use GxE or Fst Outlier analysis to identify genome-wide candidates which show exceptional association with the identified environment or trait (Hoban et al. 2016)

STEP 3: Identify loci in top quantiles or candidate loci and quantify overlap of loci

Categorize candiate loci from Step 2 using top quantiles or Z-score tests to identify final dataset to test for repeated adaptation

Identify genomic loci associated with repeated adaptation in two or more lineages

Use parametric tests to validate if the observed number of genomic loci associated with repeated adaptation are more than expected under chance

Following cross-validation indices can quantify the observed amount of repeatability relative to expectations under a null hypothesis

Metric	Description	Test data	Author
SuperExactTest	Calculates probabilities of multi-set intersections based on combinatorial theory	Single nucleotide variants data	Wang et al. (2015)
Jaccard Similarity Index	Describes that likelihood that the same gene is mutated in two independent lineages	Single nucleotide variants data	Bailey et al. (2015)
Pairwise Hypergeometric Test	Estimates the probability of SNV or gene overlap among lineages as compared to a null expectation	Gene sets	Plaisier et al. (2010), Cheng et al. (2021)
Null-W Method	Estimates strength of association for SNVs in candidate orthologs; null distribution from non-candidate orthologs	Single nucleotide variants in orthologous genes	Yeaman et al. (2016)
C-scores and $P_{a,lik}$	Estimates the probability of SNV or gene overlap among lineages as compared to a null expectation	Orthologous genes	Yeaman et al. (2018)
X-Fold Enrichment Metric	Calculates probability of observed SNP overlap associated with host plant use and climatic adaptation	Single nucleotide variants data	Chaturvedi et al. (2018, 2023)
PicMin	Calculates significance of repeated molecular evolution at individual genes by considering all orthologues	Genome scan data	Booker et al. (2022)

Figure 2: A circular representation showing genetic variants found in different species. The bars are arranged in three rings, where the inner ring shows shared variants (dark bars), middle ring shows trait-associated variants (medium opacity bars), and outer ring shows total variants (light bars) for each species. Different colors represent different types of variants: SNPs or SNVs (blue), QTLs (green), genes (orange), transcripts (red), mutations (purple), and structural variants (brown). Species names are colored based on their phylum grouping. Black symbols at the bottom of each bar depicts the trait type studied: physiology (circle), morphology (square), behavior (triangle), and life history (diamond). All values are shown in log10 scale with original values written on the bars.

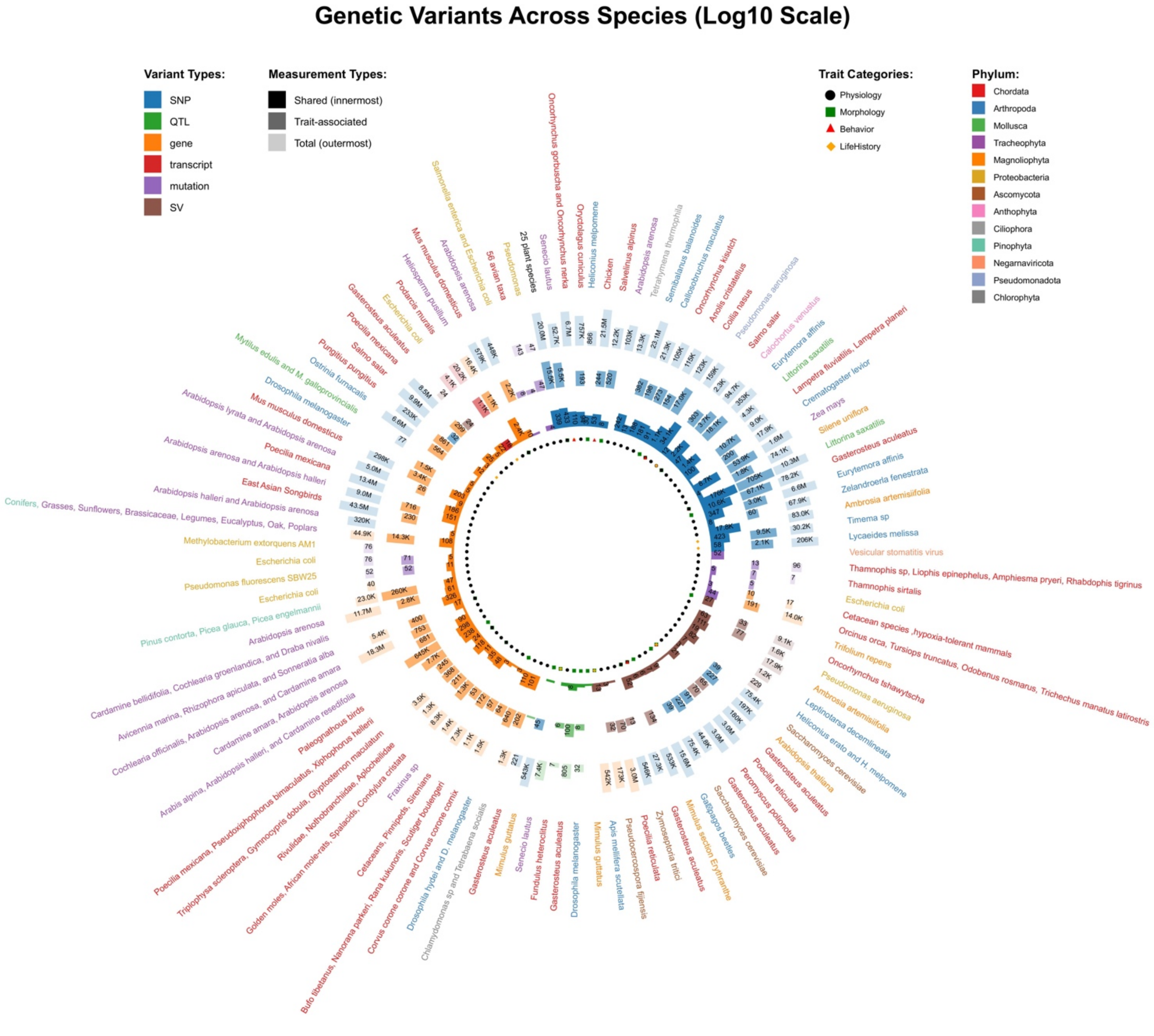
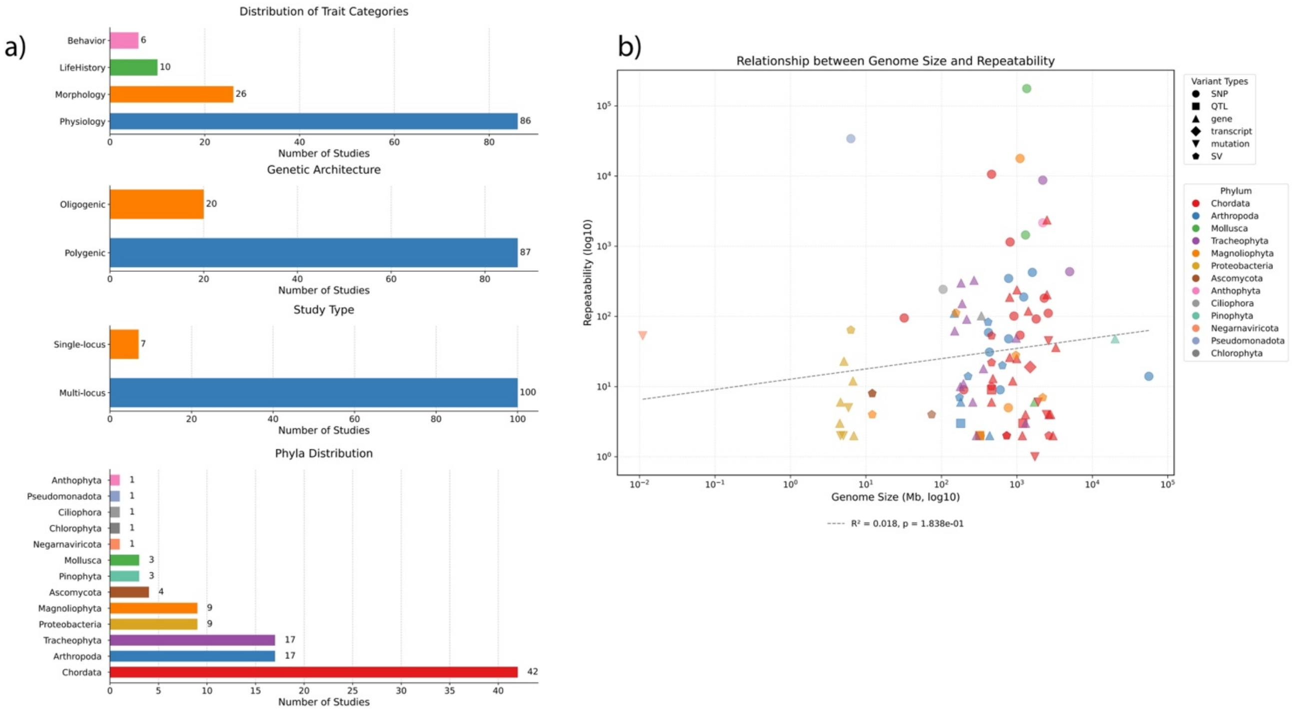


Figure 3: Analysis of trait categories, genetic architecture, study type, phylum distribution, and genetic variants patterns. (a) Bar plots showing distribution of studies across trait categories (behavior, life history, morphology, and physiology), genetic architecture (oligogenic vs polygenic), study approach (single-locus vs multi-locus), and phylum distribution across the surveyed literature. Numbers at the end of each bar indicate total count of studies. (b) Scatter plot showing the relationship between genome size (Mb, log10) and repeatability (log10). Different shapes represent variant types (SNP, QTL, gene, transcript, mutation, and SV) and colors indicate different phyla. A linear regression line is shown ($R^2 = 0.016$). Both axes are in log10 scale. Each point represents data from an individual study.



SUPPLEMENTARY METHODS

Selection of papers

We conducted an objective survey of the published literature for studies that tested genomic basis of repeated adaptation. To obtain a set of representative articles, we searched the online Semantic Scholar database for all studies in the subject area of evolutionary biology (spanning 2010-2024) that included the topic repeated evolution* parallel adaptation* genome* (a ‘*’ at the end of a search term includes all words beginning with the preceding letters). We reasoned that these search terms would detect many studies that had tested and quantified the genomic basis of parallel or convergent evolution regardless of outcome. In total, the search yielded 159 publications, of which 83 met further criteria for inclusion in the study. To be included, we required that a study addressed the genomic basis of repeated evolution between two different lineages generating data that includes at least one of the genomic entities mentioned earlier in the text. We included only studies with original data, rather than reviews. It was also necessary that the studies included to quantify the shared loci using proper tests since we are trying to design a framework to examine repeated adaptation. However, we did notice that the search missed several papers which had explicit quantification of degree of parallel genetic changes. We conducted an additional search on Google Scholar by using the keywords “quantifying genomic basis of parallel adaptation” and shortlisted 40 additional papers which met our criteria and had explicitly quantified degree of parallelism in their methods. While parsing data for our analysis, we excluded papers that lacked sufficient information about genetic variants or reported only phenotypic data without corresponding genomic evidence, resulting in a final dataset of 107 papers. We acknowledge that perhaps we missed some papers in our search, but our final set of papers provided a good representation across taxa and traits, something which was crucial for our review.

Final table

We summarized the specific information from the final set of papers which we expected to influence the degree of genomic parallelism. We created broad categories for some information. These categories align with the column names in our final spreadsheet (Supplementary Table 1). We describe these below:

1. Title – The title of the published paper.
2. Author – First author information of the paper.
3. Journal – Journal in which the paper was published.
4. Year of publication
5. Species - Focal study species was identified from each paper. We ended up with approximately 120 unique species from the final set of papers.
6. Phylum – Phylum classification of the focal species of study.
7. Kingdom – Kingdom classification of the focal species of study.

8. Genome size – Estimated genome size of the focal study species. We identified the genome size of the reference genome used in the study. Some studies provided this information in their paper. For others, we searched the genome size on NCBI Sequence Archive. We report genome sizes in Megabases (Mb).
9. Divergence_level – We classify the divergence level between the focal lineages used to compare gene reuse in the study. We classify them in three categories: (i) population; meaning populations belonging to same species were compared (ii) species; meaning multiple species of the same genus were compared, and (iii) genus; multiple genus including different species were compared.
10. Num_Lineages - We follow Bohutínská & Peichel 2024 and define lineages as a genetically distinguishable unit that can encompass populations, species, or even different kingdoms, representing a branch in the tree of life. We identified the total number of lineages used to test for genomic parallelism.
11. Trait – Specific trait studied in the paper which has repeated evolved in the test lineages.
12. Trait_category – Traits were broadly classified into four categories: (i) morphological (ii) physiological (iii) life-history (iv) behavior.
13. Data – Test genomic data was classified into six categories based on the genomic entities used to test for repeated gene reuse: (i) Single nucleotide variants (SNVs) (ii) Quantitative trait loci (QTLs) (iii) Genes or orthologues (iv) Transcripts (v) Mutations (vi) Structural variants (SVs).
14. Total_loci – Total number of genetic loci included in the study.
15. Trait_loci – Subset of the total genetic loci which were found associated with the trait being studied.
16. Shared_loci – Final number of genetic loci associated with gene reuse or shared between given set of lineages.
17. Percent_trait – Percentage of loci associated with trait out of the total loci used in the study.
18. Percent_shared – Percentage of loci shared between lineages out of the trait associated loci identified using outlier analysis.
19. Notes_on_data – Notes on categories of data used to identify shared loci.
20. Trait_type – Focal study trait was multilocus or single-locus.
21. Genetic architecture – The genetic architecture of the studied trait could be (i) oligogenic or (ii) polygenic.
22. Indices – Indices used to validate that the observed loci underlying repeated adaptation and more than expected under a null hypothesis. Not standardized, not available for all studies.

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