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Replicated Evolution in Plants

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Keywords

convergent, parallel, adaptation, speciation, constraints, plants

Abstract

Similar traits and functions commonly evolve in nature. Here, we explore patterns of replicated evolution across the plant kingdom and discuss the processes responsible for such patterns. We begin this review by defining replicated evolution and the theoretical, genetic, and ecological concepts that help explain it. We then focus our attention on empirical cases of replicated evolution at the phenotypic and genotypic levels. We find that replication at the ecotype level is common, but evidence for repeated ecological speciation is surprisingly sparse. On the other hand, the replicated evolution of ecological strategies and physiological mechanisms across similar biomes appears to be pervasive. We conclude by highlighting where future efforts can help us bridge the understanding of replicated evolution across different levels of biological organization. Earth's landscape is diverse but also repeats itself. Organisms seem to have followed suit.

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REPLICATED EVOLUTION

Evolution is a scattering process, one where populations diverge into separate groups and where phenotypic differences accumulate among them as they adapt to their surroundings (55). The genetic makeup of most populations also changes stochastically over time (96), which can add further variation to the range of phenotypes. Surprisingly, despite long extended periods of independent evolution, many taxa have evolved or maintained strikingly similar features in response to similar environmental challenges or due to mutation limitation and developmental constraint (73, 120, 195, 196). The processes responsible for this pattern are complex but suggest that deterministic forces, such as natural selection and constraint, drive many of the differences and similarities between separate organisms and ultimately the origin and maintenance of adaptations.

Replicated evolution (**Figure 1**) is a process in which outcomes of evolution arrive at similar places in phenotypic space or function, or travel the same evolutionary path many times independently (75). These processes exist in the conceptual sphere of convergent and parallel evolution (see 6, 23, 61, 84, 116, 171, 193, 194, 198 for details) (see the sidebar titled Removing Term Ambiguity). Regardless of the process driving similarity, replication occurs at various levels of biological organization, including genes, pathways, networks, single and multivariate phenotypes, ecological traits, and biomes (**Figure 2**), and can lead to simple kinds of replicated evolution, such as the same mutation causing pest resistance in crops (131), or more complex examples, such as ecological strategies creating similar vegetation types (e.g., 160, 161, 223) and the development of distinct anatomical structures in the leaves of plants to deal with harsh environmental conditions (e.g., 54, 59, 231). Replicated evolution also occurs at different scales of divergence, and, in some cases, it can be challenging to distinguish it from similarity arising from common ancestry, which can be especially problematic in young lineages (89).

Understanding the evolution of similarity relies on our ability to connect the genotype to the phenotype (138) and how it interacts with the surrounding environments (209). To date, discovering causal paths between genotype and phenotype remains out of reach of most research programs, although developmental biologists studying the *Arabidopsis* model system (e.g., 66) and

Mutation limitation: the limited supply of new mutations in a population, which in turn can limit the rate of adaptation

Developmental constraint: any limitations or restrictions that impact the development of a phenotypic trait, such as the interactions between genes

Replicated evolution: the evolution of similar features in independent lineages encompassing both young and distant lineages

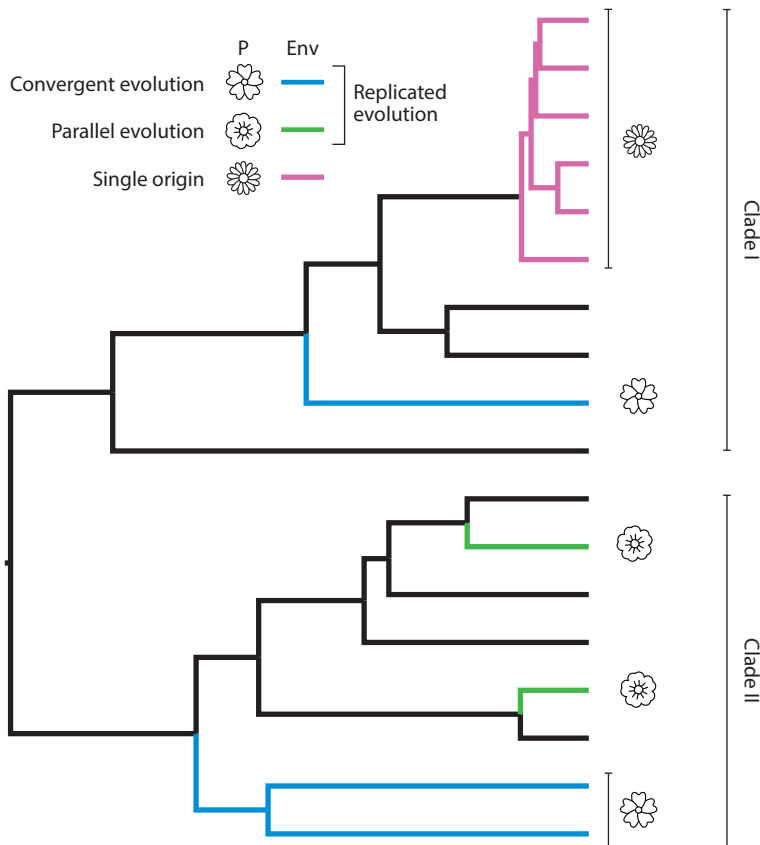


Figure 1

Replicated evolution in nature. The evolution of similar adaptive phenotypes (P) in response to similar selective pressures (Env) can arise across different evolutionary timescales. Convergent evolution occurs when similar phenotypes independently evolve in distantly related lineages. This is shown as two origins of the same flower shape due to adaptation to the blue environment in clade I and clade II. Similar phenotypes can also arise from closely related ancestors, which is typically termed parallel evolution, such as the evolution of the same flower shape in the two green lineages in clade II. We use the term replicated evolution to describe the evolution of similar features regardless of the age separating the taxa. Adaptive phenotypes can also originate once and spread across multiple lineages, as represented by the selective pressure, shown in pink, in clade I. These are not cases of replicated evolution, as the adaptive phenotype only has a single independent origin.

plant breeders creating elite cultivars (e.g., 38, 52) have developed a profound understanding of how both mutant and natural variants control certain phenotypes across multiple environments. Studies of replicated evolution provide a framework to reveal common paths of causality between genotype and phenotype, thus helping us understand the origins of similarity at distinct levels of biological organization. Systems of replicated evolution shed light on the relative importance of deterministic and stochastic processes in shaping biological functions and how biological constraints may limit evolutionary paths of adaptation (21, 42, 116, 117, 120, 171, 191, 192, 239). Such knowledge helps predict how populations adapt as new traits increase conformity to their environment, thereby tackling longstanding questions in evolutionary biology, such as, If we were to “replay the tape of life” (75), to what extent does evolution repeat itself?

Convergent evolution: the evolution of similar features in independent lineages from different initial conditions, which is typical of distantly related taxa; also known as convergence

REMOVING TERM AMBIGUITY

Convergence and parallel evolution (or parallelism) are contentious terms (for further discussion, see 6, 23, 61, 84, 116, 171, 193, 194, 198). Traditionally, convergence refers to the evolution of similar forms from distantly related lineages, whereas parallelism is the evolution of similar forms in closely related lineages (23, 191; but see 116, 194). However, confusion arises because it is difficult to draw a line between young and old lineages, and the evolution of similar features can occur via a range of genetic mechanisms. Some researchers argue that terminology should also encompass the underlying genetic mechanisms (e.g., 171). However, the fact that many different genetic processes can produce similar phenotypic features makes this unfeasible. Convergence and parallelism are better thought of as part of a continuum (**Figure 1**), which can be described by a single term—replicated evolution—to denote the evolution of similar forms in independent lineages. When researchers use the term replicated evolution, however, they must explicitly describe the evolutionary drivers and potential mechanisms of the observed patterns of similarity.

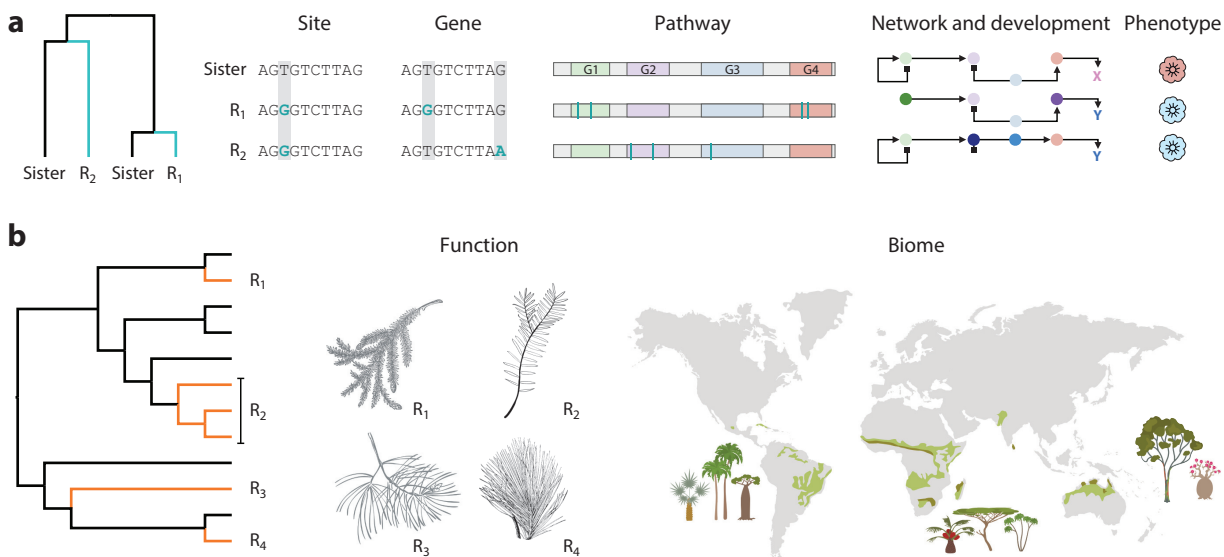


Figure 2

Levels of replicated evolution in nature. Replicated evolution can manifest at various levels of biological organization. (*a*) Across independent lineages (R_1 and R_2), replicated evolution can arise due to selection upon the same nucleotide site (which may arise via new mutations or standing genetic variation or may be introduced via gene flow), different nucleotide sites on the same gene, different genes within the same pathway, different pathways in the same network, different networks that have similar developmental outcomes, or similar traits and phenotypes. (*b*) Replicated evolution can arise at the level of the function, where independent lineages (R_1 to R_4) have different phenotypes, yet they are functionally equivalent, as shown by the repeated evolution of different slender leaf phenotypes as a strategy to prevent water loss. Replication can manifest at the level of the biome, where groups of organisms are adapted to similar terrain and climate, often with distinct adaptive strategies, which are repeated across biomes. For instance, adaptation of species to savanna habitats across separate regions of the world involves different mechanisms to cope with low rainfall (e.g., water storage in the stems of baobabs and boabs or vertical and hard leaves of eucalyptus trees and acacias). The higher the level of biological organization the greater the number of ways equivalent functions can be achieved. Images in panel *b* adapted with permission from Shutterstock and Adobe.

In the next section, we discuss theories and data explaining the genetics of replicated traits and functions and how genetic architectures and evolutionary forces interact to produce similar outcomes of evolution. We also refer the reader to recent, complementary reviews that emphasize replicated evolution of genome structure (236) and cellular phenotypes (197), as well as the repeated domestication of crops (131), to expand their views on replicated evolution in plants.

GENETICS OF REPLICATED EVOLUTION

Hemiplasy, or the probability that two DNA sequences from different taxa are the same because of incomplete lineage sorting (80) or gene flow (114), can create the appearance of replicated evolution at the locus level. These two processes—incomplete lineage sorting and gene flow—violate a strict definition of evolutionary replication, which requires that beneficial mutations must originate independently in different populations as they adapt to similar conditions. Ruling out hemiplasy is challenging but possible (80, 88), yet it might sometimes be unnecessary for the study of replicated evolution. Analyses of replicated spread of the same allele as populations adapt to similar environments, for instance, do not require the complete independence of the origin of the mutation (115), making replication frequent in nature. Regardless of how strict we are on its definition, to understand the genetics of replicated adaptation we require substantial knowledge of the actual alleles and their effects. This is not a simple task, but theories of adaptation can guide our experiments as we try to identify the loci of adaptation.

Genetic Trajectories of Replicated Evolution

The simplest genetic basis of replicated evolution occurs when two populations independently fix the same mutation. Theory indicates that this probability is $P = 2/(n + 1)$, where n is the number of possible beneficial mutations (139). This intuitive result implies that oligogenic adaptation (42, 238) should be more likely to create replicated genotypic evolution than polygenic adaptation (120, 239). A classic example of adaptation via a single locus of large effect occurs in monkeyflowers with different flower colors that attract specific pollinators. Genetic experiments found that the yellow upper (YUP) locus alone can explain major shifts in flower color and thereby in pollinator preferences (29). Similarly, the evolution of herbicide resistance in different agricultural species (e.g., 104) and the evolution of metal tolerance in mustards rely on the recurrent recruitment of a few mutations (85, 148). Such cases of replication can also occur between highly divergent taxa. For instance, a recent study on the genomics of replicated adaptation of plants to extreme environments (see 236, table 1) reported that multiple monocot lineages found in dry, tropical environments have evolved carbon cycling via 4-carbon sugar compounds (C_4) before entering the Calvin-Benson cycle. In some grasses, the key C_4 enzyme phosphoenolpyruvate carboxylase was found to have arisen independently at least eight times from the same non- C_4 phosphoenolpyruvate carboxylase and involved the evolution of the same 21 amino acids (47).

When the genetic architecture of adaptation is complex, the probability of fixing the same mutation across replicate populations can be small. Replicate populations reach a phenotypic optimum through unique adaptive walks where the allelic effects have redundant effects on a phenotype (112, 238). In general, during polygenic adaptation, diverse genetic changes can lead to similar phenotypic outcomes (2, 8). During the evolution of polygenic adaptations, replicated evolution often manifests at higher levels of organization, such as a signaling pathway or genetic network (8, 42, 238). Recent genomic work suggests that this flexible use of genes from a pathway might be common. In *Senecio lautus*, unique genes from the auxin pathway are responsible for the repeated evolution of prostrate growth habit in coastal ecotypes (89, 91, 166, 225), while in *Arabidopsis*, *Oryza*, and *Heliosperma* (Table 1) ecotypes, repeated divergence in different stress

Parallel evolution:

the evolution of similar features in independent lineages from similar initial conditions, which is typical of closely related taxa; also known as parallelism

Genetic architecture:

all the loci that contribute to a trait, including their number, effect size, allele frequency, and genetic and environmental interactions

Incomplete lineage sorting:

the sharing of alleles between two lineages due to recent common ancestry

Oligogenic adaptation:

adaptation that proceeds via few alleles of large effect size

Polygenic adaptation:

adaptation that proceeds via many different alleles of small effect size

Adaptive walk:

the way a population fixes beneficial mutations over time to reach a phenotypic or fitness optimum

Ecotypes:

non-reproductively isolated populations (typically young lineages) that have evolved similar features in response to adaptation to similar environments

Table 1 Candidate examples of replicated speciation in plants due to divergent ecological selection

Species	Taxonomic category ^a	Minimum number of origins (replicates) ^b	Major replicated trait(s)	Replicated selection	Genetic mechanism	Reproductive isolation	Compatibility/incompatibility ^c	Mode of speciation	Reference(s)
<i>Arabiopsis arenosa</i>	Non-serpentine vs serpentine	3 (5) ^{***}	Edaphic tolerance	***	***	**	NA	NA	99, 101
<i>Arabiopsis arenosa</i>	Foothill versus alpine	4 (5) ^{***}	Habitat type (elevation), plant size, flower size	***	***	**	NA	NA	16, 22, 93, 97, 98, 227–230
<i>Cerastium alpinum</i> ^d	Non-serpentine versus serpentine	2 (2) ^{**}	Edaphic tolerance	***	NA	*	NA	NA	13, 135
<i>Deschampsia cespitosa</i> ^d	Non-mine versus mine	2 ^{**}	Edaphic tolerance	*	NA	*	*	ES	36, 128
<i>Euacliptus globulus</i> ^d	Tall versus dwarf	3 (3) ^{***}	Dwarfed morphology, early flowering, drought tolerance	**	NA	**	*	ES	53, 57, 65
<i>Fucus vesiculosus</i> , <i>Fucus radicans</i>	Tall versus dwarf	2 (6) ^{**}	Dwarfed morphology, habitat type, light harvesting	*	NA	**	NA	NA	83, 143, 144
<i>Genoma macrostachys</i> ^d	Floodplain versus terra firma	3 (3) ^{**}	Habitat type, reproductive strategy, leaf shape	**	NA	***	*	ES	25, 168, 169
<i>Heliosperma pusillum</i>	Alpine versus montane	5 (6) ^{***}	Habitat type (elevation), growth habit, trichome density	**	***	***	***	ES	14–18, 201, 205
<i>Hemerocallis citrina</i> var. <i>vespertina</i> ^d	Inland versus coastal	3 ^{**}	Nocturnal flowering	NA	NA	*	*	ES	133, 152
<i>Lasthenia californica</i> ^d	Race A versus race C	2 ^{***}	Edaphic tolerance	**	NA	**	**	ES	153–156, 241
<i>Microveris lanceolata</i> ^d	Murnong versus alpine	2 ^{***}	Habitat type (elevation), root type, flowering time	*	NA	**	**	ES	187, 212, 213

(Continued)

Table 1 (Continued)

Species	Taxonomic category ^a	Minimum number of origins (replicates) ^b	Major replicated trait(s)	Replicated selection	Genetic mechanism	Reproductive isolation	Compatibility/incompatibility ^c	Mode of speciation	Reference(s)
<i>Oryza rufipogon</i> , <i>Oryza nivara</i>	Wet versus dry	2 (9)**	Habitat type, flowering time, drought tolerance	**	***	***	***	ES	37, 81, 237, 244
<i>Primula elatior</i>	Foothill versus subalpine	3***e	Leaf shape, calyx shape	NA	NA	***	NA	NA	100
<i>Rhododendron kaempferi</i> , <i>Rhododendron indicum</i>	Forest versus river	2**	Habitat type (riparian), leaf morphology	*	NA	**	NA	NA	240
<i>Schizanthus hookeri</i> , <i>Schizanthus grabhamii</i> ^d	Wet versus dry	2 (3)**	Pollination syndrome, self-compatibility, dehydration avoidance	***	NA	***	**	ES	3, 145, 164, 175
<i>Senecio glaucus</i>	Interior versus coastal	3**	Habitat type (coastal), plant size, floret number	*	NA	**	*	ES	4, 51
<i>Senecio lantius</i>	Dune versus headland	2 (8)***	Habitat type, prostrate habit, small leaves	***	***	***	***	MOS	89, 91, 130, 166, 217, 225
<i>Solidago virgaurea</i> , <i>Solidago yokusaitama</i>	Terrestrial versus rheophyte	4 (6)***	Habitat type (riparian)	*	NA	*	NA	NA	107
<i>Streptanthus glandulosus</i> ^d	Non-serpentine versus serpentine	Many**	Edaphic tolerance	**	NA	*	*	ES	44, 105, 106, 125

^aDerived taxa are listed second.

^bThe number in parentheses represents the number of replicate population pairs (i.e., separate geographic locations containing two contrasting ecotypes) for systems in which the taxa geographically occur as multiple ancestral-derived pairs.

^cFor ecological speciation, we ask whether descendent populations are reproductively compatible, whereas for mutation order speciation, we ask if they are incompatible.

^dExample from Ostevik et al. (141).

^eAlthough the authors claim multiple origins, there is extensive gene flow between ecotypes at each locality, so this case should be treated with caution.

* Indirect evidence (per Reference 141).

**Weak direct evidence (per Reference 141).

***Strong direct evidence (per Reference 141).

Abbreviations: ES, ecological speciation; MOS, mutation order speciation; NA, no available published data.

response genes has been reported between replicate pairs of populations (81, 201, 228). The evolution of pathways creating the same phenotype can also consist of radically different biochemical solutions, such as the evolution of alternative solutions to CO₂-concentrating mechanisms in flowering plants (45, 174). Such contrasting solutions are better understood under the umbrella of physical constraints in which there are very few ways to solve a problem.

Replicated evolution can also manifest at the level of the network. Networks can be seen as biological circuits that transmit information throughout ontogenetic development and control the emergence of specific phenotypes. They therefore can have an impact on the probability of two populations evolving the same trait. For instance, networks facilitate replicability when mutations can be quickly compensated through gene duplicates or when there are alternative ways to accomplish or disable a function. An example of the latter comes from *Ipomoea* (221), where repeated flower color transitions are caused by independent loss-of-function mutations in multiple taxa (11). Gene regulatory networks can also act by modifying preexisting plant organs via cell- and tissue-specific expression of genes during development, as in the case of the repeated evolution of many flower forms and structures (for a review, see 220). Such study of evolutionary systems biology is gaining traction in agriculture (78, 151) and holds promise for increasing our understanding of replicated evolution in natural populations.

Genetic Constraints on Replicated Evolution

As alluded to before in the section titled Replicated Evolution, how adaptation proceeds is bounded by developmental, genetic, and physical constraints (124). Physical laws govern how habitats are assembled, limiting the evolution of many phenotypes. Phenotypic or genotypic trajectories of evolution can be severely restricted when there is mutation limitation even if environments are favorable. Mutation limitation can arise from low mutation rates or when developmental processes impose limitations on the steps to build an organism (40, 186). On many occasions, the availability of mutations and favorable environments can lead to rapid diversification, such as adaptive radiations (e.g., 203). As environments are not always stable, genetic and developmental constraints can evolve over time as organisms adapt to new conditions. Together, genetic, developmental, and physical constraints impact the level and likelihood of replicated evolution within or between species as they modulate the probability of similarity among replicated trajectories of evolution (**Figure 3**).

Physical and genetic constraints can sometimes be severe, thus leading to similarity among unrelated organisms (112, 120). Gene duplication is a powerful mechanism to overcome such constraints (216). A famous example comes from the highly conserved *ABC* genes, which control major aspects of flower morphology and evolved only once (26). In angiosperms, paralogs of the B class, which contribute to petal, stamen, and carpel formation, have proliferated (188) and led to the independent evolution of modified petals in the Ranunculales (243) and orchids (142, 199). So, although the incorporation of nonhomologous genes of the ancestral ABC system is difficult, it seems relatively easy, on an evolutionary timescale, to modify it through the production of paralogs for novel functions. The creation of gene families might result from general constraints that affect the tempo and mode of evolution of traits across taxa.

Replicate lineages that arrive at a similar phenotypic optimum can persist in this phenotypic space for extended periods and experience strong functional constraints from selection (215). Such cases represent useful experimental systems for studying the variability and constraints of the underlying gene networks. On one hand, gene networks can continue to evolve via drift and selection if they maintain their function (206). This additional interplay of selection and drift can lead to low replicability at the nucleotide site or gene despite the high replicability of traits (206). These

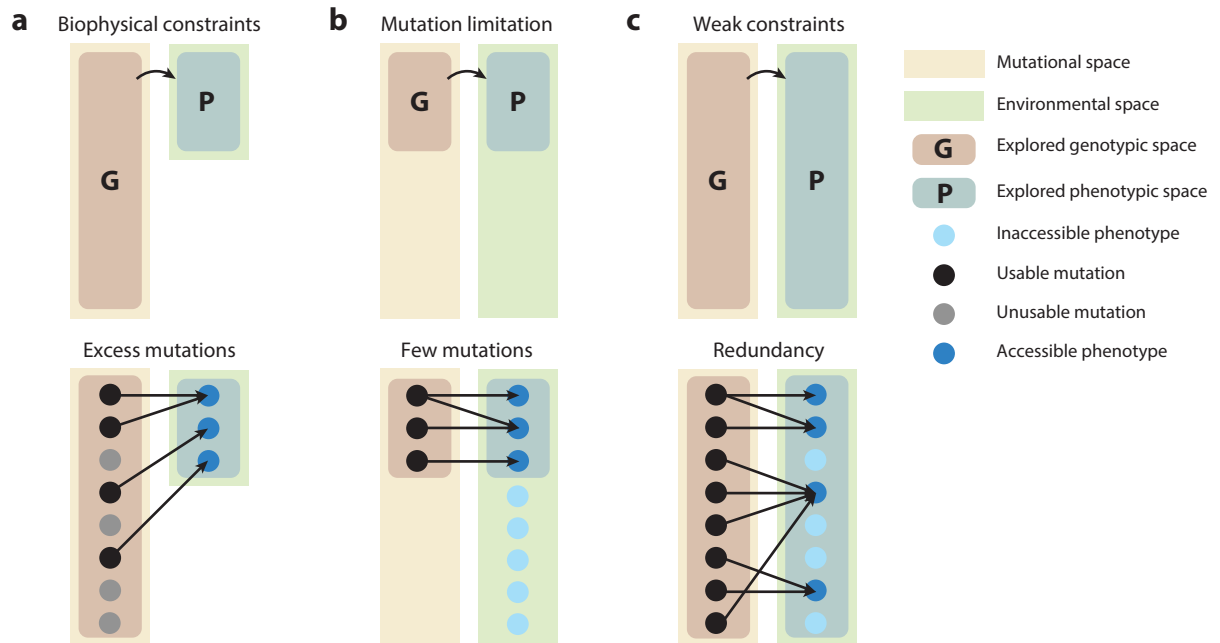


Figure 3

Examples of constraints affecting the relationship between genotype and phenotype in nature. (*a,b*) Biophysical constraints can limit the number of phenotypes that a population can explore and lead to an excess of mutations that might spread elsewhere. (*b*) Lack of genetic variability (i.e., mutation limitation) can constrain the phenotypic space and lead to unexplored phenotypes over time. High replicability at both the genotypic and phenotypic levels is likely to occur when there are strong biophysical constraints in combination with mutation limitation, as genetic architectures are likely to involve few genes. (*c*) Lack of genetic and biophysical constraints facilitates greater exploration of both genotypic and phenotypic spaces. Here, genetic architectures of adaptation are polygenic, where redundancy and robustness of interconnected genotypes will often create replication at higher levels of genetic organization, such as the genetic pathway or network.

fluid genetic architectures (90, 177) might not affect phenotypic traits but can incidentally create reproductive isolation between populations adapting to similar conditions due to drift at the genetic level. Overall, the effects of drift and stabilizing selection on traits might lead to erratic yet bounded trajectories of evolution across replicate populations. One opposite effect of the interplay between drift and selection occurs when there are evolutionary sieves for mutations that can reach high frequency in a population. When populations are small, drift can overcome the deterministic effects of selection, except for a subset of strongly selected alleles (**Figure 3b**). Under this scenario of excess mutations, populations can become similar to one another as drift imposes constraints on what mutations can spread during adaptation. Overall, our interpretations of similarity at the genetic level must be exercised with caution, as constraints impact how adaptation can proceed at various levels of biological organization over evolutionary time.

Although mutation rate, population size, and migration will affect levels of standing genetic variation, replicate evolution can also arise from nonconventional sources of genetic variation. Novel genes can be introduced into distant lineages, even between separate kingdoms, via horizontal gene transfer. Previously considered rare in multicellular eukaryotes, recent work implies that horizontal gene transfer has played a significant role in the evolutionary history of plants (for reviews, see 41, 224). Although C_4 photosynthesis has evolved multiple times in monocots

Reproductive isolation: the inability of individuals of a population to interbreed with other populations due to either intrinsic or extrinsic barriers

Stabilizing selection: a form of natural selection that favors the average phenotypic value of the population and reduces extreme trait values

Horizontal gene

transfer: the transfer of genetic material between organisms in ways other than sexual reproduction, such as between bacteria and plants

Homoploid hybrid

species: the origin of a new species via the process of hybridization between two species but without a change in ploidy level

via traditional mechanisms of inheritance, there is evidence that horizontal gene transfer can also contribute to replicability across lineages, such as in grasses from the genus *Alloteropsis*, which possess C₄ genes from multiple unrelated species (46). Similarly, bacteria and fungi have donated a variety of genes to green plants multiple times, facilitating adaptation to diverse environments (see 41, table 1). These cases of replicated evolution highlight the importance of identifying the genomic region(s) underlying replicate adaptations, as well as the selective pressures favoring their spread.

The tempo and mode of evolution influence the origin of natural replicates and affect how we interpret the causes of replicated evolution. While short- and long-term scales of replication might seem decoupled, an understanding of genetic architecture, genetic constraints, evolutionary history, and developmental evolution can help elucidate how patterns of replication manifest within and between lineages and at distinct levels of organization (116, 120, 124, 171, 193). Quantitative genetic theory, for instance, has shown that genetic variance and covariance are good predictors of phenotypic evolution in the short term but not over long periods of evolution (216). Also, studying why some organisms resemble one another can reveal genetic and evolutionary bridges between micro- and macroevolution (86). Thus, replicated evolution, even if challenging to characterize at the genetic level, is a natural phenomenon that deeply intrigues biologists and that requires interdisciplinary explanation.

REPLICATED ADAPTATION AND THE ORIGIN OF NEW SPECIES

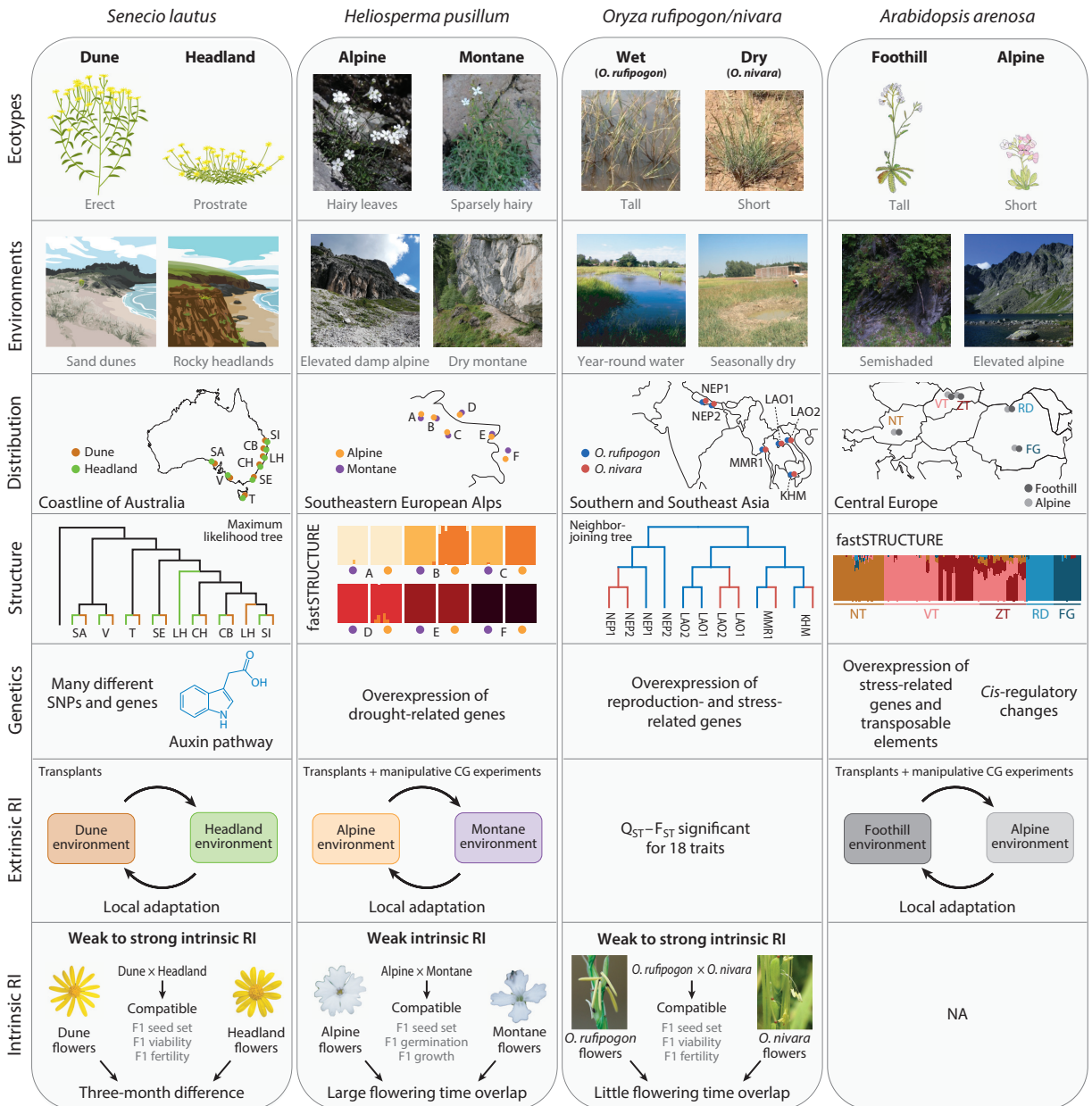
The evolution of similar phenotypes can arise between populations within a single species. Such systems provide insight into the dynamics of replicated evolution during the initial stages of adaptation and divergence, such as the repeated origin of ecotypes (see **Figure 4** for key clear-cut systems with extensive genetic and ecological data; see **Table 1** for empirical cases of replicated evolution within species).

Ecotype formation is thought to represent an early stage in the speciation process (48, 121), and many of the traits that exhibit replicated evolution in young lineages also contribute to reproductive isolation. For example, changes in flowering time can cause assortative mating (e.g., 184), and adaptation to different soil conditions can lead to reduced viability of both immigrants and hybrids (e.g., 140). Thus, replicated speciation is likely a frequent consequence of the replicated evolution of traits in young lineages. Despite this, an early review of the plant literature found few convincing examples of replicated ecological speciation—the classic form of replicated speciation—and far fewer good cases than those known from animals (141). Whether the scarcity of such cases is due to the rarity of replicated ecological speciation in plants or a lack of appropriate experiments remains unclear.

While previous discussions of replicated speciation have focused on replicated ecological speciation, replicated speciation can occur via hybridization and polyploidy as well (181, but see 200). Indeed, the recurrent origins of polyploid species appear to be common and represent the most frequent form of replicated speciation (141, 189). In most of these cases, polyploids deriving from separate origins, but involving the same parental genome(s), are compatible yet reproductively isolated from progenitor species due to the change in ploidy level. Thus, they meet the criteria for replicated speciation (see the section titled Replicated Ecological Selection below). Likewise, homoploid hybrid species often originate multiple times and represent another kind of replicated speciation (30, 189). However, while ecological selection often plays a key role in establishing new polyploid and homoploid hybrid lineages (28, 180), it may not be the chief driver of reproductive isolation. Hence, the focus of this section is on replicated ecological selection and its outcomes, which include ecological and mutation-order speciation (179).

Replicated Ecological Selection

Replicated speciation occurs when the evolution of similar traits in closely related but phylogenetically independent populations creates reproductive isolation from progenitor populations (141, 172). As first noted by Schluter & Nagel (181) and followed by Ostevik et al. (141), replicate populations can become isolated in multiple ways, and we refer the reader to their detailed discussions. Here, we review the criteria used to distinguish replicated ecological speciation from other forms of replicated speciation (141, 181).



(Caption appears on following page)

Figure 4 (Figure appears on preceding page)

Top empirical systems of replicated evolution within species demonstrating evidence for phylogenetic independence, extrinsic and intrinsic reproductive isolation, and the genetic mechanisms underlying the replicated phenotypes. For the latter, expression shifts are in the direction of the derived ecotype, which is listed second in each comparison (see **Table 1** for further details). Locations and colors of populations correspond to those used in the structure/phylogenetic analyses. For *Arabidopsis*, multiple populations were sampled for each of the five regions, although only one population per region is represented on the map. Intrinsic RI crossing data are between ecotypes/species at each locality. *Senecio*: the phylogeny of 9,658 neutral SNPs is adapted with permission from Reference 165; flower photos taken by Candice Bywater. *Heliosperma*: ecotype pictures are adapted with permission from Reference 14; environment pictures taken by Ovidiu Paun and Aglaia Szukala; the fastSTRUCTURE plot of 3,401 SNPs is adapted with permission from Reference 205. *Oryza*: ecotype pictures are adapted with permission from Reference 68; environment and flower pictures taken by Song Ge, the neighbor-joining tree of 16 nuclear neutral genes is adapted with permission from Reference 37. *Arabidopsis*: plant illustrations copyright 2022 by Magdalena Bohtínská; habitat pictures are adapted with permission from Reference 22; the fastSTRUCTURE plot of 4,341 SNPs is adapted with permission from Reference 97. Abbreviations: CG, common garden; F_{ST} , a measure of genetic differentiation; NA, no available published data; Q_{ST} , a measure of genetic differentiation associated with a quantitative trait; RI, reproductive isolation; SNP, single nucleotide polymorphism. Letters on the geographic maps correspond to the population codes used in the respective studies and to codes on the structure/phylogenetic analyses.

Independent lineages: distinct groups of individuals (populations, ecotypes, species) that are evolving separately from other such groups

Prezygotic isolation: reproductive barriers that occur before the formation of a zygote, such as flowering time differences

Postzygotic isolation: reproductive barriers that occur after the formation of a zygote, such as hybrid inviability

Extrinsic reproductive isolation: reproductive barriers due to environmental factors, such as the geographic separation of populations due to a mountain range

Criteria for phylogenetic independence. Descendent populations in similar environments must be phylogenetically independent lineages. This can be surprisingly difficult to demonstrate because introgression between ancestral and descendent populations in young lineages can result in misleading phylogenetic inferences (19). For example, a phylogeny based on neutral loci might mistakenly imply that descendent populations were multiply derived in sympatry or parapatry rather than having a single origin in allopatry. Likewise, a phylogeny based on adaptive loci might incorrectly suggest that multiply derived descendent populations have a single origin. However, the true phylogeny should be retained at markers linked to adaptive loci (165) or even at neutral loci if rates of introgression between ancestral and descendent populations are low (146).

Criteria for reproductive isolation. Ancestral and descendent populations must be reproductively isolated. The study of replicated ecological speciation requires that the strength of reproductive isolation be tested and include an assessment of both prezygotic and postzygotic isolation, or reproductive barriers, in natural settings and ideally an evaluation of both extrinsic and intrinsic forms of reproductive isolation (e.g., 130, 157).

Criteria for reproductive compatibility. Phylogenetically independent descendent populations must not be reproductively isolated. When this is not the case, the process is referred to as mutation order speciation and implies that different mutations arose and became fixed in populations experiencing repeated selection (179). Notice here that the genetics of replicated speciation has a major impact on the mode of speciation in a system.

Criteria for replicated selection. Schluter & Nagel (181) suggest that to distinguish replicated ecological speciation from replicated speciation through hybridization or polyploidy, there must be evidence of adaptive processes underlying isolation among replicate populations. Such evidence could include reciprocal transplant experiments showing local adaptation, selective sweeps at loci underlying adaptive traits, and inferences from common garden experiments or manipulative experiments that link differences in adaptive trait values to fitness and that can explain the origin of reproductive barriers within and between ecotypes, for instance.

Ecological Speciation in Plants

We surveyed the plant literature for cases of replicated ecological speciation and evaluated the strength of support following Ostevik et al. (141). We first asked whether any of the potential

examples of replicated ecological speciation compiled in Ostevik et al. (141) had been strengthened over the past decade. Next, we searched the literature published since 2012 for cases of replicated ecological speciation in plants.

A decade ago, there were no plant examples of replicated ecological speciation with compelling evidence for all four criteria, although several promising cases existed at the time (141). Evidence supporting three of these cases has since been strengthened (**Table 1**). There is now stronger evidence that the dwarfed morphology of coastal Australian ecotypes of *Eucalyptus globulus* (southern blue gum) contributes to drought tolerance (57). Thus, the only missing information in this system is evidence of reproductive compatibility among the dwarf populations. Likewise, selection for dehydration avoidance versus drought tolerance appears to be driving divergence between Andean butterfly flowers of the genus *Schizanthus* (164). However, further work needs to be done to establish phylogenetic independence and compatibility in this system (**Table 1**). Lastly, evidence of reproductive isolation between sympatric ecotypes of *Geonoma macrostachys* (a neotropical palm) has been strengthened in a recent article (25), but more information about the other three criteria is needed before it can be viewed as a conclusive case of replicated ecological speciation. There is also one strong new case of replicated ecological speciation, as well as some additional promising cases (**Table 1**). Cai et al. (37) showed that a wild rice species, *Oryza nivara*, evolved from *Oryza rufipogon* multiple times due to repeated adaptation to a seasonally dry habit. This included a shift to early flowering, which offers escape from drought, as well as strong prezygotic isolation from *O. rufipogon*. Lastly, populations of *O. nivara* from different origins were reproductively compatible, so all criteria for replicated ecological speciation are satisfied in this case.

Mutation-Order Speciation in Plants

Interestingly, one of the most striking examples of replicated evolution in a young plant system—the independent evolution of headland ecotypes of *S. laetus* from a widespread dune ecotype (89, 165)—did not lead to replicated ecological speciation (130). Instead, it represents a clear case of mutation-order speciation. During mutation-order speciation, alleles causing hybrid sterility or inviability accumulate stochastically in replicate populations (134). The source of stochasticity in the order of fixations in each population can arise from oscillations in cellular [conflict-driven processes (149)] or ecological [fluctuating environments (10)] environments or from the random order in which new beneficial mutations fix in replicate populations adapting to similar environments (123, 180). In *S. laetus*, a series of experiments (129, 130, 163, 217) showed that only divergent dune and headland populations were difficult to cross. In contrast, divergent dune populations were easily crossed, and could produce vigorous offspring. Surprisingly, replicate headland populations were difficult to transplant into replicate sites, even if closely related, and were difficult to cross when divergent. In other words, phenotypically similar populations need not be reproductively compatible (and occasionally are not ecologically exchangeable), suggesting that the evolution of replicate populations might include the stochastic accumulation of beneficial alleles that create genetic incompatibilities between them (117).

REPLICATED EVOLUTION AND THE ORIGIN OF BIOMES

As replicate traits and species originate, they may be found in different ecosystems where environmental challenges require similar solutions. This transition from the origin of species to the origin of biomes remains a major gap in connecting the rules of ecology and evolution across levels of biological organization. Below, we describe cases of replicated evolution in ecological strategies and functions, and we highlight key cases in **Table 2**.

Intrinsic reproductive isolation:

reproductive barriers not caused by environmental factors; for instance, genetic incompatibilities between individuals

Table 2 Examples of replicated evolution in plants adapting to similar environmental pressures across the world

Selective force	Strategy type	Traits and trait shifts	References
Low soil nutrients	Using nutrients more efficiently	Slow leaf economic strategies: high leaf mass area confers longer leaf life span, low leaf nitrogen and phosphorus concentrations both in green and senesced leaves, slow physiology, lipid substitution (partial replacement of phospholipids with low-P galactolipids and sulfolipids)	1, 109, 136, 159, 160, 232, 233, 235
	Enhancing nutrient uptake	Higher expenditure belowground: higher root:shoot ratio, cluster roots, higher expenditure on mycorrhizas, phosphatases, etc.	108, 110, 211
	Reducing need for nutrient uptake	More complete nutrient resorption prior to leaf fall	95, 210, 234
	Using alternative/additional nitrogen sources	N ₂ fixation, carnivory	94, 110
Low rainfall	Avoid drought altogether	Life history choices, e.g., short-lived desert ephemerals, geophytes	64, 82
	Water storage	Succulence of leaf and stem tissues, stem storage (e.g., baobab), storage in inner bark (e.g., savanna species)	24, 170, 182
	Reduce evaporative surface	Reduce leaf area during drought/dry season, operate with lower canopy leaf area and leaf area index	60, 226
	Reduce water loss through stomata and cuticle	Sunken stomata, interlocking papillae, trichomes, crassulacean acid metabolism photosynthesis (open stomata at night)	54, 59
	Tolerate dry conditions	Xylem adaptations (e.g., thick vessel walls prevent collapse), narrow vessels and tracheids to restrict water flow but protect against embolism, physical and chemical features to allow leaves to operate at more negative turgor loss points and leaves and stems to operate safely at more negative water potentials	43, 72, 208
	Use water in photosynthesis more efficiently	Operate with stomata partly closed (enhances water use efficiency), economize on water use by spending more on N-rich enzymes (least-cost theory)	63, 70, 232
Low temperatures	Avoid the coldest time of year	Shed leaves in winter (e.g., deciduous trees and shrubs), die back aboveground parts over winter and resprout in spring (e.g., geophytes), spend the winter as seeds (e.g., herbaceous annuals)	82, 102, 242
	Tolerate the coldest times of year	Thick bark, hard leaves, different pigments, cushion morphologies, smaller (narrower) leaves (less prone to frost damage), narrow tracheids and vessels (less prone to freeze-thaw embolism)	12, 92, 102, 150, 183, 231, 242
High temperatures	Minimize incoming radiation	Steeper leaf angles, higher reflectance	58, 71, 127
	Increase outgoing energy flux	Faster transpiration (problem 1: high temperatures and low water availability often occur together; problem 2: transpiration is slowed when surrounding air is very humid)	67, 71
	Reduce leaf-to-air temperature differences	Smaller leaves (thinner boundary layer, tighter coupling of leaf-to-air temperatures)	67, 69
	Tolerate high temperatures	Heat shock proteins (maintain function at high temperatures), membrane chemistry (maintain integrity at higher temperatures)	7, 132

Ecosystem Replication

More than 200 years ago, von Humboldt & Bonpland published *Essai sur la géographie des plantes* (Essay on the geography of plants) (214). This seminal work first recognized that similar shifts in vegetation zonation occur along elevational and latitudinal gradients (higher elevations being analogous to higher latitudes), as described in their *Tableau physique des Andes et Pays voisins* (Physical table of the Andes and neighboring countries) (214). In this and other works, von Humboldt used the term floras to describe vegetation zonation at broad scales, which today we would call biomes—a term coined by the famous twentieth-century plant ecologist, Frederic Clements, in 1939 (49). These zones represent one of the largest geographic descriptors of repeated environments, which can exert similar selection pressures on organisms inhabiting them, thereby leading to replicated evolution at functional and ecological levels, such as functionally equivalent suites of traits.

Biomes are determined by climate, especially rainfall, temperature, and the degree of seasonality (178, 218, 223), but geology, soil properties, and fire history may also play a role (54, 122). Similar biomes are found repeatedly across the world, and the species inhabiting them often have clear similarities in form and function. This level of replicated evolution involves many closely and distantly related species that evolved similar or equivalent phenotypes as they coped with similar environmental challenges. A classic example is Mediterranean ecosystems, which are characterized climatically in terms of cool wet winters and warm summer droughts. This type of ecosystem occurs in Southwest Australia (kwongan vegetation), the western United States (chaparral), Chile (matorral), South Africa (fynbos), and the true Mediterranean (e.g., maquis and garrigue in France, tomillares in Spain, phrygana in Greece). These vegetation types are often dominated by evergreen shrubs, subshrubs, and small trees, with many species having small, thick, leathery leaves.

Ecological Replication

As exemplified above in **Figure 2**, replicated evolution of functions that enable adaptation to common environmental pressures manifests as particular similarities in outward appearance. More subtly, replication of function takes the form of adoption of similar ecological strategies and similar morphological, chemical, and physiological features of tissues and organs (161, 222). For example, adaptation to seasonally low temperatures can be thought of as falling into two broad classes: combinations of traits for avoiding low temperatures [e.g., overwintering as seed or a belowground storage organ (82, 102)] and other combinations for tolerating low temperatures [e.g., protecting stems with thick bark (102, 183)] (**Table 2**). Adaptations to elevated temperatures include trait combinations for reducing incoming radiation [e.g., pendulous leaves (71, 127)], increasing outgoing energy fluxes via faster transpiration (67, 71), or better tolerating elevated temperatures [e.g., with specialized heat shock proteins (7, 132)]. Dry or seasonally dry climates provide numerous well-understood examples of recognizable adaptation. Again, these tend to cluster around trait combinations relating to a small number of unique plant ecological strategies (**Table 2**). Some plants avoid drought altogether [e.g., short-lived desert ephemerals (64, 82)] and others store water in specialized tissues (24, 170, 182). There are many ways in which plants can reduce water loss and are engineered to tolerate tissue water deficit. Understanding these replicated assemblages of similar and equivalent traits will require transdisciplinary approaches to comprehend both the origin of traits and their interplay with species interactions.

Another well-understood type of ecological replication is the adaptation to low soil nutrients (**Table 2**). A classic example is for plants to physically reinforce their tissues against herbivores and abiotic stressors, thereby enhancing tissue longevity and subsequently reducing nutrient uptake requirements (39, 77, 79, 207). In later parlance this became known as adopting slow leaf (or plant)

economic strategies (158, 233), that is, evolving trait combinations that lead to slow economic returns on investments of dry mass and nutrients in leaves but a longer overall revenue stream derived from those investments. Key traits of perennial species on low-nutrient soils include

- high leaf mass per area, connoting enhanced physical robustness of leaves, contributing to longer leaf life spans (often along with substantial accumulation of carbon-based defense compounds) (136, 160, 235);
- low leaf nitrogen and phosphorus concentrations, which reduce nutrient uptake requirements and reduce attractiveness to herbivores but also limit photosynthetic rates (50, 160); and
- nearly complete (or highly proficient) withdrawal of key nutrients before leaf fall (1); for example, on low phosphorus soils of eastern Australia, some evergreen species reduce leaf phosphorus concentrations to <0.002% prior to leaf fall (234), which are some of the lowest values recorded worldwide.

Not surprisingly, slow leaf economic strategies tend to be coordinated with traits that use existing nutrients more efficiently (109) and with traits that enable better access to soil nutrients. These traits include adopting higher root:shoot ratios (147), spending a larger proportion of the plant carbon budget on mycorrhizal symbioses (211), or exuding various chemical compounds to solubilize recalcitrant forms of soil phosphorus, for example, phosphatase enzymes produced by many eucalypts or the carboxylate compounds exuded from specialized cluster roots found in many Proteaceae and Cyperaceae species (110). Another classic example of replicated evolution to cope with nutrient-deficient environments is carnivory. The pitcher plant, containing a pitfall trap filled with digestive fluids, has evolved independently multiple times in order to trap prey and extract nutrients such as nitrogen (202) (**Figure 5a**). Studies on the genetic basis of these traits as well as their genetic correlations will be key for understanding how ecological coordination evolves, thereby creating a platform for understanding the ecological assembly of biomes.

Functional Replication

The anatomical features underlying coordinated traits, such as leaf physiognomic traits (**Table 2**), can explain some of the mechanisms that increase the adaptation of individuals to their environment (43, 208). Some of the main anatomical features of plants have evolved independently multiple times, suggesting that replicated evolution might be a key feature of organic evolution. Some of these structures include leaves (28, 204), roots (87), many aspects of flower development [such as bisexual flowers (176), nonsymmetric flowers (162), and flower organ fusion (see 190)], and structural systems required for proper physiological function such as the water transport system (24, 182).

Specific anatomical or ultrastructural features that increase the reliability and efficiency of water supply (e.g., 24, 182) provide clear examples of how anatomy, function, and ecology come together during replicated evolution. In perennial plants that must endure dry conditions, there is convincing evidence that species growing in low or sporadic rainfall environments evolved water transport systems capable of resisting damage from xylem cavitation (the process whereby air bubbles fill the xylem under excessive water deficit). Strong relationships between rainfall and xylem resistance to cavitation have recently been demonstrated in several clades of trees including oaks (185) and conifers (35, 111). Furthermore, this trait has been clearly linked to the ultrastructure of the pit connections between xylem conduits (118), suggesting a common anatomy across species with very divergent wood features. Thus, very small changes in the properties of the xylem cell wall lie at the foundation of a major functional replication often found in dry climates. Like

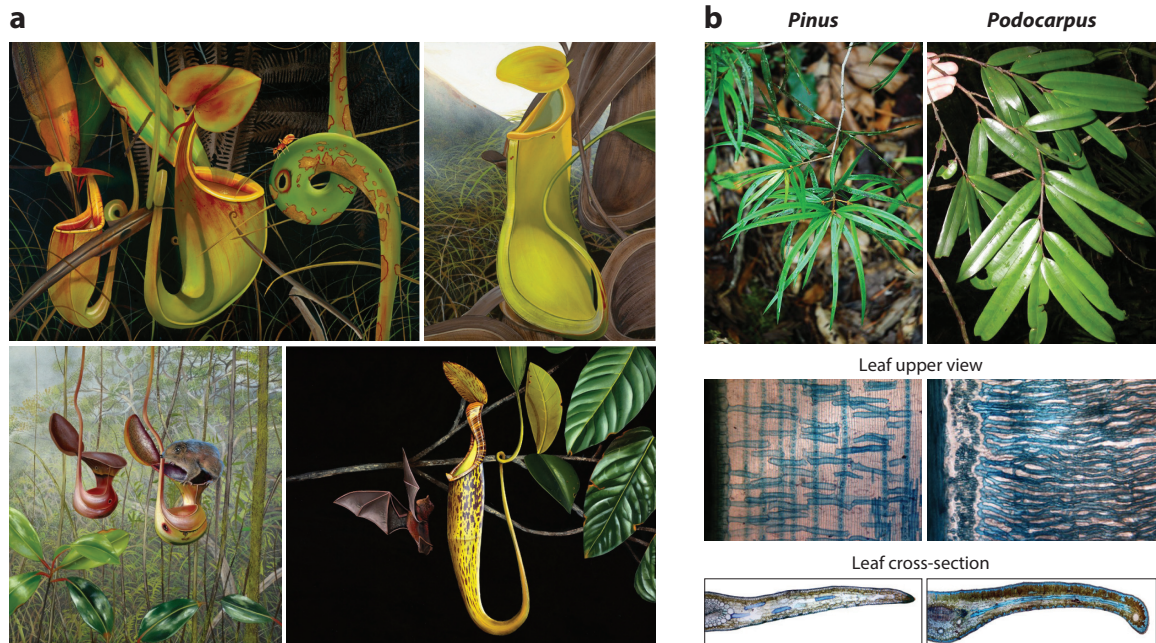


Figure 5

Replicated evolution in distant taxa. (a) Carnivory has repeatedly and independently evolved as a mechanism to gain nutrients (such as nitrogen) in nutrient-deficient environments. We show examples of pitcher plants that have repeatedly evolved similar pitfall-trapping mechanisms (202). (Top to bottom, left to right) *Nepenthes bicalcarata* with a mutualistic ant (*Colobopsis schmitzi*), *Nepenthes extincta*, *Nepenthes lowii* with a tree shrew (*Tupaia montana*), a roosting bat (*Kerivoula bardwickii*) alongside a pitcher of *Nepenthes hemsleyana*. Images painted by Chris Thorogood and adapted with permission from Reference 202. (b) Conifers from separate families have independently evolved flattened leaves to improve light capture by modifying mesophyll tissue to become an alternative water transport tissue from the midvein to the leaf margins. This anatomical adaptation of elongated and lignified cells is seen in the leaf upper view and the leaf cross section of the blue-stained cells in *Pinus* and *Podocarpus*. Photos taken by Tim Brodribb; figure adapted from Reference 30.

other replications of trait combinations, the genetics of replicated anatomies, functional traits, and ecological strategies remains a fascinating topic of exploration, particularly for evolutionary developmental biologists scouting the origin of complex traits in the deep past and the trade-offs that manifest during their evolution.

Replication of Trade-Offs

Replicated evolution can also arise in the form of alternative solutions to basic functional trade-offs. An example can be observed in the ways diverse lineages produce wide, flat leaves with high photosynthetic rates (Figure 5b). This is a complex physiological challenge because high rates of photosynthesis on land can only be achieved with the sacrifice of copious water, lost as transpiration, that escapes the leaf through the entry pathway (stomata) for photosynthetic CO₂. For this reason, species with high photosynthetic rates also possess highly efficient water transport to photosynthetic tissue in the leaf (33, 173). Angiosperms solve the problem of water transport to a flattened two-dimensional surface by producing a highly ramified venation network (27, 32), but conifers are typically restricted to one or a few veins in the leaf. In an extraordinary case of replicated evolution, conifers from three distinct families (Podocarpaceae, Pinaceae, and Taxaceae) can produce flattened leaves, not by vein ramification but by modifying mesophyll tissue to

become an alternative water transport tissue from the midvein to the leaf margins (**Figure 5b**). This anatomical replication, called accessory transfusion tissue (76), is present in multiple clades of the southern rainforest conifer family Podocarpaceae and several rainforest genera of Taxaceae (*Amentotaxus* and *Austrotaxus*). Most surprising of all, it appears in a single species of *Pinus* that produces highly flattened needles and grows in tropical rainforests in Vietnam (31). This is the only example of a *Pinus* species being able to produce flattened leaves or to compete successfully in undisturbed tropical rainforest.

Replication of Trait Associations

The process of replicated plant strategy can be understood when the impacts of adaptive evolution in one trait are considered relative to other associated functional elements. A good example in plants is the commonly observed evolution of vascular tissue that resists cavitation damage during drought (34, 111). The production of resilient xylem provides a limited advantage if other tissues have not evolved in a way that allows the plant to function under conditions of increased water deficit. Features such as greater lignification of leaves (20) and stems (56, 119), which prevents the collapse of tissues under tension, together with enhanced leaf osmotic potential (9), which enables tissues to maintain functionality during dehydration, are typically associated with cavitation-resistant xylem. This pathway toward the greater capacity to extract water from the soil and survive water deficit is further linked to stomatal behavior because prolonged activity under water stress requires stomata that are insensitive to water deficit (126). Thus, there may be a degree of evolutionary tinkering on trait covariation once a lineage begins to move along a trajectory toward increasing resistance to water stress. This culminates in commonly observed traits of mechanical strength (in wood and leaves), leaf physiognomy, and leaf life span in dry forest trees. Quantitative, developmental, and population genetic studies of such trait combinations can shed light on how natural selection might build up trait combinations that are common across biomes and point toward a whole-plant view of adaptation, where genetic correlations and their covariance with fitness sit at the heart of studies of replicated evolution.

FUTURE DIRECTIONS

Our examination of replicated evolution in plants suggests several avenues of research that can shed light on how similarity arises in nature. Major lines of inquiry are how predictable evolution can be and at what levels of biological organization it arises (2, 21, 74, 75, 124, 137). Answering these questions requires new mechanistic models to explain the flow of information from alleles to traits and from traits to ensembles of species, while considering how constraints shape evolution at different biological scales (120, 124, 193). This will require models that integrate developmental processes within one generation with the inheritance of traits across thousands of generations, as well as the incorporation of quantitative genetics theory to explain interactions among traits and their response to selection. Such a formidable challenge could benefit from adopting tools from systems biology (5, 219), computer science (113), and mathematics (216) to link mutational effects with trait evolution under a variety of selection regimes.

A corollary from the previous point is that clarifying the relationship between different levels of biological organization and evolutionary processes would benefit our understanding of similarity in nature. To what extent are networks under strong stabilizing selection? Which traits are expected to exhibit genetic and phenotypic correlations, and how long are such correlations expected to persist? Are answers to these questions specific to mating system and life history strategy? Traditionally, population genetics has focused on tracking the evolution of allelic frequencies, often of a few loci at the same time. By contrast, quantitative genetics has focused on studying how

variance changes over time, which comprises the aggregate change of allelic frequencies at many loci. Finally, developmental models often describe genetic and phenotypic dependencies within the lifetime of an organism, or they describe steps for the origin of complex traits over hundreds of millions of years. It is time we seek unification of these approaches within a cohesive framework of evolution (see also 62). The origin of similarity provides a natural experiment for such exploration, as replication occurs across many different levels of organization and time scales.

Although instances of replicated evolution at ecological and genetic levels are not analogous, they do have common abstractions; for example, there are rules to assemble an organism, and for a population to evolve, there are rules for assembling a community and for an ecosystem to change over time (103, 167). The principles governing genetic and ecological evolution might be different. Still, they are nested within each other by providing raw material (genetic variability) and selective regimes (biotic and abiotic environments) for evolutionary dynamics within and between species. With respect to ecological speciation, an interesting future direction would be to determine the role of ecology in driving replicated hybrid and polyploid speciation. How common is this, and what impact does it have on ecological replication? When considering replication across biomes, future research might investigate how often the repeatability of ecological strategies is due to independent adaptation within biomes versus dispersal and subsequent filtering of successful strategies.

At a more fundamental level, understanding the genetics of adaptation continues to be a critical problem in evolution and for the origins of replication. Without knowledge of the rules for building complex adaptations, our models of evolution will remain phenomenological. While useful for specific populations or species, they will remain limited for generalizing about the principles of diversification. Efforts to determine the genetic basis of polygenic traits continue to be hampered by challenges associated with isolating variants of small effect, especially in nonmodel systems. Likewise, genome-wide association approaches have proven powerful for understanding the genetic basis of variation within species, but extending this approach across species boundaries has proven difficult. The development of new model systems could help fill these knowledge gaps, particularly if new systems were to include cross-compatible species, as well as natural replication, both within and between species. Replication can help to avoid false positives due to stochasticity, population structure, or limited power, while also providing insights about the repeatability of genetic changes associated with the evolution of polygenic traits. Replicated evolution is not only a phenomenon to understand in and of itself, but also a scientific tool to solve fundamental biological questions.

SUMMARY POINTS

1. The term replicated evolution can be used to encompass both convergence and parallelism.
2. Replicated evolution exists at multiple scales as well as levels of biological organization. Studies of replicated evolution call for an integrated approach where the repeated and independent flow of information from genes to traits to populations to communities and biomes can be tracked and explained.
3. Empirical examples of replicated evolution are common in plants and occur at many levels of biological organization, including genes, traits, and functions.
4. Similar forms and functions observed in systems of replicated evolution provide robust evidence of the pervasive role of natural selection in shaping plant diversity in nature.

5. The extent of replicated evolution that we observe in nature suggests developmental constraints and limitations on how natural selection solves organismal challenges.
6. Systems of replicated evolution lay the foundations for understanding how natural selection shapes the diversity that we see in nature, the role of robustness and redundancy during adaptation, and whether evolution itself is deterministic and repeatable.

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171. Comprehensive review on replicated evolution and the factors that influence the underlying repeated molecular mechanisms within natural systems.

181. Coined the term parallel speciation, whereby independent lineages repeatedly evolve reproductive isolation, and provided an overview of the criteria to distinguish it from other forms of speciation.

186. An in-depth perspective on the sources of developmental constraints and how they impact natural selection and evolution.

214. First description of the similar vegetation zonation shifts that occur along broad elevational and latitudinal gradients (higher elevations are analogous to higher latitudes).

218. First comprehensive description of the main world biomes, their plant features, and the role of climate in driving these patterns.

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