# Convergent evolution in plant adaptations to extreme environments

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**Abstract**. Convergent evolution in plants provides a robust framework for understanding how natural selection shapes adaptive responses under extreme environmental conditions. This mini-review synthesizes current evidence on plant adaptations to habitats characterized by high salinity, drought, low temperatures, and metalliferous soils. Across phylogenetically distant lineages, these environments impose recurrent selective pressures that favor similar functional solutions, resulting in the repeated emergence of shared adaptive trait syndromes. While convergence at the level of individual genetic mutations is relatively rare, substantial evidence indicates that it is widespread at higher levels of biological organization, including gene families, metabolic pathways, and gene regulatory networks. This hierarchical pattern suggests that evolutionary outcomes are partially predictable, constrained by both environmental factors and pre-existing genomic architectures. Additionally, epigenetic regulation and phenotypic plasticity play critical roles in facilitating rapid and flexible responses to stress, potentially contributing to long-term evolutionary trajectories through mechanisms such as genetic accommodation. Phylogenetic constraints further influence adaptation by limiting the range of available evolutionary pathways, although extreme conditions can override these constraints for key functional traits. The integration of genomic, physiological, and ecological data highlights the existence of a conserved "adaptive toolkit" recurrently recruited across extreme environments. Beyond its theoretical significance, understanding convergent evolution in extremophile plants has important implications for crop improvement and the development of stress-resilient varieties in the context of global climate change.

**Keywords**: convergent evolution, extremophile plants, abiotic stress, adaptive traits, gene regulatory networks, phenotypic plasticity, epigenetic regulation, phylogenetic constraints, stress tolerance, climate change adaptation.

**Introduction**. Convergent evolution represents one of the most compelling lines of evidence for the role of natural selection in shaping biological diversity, particularly under conditions of strong and recurrent environmental constraints (Satterlee et al., 2024; Oroian et al., 2025). In plants, extreme environments—such as high salinity, chronic drought, low temperatures at high altitudes, and metalliferous soils (Gavriloaie et al., 2025; Farooq et al., 2015)—constitute powerful selective filters that repeatedly favor similar adaptive solutions across phylogenetically distant lineages (Hjertaas et al., 2023). These systems therefore function as natural evolutionary replicates, enabling the investigation of the extent to which evolution is predictable versus historically contingent (Pandey et al., 2026; Popescu & Tripathi, 2026; Petrescu-Mag, 2025abc, 2026ab).

A central question in evolutionary biology concerns whether adaptation follows deterministic pathways when organisms are exposed to comparable selective pressures (Xu et al., 2020; Greenway et al., 2020). In the case of extremophile plants, accumulating genomic, physiological, and ecological evidence suggests that convergence is more prevalent at higher levels of biological organization—such as metabolic pathways, gene regulatory networks, and functional trait syndromes—than at the level of individual nucleotide substitutions (Xu et al., 2020; Artur & Kajala, 2021; Heyduk et al., 2019;

Greenway et al., 2020). This pattern indicates that while the precise genetic routes may vary, evolution often targets a limited set of functional solutions, constrained by both the physicochemical nature of stressors and the pre-existing genomic architecture of organisms (Xu et al., 2020; Artur & Kajala, 2021; Greenway et al., 2020).

Extreme environments impose multifactorial stresses that act simultaneously, including osmotic imbalance, oxidative stress, limited water availability, and cellular toxicity (Bora et al., 2005ab; Bordea & Popescu, 2023). As a consequence, adaptive responses tend to involve integrated trait complexes rather than isolated modifications. For instance, tolerance to salinity or drought frequently requires coordinated regulation of ion transport, osmoprotection, and reactive oxygen species detoxification. Similarly, adaptation to alpine environments involves the interplay of cold tolerance, UV protection, and altered phenology. These recurring trait assemblages suggest the existence of a shared “adaptive toolkit” that is repeatedly co-opted and modified across independent evolutionary lineages.

At the same time, the evolutionary trajectories leading to similar phenotypes are shaped by phylogenetic constraints, including inherited gene repertoires, regulatory network architectures, and developmental pathways. Thus, convergent evolution in plants reflects a dynamic balance between determinism imposed by environmental selection and contingency imposed by evolutionary history (Agrawal, 2017; Păsărin et al., 2025; Petrescu-Mag et al., 2024). Understanding this balance is essential not only for elucidating the mechanisms of plant adaptation but also for predicting responses to ongoing global environmental change.

This mini-review synthesizes current knowledge on convergent evolution in plant adaptations to extreme environments, with a particular focus on the predictability of evolutionary outcomes, the role of shared functional modules, and the influence of phylogenetic constraints across multiple levels of biological organization.

**Predictability of Evolution in Extreme Environments**. Genomic comparisons across diverse extremophiles indicate that convergence at individual amino acid sites is relatively rare and prone to false positives, whereas convergence at higher levels (pathways, gene families, expression programs, genome composition) is frequent, suggesting partially predictable evolutionary trajectories (Xu et al., 2020).

In alpine floras worldwide, species assemblages are phylogenetically clustered, indicating repeated recruitment of a limited set of cold-tolerant lineages and thus predictable niche conservatism at the clade level (Qian et al., 2021).

For alpine plants, independent lineages repeatedly show contraction of disease-resistance gene families and convergent positive selection on genes linked to reproduction, respiration, cell wall modification, DNA repair and stress resistance, implying predictable genomic targets under cold, high UV and hypoxia (Zhang et al., 2023; Zhang et al., 2022; Zhang et al., 2024). Experimental selection under zinc stress demonstrates rapid adaptive divergence in functional traits within a single generation, supporting strong, directional selection in metalliferous habitats (Nowak et al., 2018) (Table 1, Figure 1).

In grasses, desiccation tolerance shows substantial convergence in gene duplication and expression, often activating syntenic orthologs (parallel evolution), while sometimes recruiting different genes in the same pathways (phenotypic convergence) (Marks et al., 2024). Across xerophytes, at least 118 genes are shared among aridity-tolerant species, with a subset repeatedly co-opted during local adaptation, indicating a reusable “xerophytic toolkit” (Fu et al., 2024).

Alpine species independently evolve thick cuticular waxes and flavonoid-rich “greenhouse” structures via convergent expansion and upregulation of associated pathways (Zhang et al., 2023; Zhang et al., 2022; Zhang et al., 2024). In halophytes and metal-hyperaccumulators, different lineages repeatedly exploit common physiological modules—ion transport, detoxification, oxidative stress responses—even when the precise genes and regulatory details differ (Flowers et al., 2010; Flowers & Colmer, 2015; Manara et al., 2020; Mann et al., 2023; Van Zelm et al., 2020; Xu et al., 2026).

Table 1

Recurrent adaptive trait sets across extreme habitats:
shared trait syndromes in four extreme habitats

| *Environment* | *Recurrent adaptive traits (physiology / genome)* | *References* |
|---|---|---|
| Saline (halophytes) | Ion exclusion/compartmentation, compatible solutes, ROS control; repeated use of general salt-tolerance pathways; extensive gene duplication and regulatory rewiring in model halophytes | Flowers et al., 2010; Flowers & Colmer, 2015; Mann et al., 2023; Van Zelm et al., 2020; Xu et al., 2026 |
| Drought / xeric | Desiccation tolerance, CCMs (C4, CAM), root barriers; convergent co-option and re-wiring of gene regulatory networks; shared xerophytic gene sets reused in local adaptation | Marks et al., 2024; Fu et al., 2024; Artur & Kajala, 2021; Artur & Kajala, 2020 |
| Alpine / high altitude | Contraction of immune (R-) genes, enhanced cuticular wax and flavonoid pathways, genes for cold/UV/hypoxia tolerance; convergent phenological strategies (earlier, synchronized flowering) | Zhang et al., 2023; Zhang et al., 2022; Qian et al., 2021; Zhang et al., 2024; Tamburrino et al., 2026 |
| Metalliferous soils | Hyperaccumulation and hypertolerance backgrounds, local refinement into distinct ecotypes; modest but real convergence in candidate genes and functional networks; parallel selection on specific SNPs in some genes | Preite et al., 2018; Manara et al., 2020; Schvartzman et al., 2018; Feng et al., 2024; Nowak et al., 2018. |

**Epigenetic Regulation and Phenotypic Plasticity in Extreme Environments**. Beyond genetic adaptation, increasing evidence highlights the critical role of epigenetic regulation and phenotypic plasticity in facilitating plant survival under extreme environmental conditions (Abdulraheem et al., 2024; Wood et al., 2021; Chang et al., 2019). Epigenetic mechanisms—including DNA methylation, histone modifications, and small RNA-mediated pathways—enable rapid and reversible changes in gene expression without altering the underlying DNA sequence (Liu & He, 2020; Wood et al., 2021; Akhter et al., 2021; Chang et al., 2019). These mechanisms can modulate stress-responsive pathways and may contribute to both short-term acclimation and longer-term evolutionary processes (Liu & He, 2020; Abdulraheem et al., 2024; Wood et al., 2021; Akhter et al., 2021; Ma et al., 2024; Hu et al., 2023; Chang et al., 2019).

In extreme habitats, where environmental conditions can fluctuate unpredictably or exceed physiological thresholds, phenotypic plasticity provides an immediate buffer against stress (Abdulraheem et al., 2024; Wood et al., 2021; Chang et al., 2019). For example, plants exposed to drought or salinity can dynamically adjust stomatal conductance, osmolyte production, and antioxidant defenses through regulatory changes that do not require genetic mutation (Seleiman et al., 2021; Lodhi & Srivastava, 2025; Alzahrani et al., 2025; Alzahrani, 2024; Alsamadany et al., 2024; Dehnavi et al., 2024). Importantly, such plastic responses are often underpinned by conserved gene regulatory networks, which are repeatedly activated across diverse taxa, contributing to functional convergence (Abdulraheem et al., 2024; Wood et al., 2021; Hu et al., 2023; Chang et al., 2019).

Epigenetic modifications may also exhibit a degree of heritability, thereby influencing transgenerational responses to stress (Liu & He, 2020; Cao & Chen, 2024; Abdulraheem et al., 2024; Karalija et al., 2025; Wood et al., 2021; Lodhi & Srivastava, 2025; Harris et al., 2023; Nijhout et al., 2020; Akhter et al., 2021; Aswathi et al., 2025; Lagiotis et al., 2023). In this context, stress-induced epigenetic states can prime offspring for similar environmental conditions, effectively bridging ecological and evolutionary timescales (Liu & He, 2020; Abdulraheem et al., 2024; Karalija et al., 2025; Wood et al., 2021; Lodhi & Srivastava, 2025; Harris et al., 2023; Aswathi et al., 2025; Lagiotis et al., 2023). Although the stability and evolutionary significance of such inheritance remain debated, it is increasingly clear that epigenetic variation represents an additional layer of biological complexity shaping adaptive trajectories (Liu & He, 2020; Cao & Chen, 2024; Abdulraheem et al., 2024; Karalija et al., 2025; Wood et al., 2021;

Lodhi & Srivastava, 2025; Harris et al., 2023; Akhter et al., 2021; Aswathi et al., 2025; Lagiotis et al., 2023; Chang et al., 2019).

Furthermore, the interaction between plasticity and genetic evolution may itself be subject to convergence. Lineages inhabiting extreme environments often show repeated patterns of plastic responses that later become genetically assimilated, a process known as genetic accommodation (Cao & Chen, 2024; Wood et al., 2021; Nijhout et al., 2020; Scheiner & Levis, 2021; Hu et al., 2023). This suggests that phenotypic plasticity is not merely a transient phenomenon but may actively guide the direction of evolutionary change (Cao & Chen, 2024; Wood et al., 2021; Nijhout et al., 2020; Scheiner & Levis, 2021; Hu et al., 2023).

Overall, integrating epigenetic and plastic responses into the framework of convergent evolution provides a more comprehensive understanding of how plants cope with environmental extremes, highlighting the importance of regulatory flexibility alongside genetic adaptation (Cao & Chen, 2024; Abdulraheem et al., 2024; Wood et al., 2021; Akhter et al., 2021; Ma et al., 2024; Hu et al., 2023; Chang et al., 2019).

**Phylogenetic Constraints and Evolutionary Lability**. At community scale, alpine floras are assembled from a limited set of clades preadapted to cold, demonstrating strong phylogenetic niche conservatism: alpine floras are more phylogenetically clustered than their surrounding regional floras and the global pool, especially in temperate regions (Qian et al., 2021). However, within alpine communities, flowering phenology shows weakened phylogenetic signal and strong functional convergence at higher elevations, implying that harsh conditions can override ancestral constraints for key traits (Tamburrino et al., 2026). In metallicolous *Arabidopsis*, related pseudo-metallophytes share pre-existing hyperaccumulation and hypertolerance backgrounds, but independent colonizations of calamine soils show only modest gene-level convergence and substantial species- and site-specific solutions, suggesting phylogenetic “starting points” constrain but do not fully canalize adaptation (Preite et al., 2018; Manara et al., 2020; Schvartzman et al., 2018).

Genome-scale surveys across extremophile plants further indicate that deeply conserved gene regulatory networks are repeatedly co-opted and modified, rather than entirely novel networks evolving de novo, highlighting phylogenetic constraint at the level of available GRNs combined with considerable regulatory flexibility (Xu et al., 2020; Artur & Kajala, 2021; Artur & Kajala, 2020).

**Implications for Crop Improvement and Climate Change Resilience**. Insights into convergent evolution in extremophile plants have significant implications for agriculture and ecosystem management in the context of global climate change. As crops are increasingly exposed to abiotic stresses such as drought, salinity, and temperature extremes, understanding the recurrent adaptive strategies evolved by wild plant lineages provides a valuable framework for developing stress-resilient cultivars.

One key implication is the identification of conserved functional modules that can be targeted in crop improvement programs. Traits such as ion homeostasis, osmoprotection, and oxidative stress tolerance are repeatedly recruited across diverse plant taxa, suggesting that they represent robust and transferable solutions to environmental stress. Advances in comparative genomics and transcriptomics have facilitated the identification of candidate genes and regulatory networks that can be manipulated through breeding or biotechnological approaches.

Moreover, the recognition that adaptation often occurs at the level of gene networks rather than individual genes underscores the importance of systems-level approaches. Engineering or selecting for coordinated responses may be more effective than targeting single loci, particularly for complex traits such as drought tolerance or nutrient efficiency.

Convergent evolution also informs predictive models of plant responses to environmental change. If adaptive outcomes are partially predictable, it becomes possible to anticipate which traits or pathways are most likely to be favored under future climatic scenarios. This has direct applications in conservation biology, where identifying species or lineages with preadapted traits may guide efforts to preserve biodiversity under shifting environmental conditions.

However, the role of phylogenetic constraints highlights potential limitations. Not all species possess the same evolutionary "starting points," and thus their capacity to evolve similar adaptations may differ. This reinforces the need to consider evolutionary history when designing strategies for crop improvement or ecosystem management.

In summary, the study of convergent evolution in extreme environments not only advances fundamental evolutionary theory but also provides practical insights for addressing some of the most pressing challenges in plant science and global sustainability.

**Conclusions**. Convergent evolution in plant adaptations to extreme environments provides compelling evidence that natural selection can repeatedly drive the emergence of similar functional solutions across phylogenetically distant lineages. The synthesis of current data indicates that evolutionary convergence is rarely manifested at the level of individual mutations, but instead predominantly occurs at higher organizational levels, including gene families, metabolic pathways, and gene regulatory networks. This hierarchical pattern of convergence supports the view that evolution is partially predictable, particularly under strong and consistent environmental pressures.

Across saline, xeric, alpine, and metalliferous habitats, plants repeatedly recruit a limited set of physiological and molecular mechanisms, forming recurrent adaptive trait syndromes. These include ion homeostasis, osmoprotection, detoxification, and stress-responsive regulatory programs, which together constitute a shared and reusable adaptive toolkit. At the same time, the specific genetic routes leading to these outcomes remain diverse, reflecting both evolutionary contingency and lineage-specific genomic architectures.

Importantly, adaptation to extreme environments is not solely driven by genetic change but is also facilitated by epigenetic regulation and phenotypic plasticity. These mechanisms enable rapid and flexible responses to environmental stress and may contribute to longer-term evolutionary trajectories through processes such as genetic accommodation. Their integration into the framework of convergent evolution highlights the central role of regulatory dynamics in shaping plant resilience.

Phylogenetic constraints further modulate adaptive outcomes by limiting the range of available evolutionary pathways. While certain clades exhibit predispositions toward particular stress tolerances, extreme conditions can also promote functional convergence that overrides ancestral signals for key traits. Thus, plant adaptation emerges from a dynamic interplay between deterministic selection pressures and historically contingent starting points.

Beyond its theoretical significance, convergent evolution has important practical implications. The identification of conserved adaptive modules provides a valuable foundation for crop improvement and the development of stress-resilient varieties in the face of accelerating climate change. However, the influence of phylogenetic constraints underscores the need for lineage-specific strategies and systems-level approaches.

As a final remark, convergent evolution in extremophile plants reveals both the repeatability and the complexity of adaptive processes. Future research integrating genomics, epigenomics, functional biology, and ecological data will be essential for refining our understanding of evolutionary predictability and for translating these insights into sustainable solutions for agriculture and biodiversity conservation.

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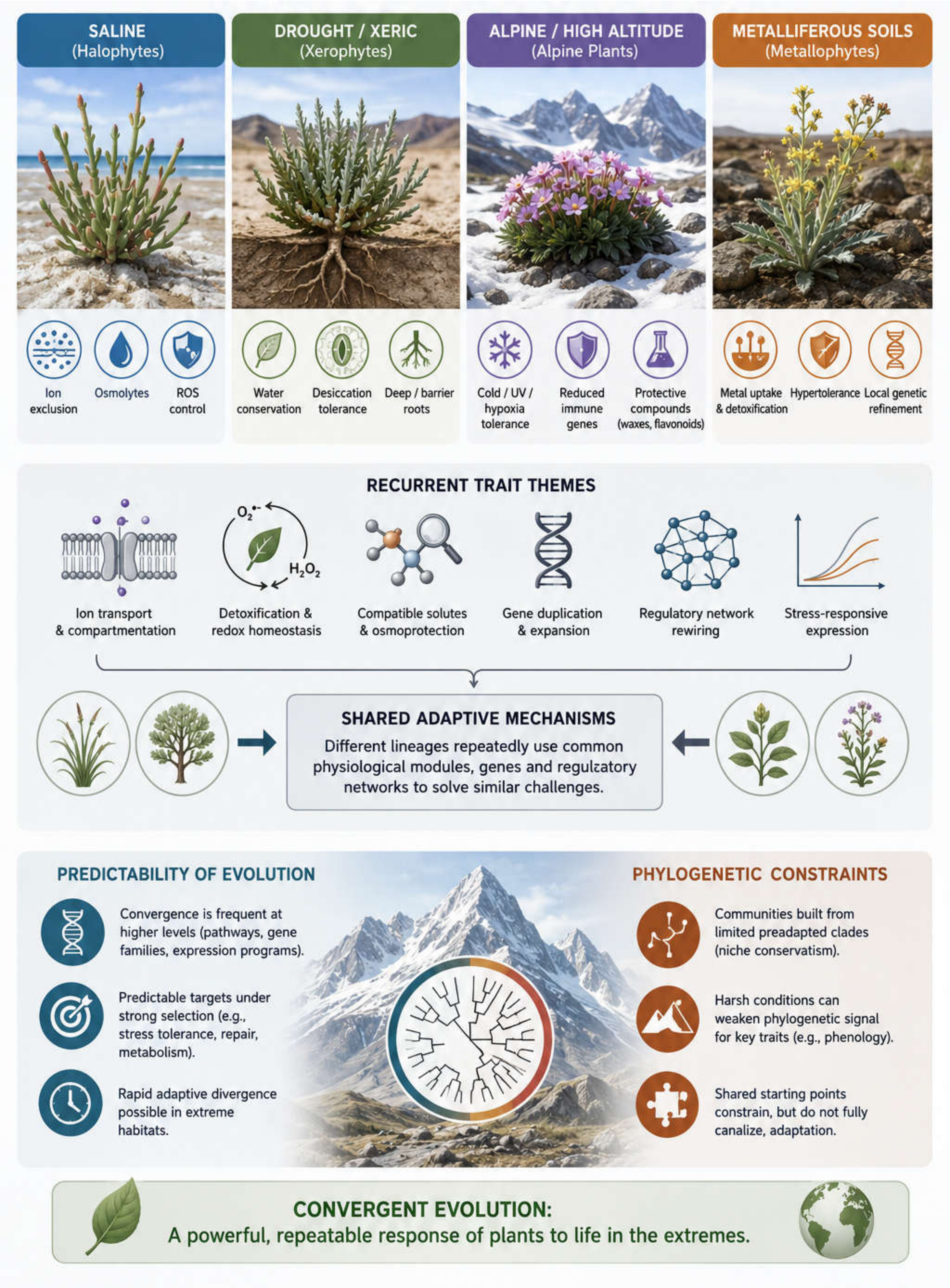

Figure 1. Convergent evolution in plant adaptations to extreme environments: similar pressures, similar solutions – across distant lineages.

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