Genomic Signatures of Environmental Adaptation in Pakistani Flora: A Multi-Species Analysis Across Diverse Ecological Gradients

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Abstract

The rich plant biodiversity of Pakistan, spanning diverse ecological zones from alpine meadows to arid deserts, presents a unique opportunity to study genomic adaptation to environmental stresses. This comprehensive review synthesizes findings from recent genome-wide studies on Pakistani native plants, revealing consistent signatures of selection across species in response to local environmental conditions. We analyzed genomic data from multiple studies encompassing species such as *Hordeum vulgare* (barley), *Triticum aestivum* (wheat), and their wild relatives, identifying selective sweeps in genes associated with drought tolerance, salt stress response, and temperature adaptation. Our analysis demonstrates that Pakistani flora has developed sophisticated genomic adaptations through selective sweeps, structural variations, and gene family expansions. Specifically, we identified repeated selection in genes related to ion homeostasis, photosynthetic efficiency, and flowering time regulation. These findings provide valuable insights for crop improvement strategies and have significant implications for biodiversity conservation in the face of climate change. The genomic resources characterized from Pakistan's native species represent a valuable resource for global efforts to develop climate-resilient crops. This expanded review incorporates additional case studies from medicinal plants, forest species, and extremophytes, providing a more comprehensive understanding of adaptation mechanisms across different plant life forms and ecosystems.

Keywords

Plant Genomics, Environmental Adaptation, Selection Signatures, Genome-Wide Association Studies, Biodiversity, Conservation Genomics

1. Introduction

Pakistan's remarkable geographic diversity creates a natural laboratory for studying plant adaptation to environmental stresses. Ranging from the high-altitude ecosystems of the Himalayas to the arid plains of the Punjab and Sindh provinces, the country's flora has evolved under diverse selective pressures including water scarcity, high salinity, and temperature extremes. The country's unique position at the crossroads of multiple biogeographic regions has resulted in exceptional species richness, with approximately 6,000 plant species recorded, including many endemics that have evolved in response to local environmental challenges. Understanding the genomic basis of these adaptations has become increasingly urgent in the context of climate change, which threatens both natural ecosystems and agricultural productivity worldwide.

Recent advances in genomic technologies have revolutionized our ability to detect signatures of environmental selection in plant genomes. Studies of crop wild relatives (CWRs) native to Pakistan have been particularly informative, revealing genetic mechanisms underlying resilience to abiotic stresses. For instance, research on wild barley (*Hordeum spontaneum*) populations from Pakistan's Thar Desert has uncovered novel alleles associated with drought tolerance. Similarly, investigations of wheat relatives in salt-affected regions of Punjab have identified genes responsible for ion homeostasis and osmotic adjustment. Beyond agricultural relatives, studies on native trees, medicinal plants, and extremophytes have revealed additional layers of genomic adaptation to specific ecological niches.

The publication of chromosome-level genomes for several Pakistani native plants, including *Cicer microphyllum* (a wild relative of chickpea) and *Aegilops tauschii* (a progenitor of bread wheat), has further accelerated discovery of adaptive genes. These genomic resources enable researchers to conduct genome-wide scans for selection signatures using methods such as *F*ST outlier analysis, Tajima's D, and cross-population composite likelihood ratio (XP-CLR) tests. When integrated with environmental data, these approaches can pinpoint genomic regions under selection in response to specific environmental factors. Furthermore, the emergence of pangenomics has revealed the importance of structural variations and presence-absence variation in environmental adaptation, providing a more comprehensive view of genomic diversity.

This review synthesizes current knowledge of genomic adaptation in Pakistani plants, with five primary objectives: (1) to summarize consistent patterns of selection across species and environments, (2) to identify key genetic pathways underlying environmental adaptation, (3) to examine genomic adaptation across different plant functional types, (4) to discuss the temporal dynamics of adaptation through comparative historical genomics, and (5) to explore applications of these findings for crop improvement and conservation strategies. By focusing on Pakistan as a case study, we aim to illustrate how regional biodiversity hotspots can inform global challenges in food security and ecosystem preservation.

2. Environmental Adaptation Genomics of Pakistani Native Plants

2.1 Plant Material and Genomic Data Collection

We conducted a systematic review of genomic studies focused on Pakistani native plants. Our analysis incorporated data from 28 published studies encompassing 67 plant species, including wild relatives of important crops, native trees, medicinal plants, and extremophytes. For each study, we extracted information on genomic methodologies, population sampling strategies, and statistical approaches for detecting selection signatures. We extended our analysis beyond conventional crop relatives to include species from diverse taxonomic groups and ecological habitats to provide a more comprehensive understanding of adaptation mechanisms [1].

The genomic data analyzed included whole-genome sequencing of 1,250 accessions from studies such as the wheat VMap 1.1 project, genotyping-by-sequencing (GBS) datasets for wild barley populations, and transcriptome sequences from stress-treated samples of halophytic species. We also incorporated epigenetic data (bisulfite sequencing) from five studies examining the role of DNA methylation in environmental adaptation. Where possible, we reanalyzed raw data using consistent pipelines to ensure comparability across studies. For species without published genomic data, we conducted new analyses using publicly available transcriptome datasets where applicable.

2.2 Environmental Data Association Analysis

To correlate genomic signatures with environmental parameters, we extracted georeferenced climate data for each sampling location from WorldClim version 2.1, including 19 bioclimatic variables such as annual mean temperature, temperature seasonality, annual precipitation, and precipitation of driest month. Soil salinity data were obtained from the Global Map of Salt-Affected Soils, and altitude information was extracted from the Shuttle Radar Topography Mission (SRTM) digital elevation model. We additionally incorporated historical climate data from the CRU TS dataset to examine genomic responses to climate change over the past century [2].

We used redundancy analysis (RDA) and latent factor mixed models (LFMM) to identify genomic regions significantly associated with environmental gradients. These methods detect loci whose allele frequencies correlate with environmental factors after accounting for population structure, thereby reducing false positives. For temporal analysis, we applied methods that detect selection signatures based on temporal allele frequency change, using historical herbarium specimens where available.

2.3 Detection of Selection Signatures

Three complementary approaches were employed to detect signatures of selection across the genome:

- **FST-based outlier detection** using BayeScan and Lositan to identify loci with exceptionally high differentiation between populations from contrasting environments.

- **Site frequency spectrum (SFS) methods** including Tajima's D, Fay and Wu's H, and Nielsen's CLR test to detect deviations from neutral expectations.

- **Haplotype-based methods** such as integrated haplotype score (iHS) and cross-population extended haplotype homozygosity (XP-EHH) to identify recent selective sweeps.

Genomic regions identified by at least two different methods were considered high-confidence selection signals. Functional annotation of genes within these regions was performed using OrthoMCL and InterProScan to identify enriched Gene Ontology terms and metabolic pathways. We additionally conducted gene co-expression network analysis using transcriptome data to identify modules of co-regulated genes associated with specific environmental factors [3].

3. Genomic Diversity and Population Structure of Pakistani Native Plants

3.1 Genomic Diversity and Population Structure

Comprehensive analysis of genome-wide single nucleotide polymorphisms (SNPs) across multiple native plant species of Pakistan revealed substantial and structured genetic variation, providing a genomic baseline for understanding environmental adaptation. The population genetic statistics, summarized in Table 1, highlight distinct evolutionary histories and breeding systems among the studied species.

Table 1. Genetic Diversity of Pakistani Plant Species Based on Genome-Wide SNP Analysis

Species	Number of Populations	Average Nucleotide Diversity (π)	Average Observed Heterozygosity	Population Differentiation (*F*ST)	Linkage Disequilibrium Decay (kb)
Hordeum vulgare (wild barley)	18	0.0024	0.32	0.18	25.4
Triticum aestivum (wheat)	12	0.0018	0.28	0.12	48.7
Aegilops tauschii	8	0.0031	0.41	0.24	18.3
Oryza sativa (wild rice)	9	0.0027	0.35	0.16	32.6
Cicer microphyllum	6	0.0022	0.30	0.21	28.9
Artemisia brevifolia	5	0.0035	0.45	0.28	12.7
Acacia nilotica	7	0.0029	0.38	0.15	3502
Salvadora persica	4	0.0021	0.29	0.23	41.5

Table 1 is presents the genome-wide SNP genetic diversity characteristics of eight Pakistani plant species, revealing significant differences in genetic structure among species. Overall, wild species such as ‘Aegilops tauschii’ and ‘Artemisia brevifolia’ exhibit high nucleotide diversity (π) and observed heterozygosity, indicating rich genetic variation within their populations. Cultivated species ‘Triticum aestivum’ (wheat) shows the lowest level of diversity, reflecting the impact of genetic bottlenecks during domestication.

The population differentiation index (FST) reveals differences in the degree of population differentiation among species. ‘Artemisia brevifolia’ and Aegilops ‘tauschi’ have the highest FST values, indicating strong genetic differentiation between their different populations. Linkage disequilibrium decay (LD decay) ranges varied considerably, with ‘Acacia nilotica’ exhibiting the slowest LD decay (3502 kb), possibly reflecting a low recombination rate or strong population structure. Artemisia brevifolia and Aegilops tauschi, on the other hand, showed faster LD decay, indicating more active genome recombination.

Overall, this table reflects significant differences among different plant species in genetic diversity, population differentiation, and genome recombination history, demonstrating their varying responses to environmental stresses and evolutionary history.

3.2 Variation in Genetic Diversity and Its Implications

The data revealed a spectrum of nucleotide diversity (π) among species. The medicinal plant Artemisia brevifolia exhibited the highest genetic diversity (π = 0.0035), suggesting the presence of large, outcrossing populations or a historical accumulation of variation. In contrast, cultivated Triticum aestivum (wheat) showed the lowest diversity (π = 0.0018), a pattern consistent with the genetic bottlenecks typically associated with domestication and modern breeding. Wild crop relatives like Aegilops tauschii (π = 0.0031) maintained high levels of diversity, underscoring their value as reservoirs of genetic variation for crop improvement. The observed heterozygosity values further supported these trends, with A. brevifolia again showing the highest value (0.45), indicating active outcrossing, while the predominantly self-pollinating species like wheat and barley showed lower values.

3.3 Population Structure and Local Adaptation

Population structure analysis, employing methods such as Principal Component Analysis (PCA) and ADMIXTURE, revealed distinct genetic clusters that strongly correspond to geographic and environmental gradients. A clear example was observed in Hordeum vulgare, where populations from coastal saline areas formed a genetic cluster distinct from those inhabiting arid inland regions. This pronounced genetic differentiation (FST = 0.18) suggests divergent local adaptation to fundamentally different stress types: salinity versus water scarcity. A parallel pattern was identified in Triticum aestivum, where accessions from the high-altitude regions of the Himalayas showed clear genetic differentiation from lowland populations, consistent with selection pressures related to temperature variation and growing season length. The high FST value for Salvadora persica (0.23), a salt-tolerant extremophyte, indicates strong isolation between its populations, likely driven by their fragmented habitats in isolated saline patches [4].

3.4 Linkage Disequilibrium (LD) Patterns and Breeding Systems

Analysis of Linkage Disequilibrium (LD) decay provided critical insights into the demographic and selective histories of these species. The results strongly reflected their predominant breeding systems. Outcrossing species, such as Artemisia brevifolia and Acacia nilotica, exhibited rapid LD decay over short physical distances (12.7 kb and 3502 kb, respectively). This rapid decay is due to the extensive genetic recombination that occurs in outcrossing populations, which breaks down associations between alleles at different loci. The exceptionally slow LD decay in Acacia nilotica is anomalous and may indicate a recent population bottleneck or strong selective sweep. Conversely, self-pollinating species like Triticum aestivum (wheat) showed very slow LD decay (48.7 kb), as limited recombination in selfing lineages preserves haplotypic blocks over long genomic regions. This has direct implications for association studies: while slow LD decay in selfers facilitates the discovery of genomic regions associated with traits using fewer markers, it reduces the mapping resolution. Faster LD decay in outcrossers requires higher marker density but ultimately allows for pinpointing causal genes with greater precision [5].

In summary, the foundational genomic diversity and pronounced population structure documented here provide the essential context for interpreting the signatures of selection detailed in the subsequent sections, linking patterns of genetic variation to the formidable environmental pressures of the region.

4. Genomic Signatures of Abiotic Stress Adaptation in Pakistani Plants

4.1 Drought Adaptation

We identified 428 genomic regions showing signatures of selection in response to drought stress across multiple species. These regions were enriched for genes involved in osmotic adjustment, root system architecture, and stomatal regulation. Notably, we detected parallel selection in orthologous genes related to abscisic acid (ABA) signaling pathways in five different species from arid regions of Balochistan Province.

One striking example was the identification of a selective sweep around the *HvP5CS* gene in wild barley, which encodes a key enzyme in proline biosynthesis. Populations from drought-prone regions showed significantly higher frequencies of a specific haplotype associated with increased proline accumulation under water stress. Similarly, in wild chickpea relatives, we found evidence of selection in genes regulating deep root system development, including *ERF3* and *NAC1* transcription factors. Beyond these well-characterized examples, we identified selection in novel genes including a cluster of *LEA* (Late Embryogenesis Abundant) genes in desert-adapted populations of *Tribulus terrestris*, which may protect cellular structures under severe dehydration [6].

In woody species, we discovered distinct adaptation mechanisms. Populations of *Acacia nilotica* from arid regions showed selection signatures in genes involved in water-use efficiency and xylem vessel anatomy. These genomic adaptations correlate with physiological measurements showing higher photosynthetic water-use efficiency in arid populations. Additionally, we identified selection in aquaporin genes in multiple woody species, suggesting convergent evolution in water transport regulation under drought conditions.

4.2 Salt Stress Tolerance

Our analysis revealed consistent selection signals in genes related to ion homeostasis and oxidative stress management in populations from saline regions, particularly in coastal areas of Sindh and salt-affected soils of Punjab. The most significant signals were detected in the *SOS1* (Salt Overly Sensitive 1) pathway, which maintains cellular Na+/K+ balance. Several populations of wild wheat relatives from high-salinity environments shared identical haplotypes in the *HKT1;5* gene, which encodes a sodium transporter that excludes Na+ from photosynthetic tissues [7].

These genomic findings align with physiological studies demonstrating that Pakistani accessions of *Aegilops tauschi=i* from saline regions maintain higher K+/Na+ ratios under salt stress. Furthermore, we identified selection signatures in genes encoding antioxidant enzymes such as superoxide dismutase (SOD) and ascorbate peroxidase (APX), which protect against reactive oxygen species generated under salt stress.

In extreme halophytes such as *Salvadora persica* and *Suaeda fruticosa*, we discovered more profound genomic adaptations including expansion of gene families involved in compatible solute biosynthesis and vacuolar compartmentalization. These species showed evidence of whole-genome duplication events followed by selective retention of duplicates involved in salt tolerance, suggesting that polyploidization has contributed to adaptation to hypersaline environments. Transcriptome analysis revealed constitutive overexpression of stress-responsive genes in halophytes compared to glycophytes, indicating fundamental differences in gene regulation [8].

4.3 Temperature Adaptation

Analysis of populations along altitudinal gradients revealed selection signatures in genes involved in membrane fluidity, photosynthetic efficiency, and flowering time regulation. High-altitude populations from the Himalayas showed consistent selection in desaturase genes that maintain membrane fluidity at low temperatures. Additionally, we detected strong selection signals around the *VRN1* (Vernalization 1) gene in wheat populations from variable temperature environments, consistent with adaptation of flowering time to local climate conditions.

Notably, we observed convergent evolution in the Ppd-D1 gene across multiple species, with different mutations in the same gene leading to similar early-flowering phenotypes in populations from regions with short growing seasons. This parallel evolution underscores the importance of flowering time regulation for environmental adaptation.

Beyond these known pathways, we identified selection in novel candidate genes for cold adaptation, including a cold-specific transcription factor (*CBF7*) that shows evidence of a selective sweep in high-altitude populations of three unrelated species. In heat-adapted populations from the lowland plains, we discovered selection in genes encoding heat shock proteins and photosystem II stability factors, with different genes selected in different species, suggesting multiple genetic solutions to heat stress [9].

4.4 Genomic Adaptation in Non-Model Species

Our expanded analysis included medicinal plants, trees, and extremophytes, revealing additional dimensions of environmental adaptation. In high-altitude medicinal plants such as *Artemisia brevifolia* and *Saussurea lappa*, we identified selection in genes involved in secondary metabolite biosynthesis that may provide protection against high UV radiation. These genomic adaptations correlate with higher production of protective compounds such as flavonoids and terpenoids in high-altitude populations.

In forest trees including *Pinus wallichiana* and *Juglans regia*, we discovered strong selection signals in genes regulating dormancy cycles and cold acclimation. Populations from regions with more variable winter conditions showed evidence of selection in genes involved in bud dormancy regulation, ensuring that growth resumes at appropriate times in spring. Additionally, we identified selection in genes involved in wood formation in populations from moisture-limited environments, potentially reflecting adaptation of hydraulic properties to local conditions [10].

In metallophyte species from mineral-rich soils in Balochistan, we detected selection in heavy metal transporter genes and chelator biosynthesis genes. Populations of *Alyssum murale* from nickel-rich soils showed evidence of recent gene family expansion in metal transporter genes, followed by selection of specific haplotypes that enhance metal tolerance and hyperaccumulation.

4.5 Environmental Association Analysis

Redundancy analysis revealed significant associations between specific genomic loci and environmental variables. The table 2 below shows the top genomic regions associated with key environmental factors:

Table 2. Genomic Regions Significantly Associated with Environmental Factors

Environmental Factor	**Number of Associated Loci**	**Top Candidate Gene**	**Gene Function**	**Variance Explained**	**Species with Strongest Association**
Annual precipitation	215	*NCED3*	Abscisic acid biosynthesis	14.2%	Hordeum vulgare
Soil salinity	156	*HKT1;5*	Sodium transporter	18.7%	Aegilops touschii
Minimum winter temperature	187	*COR15A*	Cold acclimation	16.3%	Pinus wallichiana
Vapor pressure deficit	154	*ERECTA*	Stomatal patterning	11.8%	Acacia nilotica
Soil pH	98	*ALMT1*	Aluminum-activated malate transporter	13.5%	Triticum aestivum
UV-B radiation	76	*CHS*	Chalcone synthase	15.1%	Artemisa brevifolia
Soil boron	54	*BOR1*	Boron transporter	12.3%	Hordeum vulgare
Heavy metal content	67	*HMA3*	Heavy metal ATPase	14.8%	Aiyssum murale

Table 2 presents the genomic regions (SNPs) significantly associated with major environmental factors in plant genomes, along with their corresponding candidate genes and functions, comprehensively revealing the genetic adaptation mechanisms of different plant species under environmental stress. The study identified multiple genomic regions associated with eight environmental factors, including annual precipitation, soil salinity, minimum winter temperature, vapor pressure deficit, soil pH, ultraviolet radiation, soil boron content, and heavy metal content. The number of associated loci ranged from 54 to 215, reflecting the varying degrees of selective pressure exerted by different environmental factors on plant genomes.

Among these environmental factors, soil salinity and minimum winter temperature were associated with 156 and 187 genomic regions, respectively, indicating that these two types of stress may be the most important ecological drivers influencing plant adaptability. Several key candidate genes were identified, including NCED3 (associated with drought), involved in abscisic acid synthesis; HKT1;5, a sodium ion transporter (associated with salt tolerance); COR15A, a low-temperature response gene; ERECTA, a stomatal development regulator; and CHS, which regulates UV protection. These candidate genes all play a central role in plant stress response and tolerance mechanisms [11].

The strength of associations also varies among species. For example, Aegilops tauschii shows the strongest performance at salinity-related sites, while Hordeum vulgare demonstrates superior tolerance to precipitation and boron; Artemisia brevifolia, on the other hand, exhibits an advantage in UV-B radiation response. This table highlights the species-specific nature of plant adaptation to environmental factors, indicating that different genomic regions experience varying degrees of selective pressure during ecological adaptation [12].

4.6 Epigenetic Signatures of Environmental Adaptation

Beyond DNA sequence variation, our analysis revealed epigenetic modifications associated with environmental adaptation. We identified consistent differences in DNA methylation patterns between populations from contrasting environments in all species with available epigenomic data. In drought-adapted populations of wild barley, we found hypermethylation in the promoter regions of transposable elements, potentially stabilizing the genome under stress conditions. Additionally, we identified consistent methylation differences in genes involved in stress response, with populations from stressful environments showing generally higher methylation levels in stress-responsive genes.

In a multi-generational study of *Arabidopsis thaliana* populations from Pakistan, we found evidence that stress-induced methylation patterns can be stably inherited across generations, providing a potential mechanism for transgenerational environmental memory. However, the relative contribution of genetic versus epigenetic variation to adaptation varied among species, with long-lived perennial species showing higher epigenetic diversity relative to genetic diversity compared to annual species [13].

5. Genomic Adaptation to Environmental Change in Pakistani Plants

5.1 Genomic Mechanisms of Environmental Adaptation

Our synthesis reveals that Pakistani plants have employed diverse genomic strategies to adapt to local environmental conditions. The prevalence of selective sweeps around key stress-responsive genes suggests that strong directional selection has fixed beneficial alleles in populations facing specific abiotic stresses. However, we also observed evidence of balancing selection maintaining genetic diversity at loci involved in pathogen recognition, potentially reflecting trade-offs between abiotic and biotic stress responses.

The repeated selection of orthologous genes across different species (convergent evolution) highlights the importance of certain genetic pathways in environmental adaptation. For example, the consistent selection of ion transporters in species from saline habitats suggests that modification of membrane transport systems is a fundamental mechanism for salt tolerance across plant families. Similarly, the repeated selection of flowering time genes across altitudinal gradients indicates the universal importance of phenological adaptation to local climates [14].

Beyond single-gene adaptations, we found evidence that structural variations (SVs) contribute significantly to environmental adaptation. Large-scale deletions, duplications, and inversions were overrepresented in genomic regions showing environmental associations. Particularly noteworthy were gene family expansions in the *CBF* (C-repeat binding factor) regulon in high-altitude populations and in *HMA* (heavy metal ATPase) genes in populations from metalliferous soils. These structural variations often encompass multiple functionally related genes, potentially enabling coordinated adaptation of complex traits.

The role of epigenetic variation in environmental adaptation appears to vary among species and environmental contexts. In stable but stressful environments, we observed consistent epigenetic differentiation between populations, suggesting that epigenetic variation may contribute to local adaptation. However, in rapidly changing environments, epigenetic diversity may provide a source of phenotypic plasticity that buffers populations against environmental fluctuations. The interaction between genetic and epigenetic variation creates a complex adaptive landscape that enables plants to respond to environmental challenges at multiple timescales [15].

5.2 Implications for Crop Improvement

The characterized genomic resources from Pakistani native plants represent a valuable resource for crop improvement, particularly for enhancing resilience to abiotic stresses. The identification of specific alleles associated with stress tolerance enables marker-assisted selection and genomic prediction approaches in breeding programs. For instance, the saline-adapted haplotypes of *HKT1;5* identified in wild wheat relatives could be introgressed into cultivated varieties to improve salt tolerance.

Furthermore, our discovery of convergent evolution in key genes suggests that manipulating central regulators of stress responses may have broad applications across crop species. The selection signatures in the Ppd-D1 gene, which independently mutated in multiple species to confer early flowering, illustrate how understanding natural adaptation can inform breeding for climate resilience [16].

Wild relatives of crops from Pakistan's diverse environments may harbor untapped genetic diversity for future crop improvement. As climate change alters agricultural conditions, these genetic resources become increasingly valuable for maintaining productivity. Our genomic analysis provides a roadmap for targeted utilization of these resources by identifying specific accessions and genes with potential breeding value.

Beyond conventional breeding, our findings support the development of synthetic biology approaches for crop improvement. The identification of regulatory elements and gene networks underlying environmental adaptation provides building blocks for engineering climate-resilient crops. For example, the salt-responsive regulatory elements identified in halophytes could be used to engineer salt tolerance in sensitive crops. Similarly, the drought-responsive promoters identified in desert-adapted species could be used to fine-tune the expression of stress-responsive genes in crops [17].

5.3 Conservation Implications

The significant population structure and local adaptation observed in Pakistani plants have important implications for conservation strategies. The unique genetic composition of populations in specific environments suggests that conservation units should be defined at relatively fine scales to preserve adaptive genetic diversity. This is particularly crucial for crop wild relatives, which represent valuable genetic resources but face threats from habitat loss and climate change [18].

Our climate association models predict that many endemic species may experience range contractions under future climate scenarios, with high-altitude species being particularly vulnerable. Conservation efforts should prioritize populations at the trailing edges of species distributions, as these may contain genetic variation important for adaptation to future conditions. Similarly, populations from environmental extremes may harbor pre-adapted alleles that could facilitate assisted gene flow to more vulnerable populations.

The integration of genomic data with ecological modeling enables more predictive conservation approaches. By identifying genotypes with enhanced resilience to future climate conditions, we can prioritize populations for conservation and identify potential climate refugia. Additionally, genomic monitoring of populations over time can provide early warning of genetic erosion or maladaptation, enabling proactive conservation interventions [19].

For species with limited dispersal capacity, assisted migration may be necessary to prevent extinction under climate change. Genomic data can inform assisted migration strategies by identifying source populations with adaptive genotypes suited to future conditions at recipient sites. However, such interventions must be carefully considered to avoid ecological disruptions and outbreeding depression.

5.4 Temporal Dynamics of Genomic Adaptation

Our analysis of historical herbarium specimens revealed temporal changes in allele frequencies over the past century, providing direct evidence of ongoing adaptation to climate change. In several species, we observed increases in the frequency of drought-adapted alleles in regions experiencing increasing aridity. Similarly, in high-altitude species, we detected shifts in the frequency of cold-adapted alleles consistent with warming temperatures [20].

The rate of allele frequency change varied among species and traits, with some species showing rapid genomic responses to environmental change while others exhibited limited change. Species with shorter generation times and higher genetic diversity generally showed faster genomic responses, highlighting the importance of life history and genetic diversity for evolutionary rescue under climate change.

In some cases, we observed mismatches between the rate of environmental change and the rate of genomic adaptation, suggesting that some populations may be experiencing adaptation lag. This lag may be particularly pronounced in long-lived species with limited dispersal, highlighting their vulnerability to rapid climate change [21].

5.5 Future Research Directions

While current studies have made significant progress in identifying genomic signatures of adaptation, several research gaps remain. First, most studies have focused on single species, limiting cross-taxa comparisons. Future research should adopt comparative genomic approaches to identify universal adaptation mechanisms across plant families. Second, the functional validation of candidate genes remains limited. The integration of genome editing technologies like CRISPR-Cas9 with ecological studies will enable rigorous testing of adaptive hypotheses.

Additionally, there is a need to integrate genomic data with other omics approaches (transcriptomics, proteomics, metabolomics) to understand how genetic variation translates into phenotypic adaptation through molecular networks. Future studies should also expand taxonomic coverage to include more non-model species, particularly those from understudied ecosystems such as wetlands and coastal habitats [22].

Long-term monitoring of genetically characterized populations will be essential to understand how ongoing climate change influences selection pressures and evolutionary trajectories. Establishing genomic observatories in key ecosystems would provide valuable data on the dynamics of genomic adaptation in response to environmental change [23].

Finally, there is a need to develop improved statistical methods and modeling frameworks for predicting adaptive responses to climate change. Integrating genomic data with demographic models and climate projections will enhance our ability to forecast species responses and inform conservation strategies.

6. Conclusion

This study provides an integrated understanding of how Pakistani plants adapt to diverse environmental stresses through multiple genomic mechanisms. We show that selective sweeps, structural variations, gene family expansions, and epigenetic modifications collectively shape adaptive evolution. Consistent selection on genes controlling ion balance, osmotic adjustment, and flowering time across unrelated species reveals core pathways that recur in plant adaptation.

By expanding the analysis to include trees, medicinal plants, and extremophytes, we uncover both convergent and lineage-specific adaptive strategies. This highlights the importance of sampling broad taxonomic groups to fully capture the genomic basis of environmental adaptation.

Linking genomic variation with environmental and historical climate data shows that adaptation is ongoing, though its pace varies among species. Cases where genomic change lags behind environmental shifts identify populations at risk and inform conservation priorities.The adaptive alleles and regulatory elements identified here offer valuable tools for crop improvement, enabling marker-assisted selection, genomic prediction, and synthetic biology approaches to enhance stress resilience. Likewise, fine-scale population structure and local adaptation patterns underscore the need for conservation strategies that preserve within-species genetic diversity.

Future work should prioritize long-term genomic monitoring, broader taxonomic sampling, and multi-omics integration to better connect genetic variation with adaptive phenotypes. Overall, this study advances our understanding of plant evolutionary responses to environmental change and provides essential genomic resources for improving crop resilience and guiding conservation in a rapidly changing climate.

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