

## **Ecological Epigenetics: A Complex Nexus between Environmental Factors and Genomics**

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### **Abstract**

Biological complexity emerges from interactions between genomes and their environments, which have been dissected by recent conceptual and technical advances on both short and long time scales. Phenotypic variation is limited by the internal and external features of species as a result of this genome-environment interaction. Phenotypic plasticity demonstrates how organisms form as a result of the complex interaction between genomes and environmental conditions. Different biological studies have presumed that because of DNA sequence alterations, populations of organisms are adapted to extreme environments due to heritable variations. Besides the evidences, the essential role of genetic polymorphisms, epigenetic mechanisms like chromatin modifications and DNA methylation can impact ecologically essential traits even if genetic variation is lacking. To full fill such research gap requires the utilization of integrative approaches to comprehend processes at several stages of organizations from ecosystems to genes eventually giving rise to the science of ecological epigenetics.

**Keywords:** Ecology, phenotypic variation, ecological genomics, environmental factors

### **Introduction**

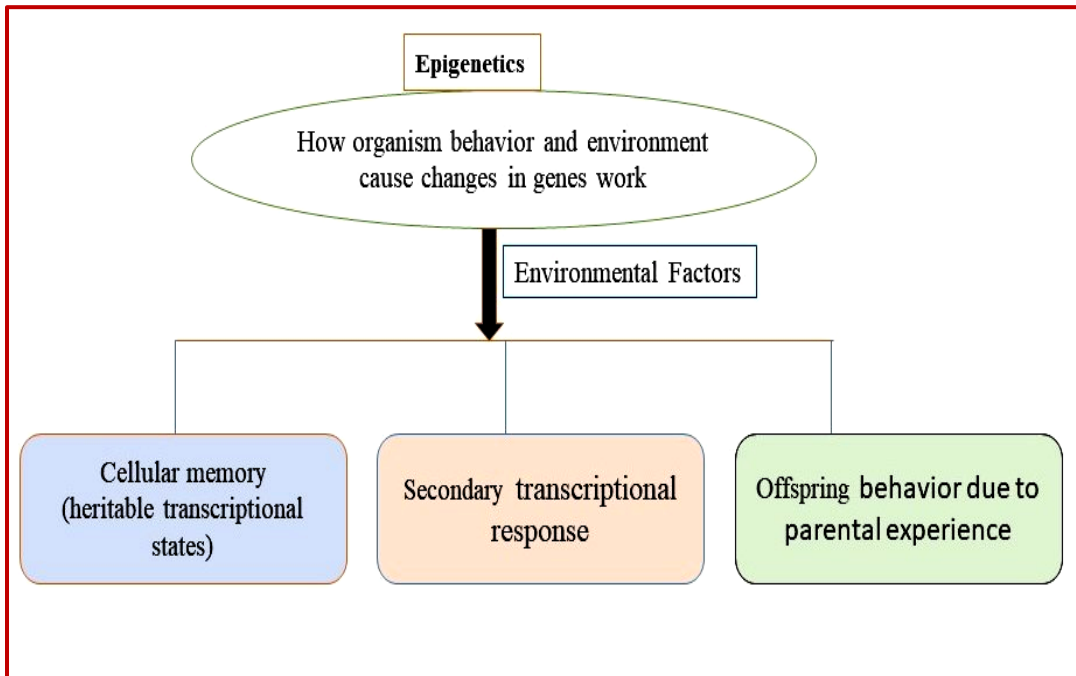
The ability of environmental factors to characterize the genome is immense, as any change in the environment, severe stress, or genomic shock events such as hybridization or genome duplication can alter an organism's epigenetic configuration, resulting in new phenotypes and some of these alterations can be passed on to the next generations (Boyko and Kovalchuk, 2011; Ramos-Lopez *et al.*, 2021). Different empirical studies within natural populations have shown that environmental factors pose a strong influence or override epigenetic signals promoting evolutionary divergence and adaptation (Flatscher *et al.*, 2012). Because genetic variability is lower in smaller or fragmented populations, epigenetic information provides an additional source of natural variation. Epigenetics is the study of heritable changes in an expressed gene that are not explained by changes in DNA sequence

(Bossdorf *et al.*, 2008). Epigenetics incorporates all processes other than DNA sequence that give rise to phenotype in organisms, whether heritable or not (Hallgrímsson and Hall, 2011). Others argue that heritability is a necessary component linked with epigenetics as it is frequently associated with "soft inheritance" (Kovalchuk, 2012). Although there are few ecological phenomenon that are yet to be elaborated by the genetic disparity but still, ecological genomics has emerged as a novel tool that provides an insight into ecologically and evolutionary relevant phenotypic variations (Ungerer *et al.*, 2008). The goal of ecological epigenetics is to figure out how epigenetic processes can play a role in population phenotypic variation (Bossdorf *et al.*, 2008). In comparison to ecological genomics, the science of epigenetics can be considered as more labile and responsive with respect to environmental factors (e.g., via DNA methylation modifications) (Angers *et al.*, 2010). The epigenome concept varies from cell to cell, and it has the potential to modify gene expression in a variety of ways by arranging the nuclear architecture of chromosomes to facilitate or inhibit transcription element access to genes and DNA expression mediation. While epigenomics refers to a comprehensive examination of chromatin constituents or gene regulation, epigenetics refers to three distinct types of memory (**Figure 1**) that use different mechanisms over different time scales (Wang and Chang, 2018). These are:

- Cellular memory that is mitotically heritable transcriptional states established during development.
- Those mitotically heritable patterns that are produced by organism in retort to environmental impetuses experiencing a more robust secondary transcriptional response.
- Those mitotically heritable variations in organism physiology and gene expression that influence offspring behavior due to parental experience.

The majority of our understanding of epigenetic processes arises from the experimental works that have been carried on model organisms (mouse) (Morgan *et al.*, 1999) and *Arabidopsis thaliana* (Lippman *et al.*, 2004). Investigations have revealed that environmental factors affect DNA methylation (Verhoeven *et al.*, 2010). Epigenetic alterations of the genome, such as DNA methylation or different histone modifications which impact gene expression and the phenotypes of organisms can eventually vary across individuals or populations of the same species, and this alteration can be heritable (Duncan *et al.*, 2014). Ecologists and evolutionary biologists have only lately realized the potential importance of epigenetic variation in their domains and have begun to investigate it in an ecological-evolutionary framework. The findings reveal that epigenetic variation is widespread within and among wild plant populations, and that these epigenetic changes can exist independently of DNA sequence variation (Hu and Barrett, 2017). Heritable variation is fostered by epigenetic difference as demonstrated by phenotypic flexibility, niche

breadth, and habitat divergence in ecologically important characteristics such as plant growth, phenology, and herbivore defence (Mounger *et al.*, 2021).



**Figure 1: Environmental factors and epigenetics**

### DNA methylation

DNA methylation is the ubiquitous mechanism of heritable epigenetic disparity maintaining the repressing state of methylated loci. In plants, asymmetric methylation (mCpHpH) is restored after each mitotic cell division, but symmetric methylation (mCpG and mCpNpG) may be maintained during mitosis and meiosis cell divisions (Martienssen and Colot, 2001). New cytosine methylation is catalyzed by de novo DNA methyltransferase. The maintenance DNA methyltransferase is responsible for symmetric methylation marks on parental DNA. The post-translational modification of histones and DNA methylation are used to study chromatin modelling and remodeling. These changes have the ability to transfer epigenetic memory both within and through generations (Vaillant and Paszkowski, 2007). This lack of methylation is usually indicative of the active state of these promoters. DNA methylation promotes the repression of expressed genes; nevertheless, demethylation is employed to enhance gene expression (Zilberman and Henikoff, 2007). Various experimental evidences have demonstrated the influence of environmental stresses on DNA methylation dynamics from time to time. In tobacco, for example, Al, salt, and cold stress cause demethylation of the glycerphosphodiesterase-like

protein (NtGpDL). Water deprivation also causes a specific type of cytosine hypermethylation (CCGG) in the pea genome (Labra *et al.*, 2002).

### **Histone modification**

Histone modification and DNA methylation are coordinated and correlated processes (Cedar and Bergman, 2009). Nucleosome, the vital unit of eukaryotic chromosome consisting of histone core complex (H2A, H2B, H3 & H4) wrapped by 146bp DNA and linker histone H1 associated with linker DNA (8 – 114 bp). Post translational modification is carried out by the N- terminal tails of core histone where histone acetylation, phosphorylation and ubiquitination promote transcription (Sridhar *et al.*, 2007). Histone variants and N- tail posttranslational modification form a combination of codes called as histone codes that provide nucleosome assemblies and combination possibilities. These codes have a greater similarity for chromatin associated proteins and hence help in genetic code expression (Fuchs *et al.*, 2006). Chromatin remodeling complexes (CRC) and ATP dependent CRCs promote chromatin modification by modifying these histone complexes that non-covalently cause histone alteration in the nucleosome (Fransz *et al.*, 2002). Although they are associated with epigenetic processes, definitive heritability in their own right is capricious and it is being presumed that RNA may be a possible determinant. Histone variants offer a means to alter histone code. For example in tomato, the linker histone H1 variant, H1-S is being induced by drought through an ABA-dependent pathway (Scippa *et al.*, 2000).

### **Micro-RNA**

Micro-RNAs are included as another regulation mechanism in epigenetics (Pearce, 2011). Keeping in view the DNA methylation and histone modifications, the impact of environmental factors on epigenetics is being studied, however concept of micro-RNA could also be explored to comprehend the mechanism of local adaptation to different habitats as such mechanism are highly dominated by the environmental conditions resulting in heritable variation in traits. This has been investigated in a recent study that found a correlation between epigenetic function and habitat. Herrera and Bazaga (2010), for example, looked at how genetic and epigenetic variations spread in and within wild populations of Spanish violets (*Viola cazorlensis*). They discovered genetic and epigenetic population differentiation, as well as the fact that epigenetic variation outweighed genetic variation. The discovery of further variance at epigenetic markers suggests that epigenetics may be liable for a large portion of the changes in these organisms. Factors like low nutrients, salt tension, jasmonic acid, salicylic acid and control treatment were used by Verhoeven *et al.* (2010) to evaluate on epigenetic variation in dandelion (*Taraxacum officinale*). It was found that substantially more methylation changes occurred genome-

wide in treated plants than in controls using MS-AFLP. The investigation further elaborated that these variations were hereditary (Verhoeven *et al.*, 2010).

### **Effect of epigenetic changes**

From many studies, evidences are gathering about the ecologically important traits like growth, phenology and herbivory where epigenetic mechanisms or modifications have resulted in heritable variation in addition to phenotypic plasticity, niche width and habitat differentiation (Chano *et al.*, 2021; Mertens *et al.*, 2021).

### **Trophic interaction**

Epigenetic mechanisms can influence trophic interactions, such as herbivory, in addition to being responsive to environmental stimuli. Investigations have revealed that in response to herbivory, Spanish populations of *V. cazorlensis* showed the variation in DNA methylation owing to long-term exposure to unregulated herbivory (Herrera and Bazaga, 2011). The impact of methylation at a particular variable loci was also connected to AFLP markers linked to herbivory levels. Such a study has been a novel one where epigenetics and genomic disparity has been compared with respect to environmental stressors.

### **Niche breadth**

Niche breadth is other ecological endeavor to figure out what triggers certain species' desire to occupy a large niche within a population. Methylation variations are a critical component of nectar-living yeast's that utilize resources from a diverse assortment of host environments, especially harsh environments. Herrera *et al.* (2012) used the demethylating agent 5-Azacytidine to grow yeast lines in a variety of media with fluctuating concentrations of sucrose, glucose, and fructose (5-AzaC). Development was inhibited by 5-AzaC, which was more pronounced with high sugar concentrations. These findings indicate that *M. reukaufii*'s DNA methylation retorts to various nectar conditions, and that the yeast's epigenetic response enables it to inhabit an extensive assortment of nectars and flowers.

### **Invasive species**

Invasive species have a remarkable ability to colonize new habitats. Invasive organisms can exhibit a wide range of phenotypic variation, which can lead to genetic paradox (Liebl *et al.*, 2013; Schrey *et al.*, 2012). The epigenetic changes or alterations have been found quite effective to compensate the reduced genetic and phenotypic plasticity. For example, In Europe, Japanese knotweed (*Fallopia japonica*) an invasive plant species has been growing at a higher rate and colonized the northeastern United States, where it can be found along roadsides, marshes, and beaches. In response to regulated salt treatments, plants from

different populations showed almost no variability but retained a higher level of epigenetic and phenotypic variation and phenotypic plasticity (Richards, 2008). A similar research was conducted to investigate the role of epigenetics in invasive nature (Dai *et al.*, 2017). These results indicate that epigenetic variation plays a pivotal role in assisting knotweed's rapid colonization in variety of ecosystems.

### **Behavior changes**

Behavior is frequently regarded as a phenotypic characteristic that is both flexible and responsive to the environment (West-Eberhard, 2003). The capability to change behavior permits for a faster and less expensive response to environmental cues (West-Eberhard, 2003). Laboratory studies have revealed that epigenetic changes, when combined with environmental factors, can influence behavioral variation. Changes in larval diets, for example, have influenced behavioral variation related to caste system in honeybees. As genetically identical larvae are fed royal jelly, they develop into reproductive queens who are more aggressive in character, whereas those who eat lower-quality diets evolve into non-reproductive workers who forage throughout their lives, as revealed by epigenetics. According to the current database, such behavior may be driven by differences in DNA methylation in the brain, with queens having lower DNA methylation of specific genes than workers. The DNA methyltransferase pathway was downregulated in larvae injected with short interfering RNA, resulting in the formation of more queens than a control group (Miklos *et al.*, 2011).

### **Hormonal signaling**

The first acumen into the molecular genetic mechanisms associated with morphological defense formation in *Daphnia pulex* and *Daphnia magna* under the predation risk by *Chaoborus* larva has been investigated by various researchers across the globe (Miklos *et al.*, 2011). For the development of inducible defense structures, insulin signaling (IS), Juvenile hormone (JH) and expression of body and morphogenetic gene patterns are involved as supported by the findings of moderately up regulated genes. Although there is strong sustenance for contribution of juvenile hormone (JH), no JH receptor has been recognized in the *Daphnia pulex* draft genome even though substantial exertions have been utilized.

### **Stress tolerance**

Abscisic acid plays a fundamental part in abiotic stress tolerance as it controls different plant developments such as growth and development affected by the non-stress conditions. Many studies have analyzed that epigenetic mechanisms are fundamental part of ABA regulated processes. Plant hormones and abiotic stresses influence the expression of several HDACs as revealed in expression of rice HDAC gene analyses as ABA suppresses the

HDT701, HDT702, SRT701 & SRT702 expression in rice due to abiotic stresses such as cold salt and mannitol inducing ABA accumulation and ultimately may repress HDACs.

### **Habitat**

Mangrove ecosystem being found in tropical and subtropical habitats are mostly subjected to daily water salinity variations (Fattorini *et al.*, 2021). Mangrove plant species must withstand a wide range of climatic circumstances, and structural and morphological features vary greatly between Ecogeographic zones (Putz and Zuidema, 2008). Plants in habitats with limiting constraints such as recurrent dryness and hypersaline soils (salt marshes) grow abnormally and reach only 1.5 to 3 metres in height, with a shrub-like shape (Lira-Medeiros *et al.*, 2010). White mangrove, *Laguncularia racemosa* (L.) Gaertn.f. (Family: *Combretaceae*), is extensively distributed in the western globe among the mangroves of America and Africa (Lonard *et al.*, 2020). Individuals of *L. racemosa* live in either a river basin or a salt marsh, and are thus constantly subjected to a variety of environmental stressors. AFLP (Amplified Fragment Length Polymorphism) markers can be used to describe such plants and track out their links to epigenomics variation.

### **Phenological plasticity and ecological genomics**

The capability of genotype to form altered phenotypes in varying environmental conditions is called phenotypic plasticity. Phenotypic plasticity has widely been documented as an important process of adaptively altering phenotypes in retort to environmental variation (Miner *et al.*, 2005). Phenotypic plasticity requires the environmentally responsive development of a phenotype, so the abiotic and biotic ecological environments that an organism encounters must be assessed and integrated into the ecological genomics of plasticity. Plasticity cannot evolve without genetic variation or certain environmental factors, just as it cannot evolve without genetic variation. The effect of the climate on demography has ramifications for the evolution of plasticity. Finally, unnatural conditions, which ecologists often dismiss, will shed light on the processes and evolutionary implications of plasticity. Plasticity is predicted to change over time in predictable conditions (Scheiner, 2004). If the climate does not change, plasticity is unlikely to adapt. If the environment changes in an unforeseen way, bet-hedging techniques can emerge (Starrfelt and Kokko, 2012). Active induction necessitates more than predictable variation; environments must also provide reliable cues for environmental change, which the organism can perceive and convert into phenotypic responses (Starrfelt and Kokko, 2012). Reliable cues must then allow for the time between the cue's response and the formation of the plastic phenotype. Non-plastic approaches may be preferred if environmental change outpaces phenotypic change, or if the time between cue reception and phenotype development is too long (Padilla and Adolph, 1996). Ecological genomics includes not only the process regulating phenotype formation, but also functional genomics (Dalziel *et al.*, 2009). In order to understand phenotypic evolution and its position in the larger population.

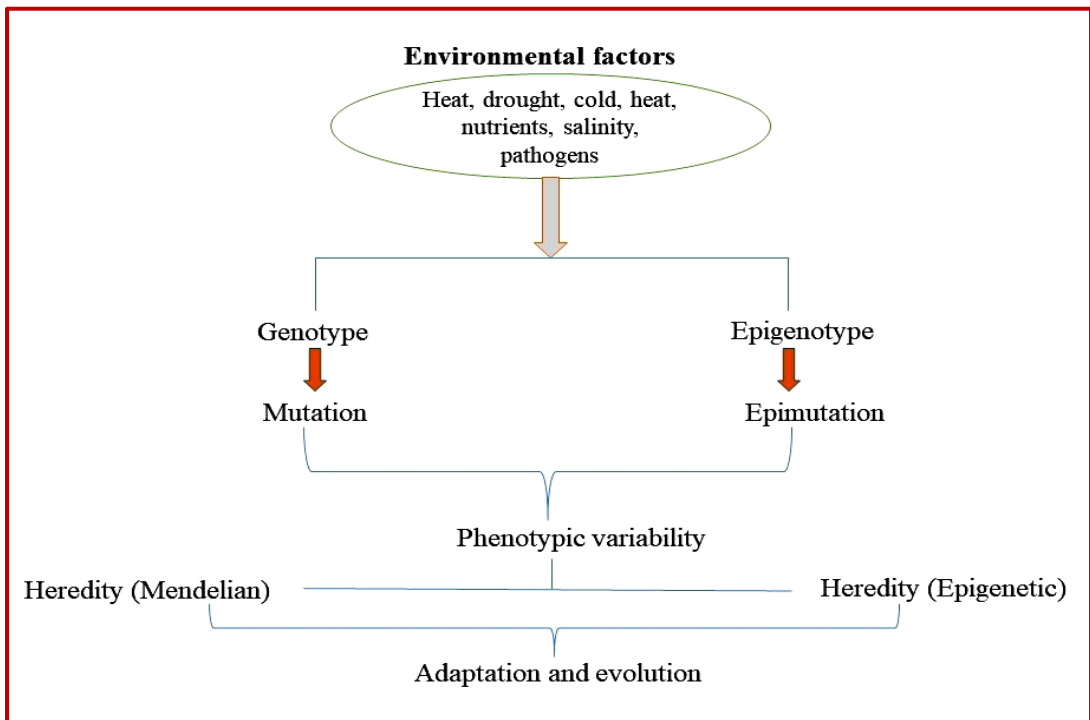
Ecological genetics has focused on the genetic and molecular origins of ecological basic traits, as well as their evolutionary implications. Furthermore, the environment has such an effect on the phenotype that it cannot be isolated from the genome, suggesting the critical role that plasticity may play in ecological genomics (Valena and Moczek, 2012). It creates novel hypotheses on how environmental factors influence phenotype formation and evolution. Despite the fact that plasticity has been the subject of multiple studies (Putz and Zuidema, 2008; Schrey *et al.*, 2012; Valena and Moczek, 2012; Verhoeven *et al.*, 2010; West-Eberhard, 2003), scientists have only lately been able to underline the significance of phenotypic plasticity in combination with ecological genomic techniques (Lonard *et al.*, 2020; Richards, 2008). Understanding the molecular basis for the development of alternative phenotypes necessitates the use of genomic methods. Understanding community-level processes attributed to plasticity would necessitate predicting the evolutionary effects and configurations of plasticity as influenced by environmental variations as indicated by the investigation involving horned beetles (Aubin-Horth and Renn, 2009). For example, Luciano Matzkin *et al.*, 2005, studied *Drosophila* adaptation to various host plants, revealing the genomic changes caused by *Drosophila mojavensis* in host cacti species challenged by various factors such as nutritional composition and toxic compounds. The study further demonstrated how the combination of genomic methods has allowed researchers to pinpoint the molecular conduits entangled in these host changes. The *Drosophila* example is a great example of how metabolic changes occur in tandem with adaptive evolution. Morphological and colour changes may drive adaptive evolution. (Araya *et al.*, 2010), compared the genome of a *S. cerevisiae* strain that developed in a sulphate-limited environment to that of its ancestor. Single-point mutations affecting the canon of *RRN3*, a gene intricated in modulating ribosomal gene expression under nutrient-limiting conditions, were discovered to be responsible for adaptation. A similar method to find prompt mutations in *S. cerevisia* that have a higher salt concentration and lower glucose tolerance have also been used (Anderson *et al.*, 2012). Population genomics, which enables the identification of natural genomic variations and the association of specific traits to these variations, is an alternative to study the mutations that underpin adaptation. Phenotypes can seldom be elucidated by constrained genetic variation, as they may be expounded under controlled settings, since environmental influences in natural populations are diverse, complicated, and extremely variable.

### **Mechanism of plasticity**

Due to change in environmental conditions, phenotypic plasticity can prompt evolution and eventually can impact genetic evolution outcome (**Figure 2**). Epigenetic variation can be modified unlike that of genetic variation by various ecological interaction and this can lead to new phenotype and hence microevolution.



Many species have adjusted their breeding and mating behaviors owing to climate change or eutrophication in aquatic habitats (Candolin, 2009). The study carried on house finches (*Carpodacus mexicanus*) throughout North America shows how physiological, morphological and behavioral plasticity is facilitated in retort to temperature variation impacting both phenotypic variance and offspring fitness paving a way for genetic evolution in new populations (Badyaev, 2009). Similarly, the colonization of dark eyed juncos (*Junco hyemalis*) was facilitated by plasticity of breeding cycles in high elevated temperate regions creating altered patterns of sexual selection on plumage coloration. Environmental induction can appear in two distinct forms. First, chemical and physical laws may cause the phenotype to be forced by the environment (passive induction). Through enzyme kinetics and diffusion rates, temperature, for example, can trigger phenotypic alterations. Nutrient accessibility also has an impact on development and morphology. It will be required to comprehend the real nature of induction in order to determine the causal relationship between genotype and phenotype. Overall phenotypic plasticity is likely attributable to changes in the quantities of environmental components required for the production of a "normal" phenotype, as well as environmental sensitivity of gene expression or protein, lipid, and RNA activities. The evolved organized response to the stimulation of environmental sensors, in turn, may be motivated by epigenetics (Richards, 2008).



**Figure 2: Environmental factors, phenotypic variability and evolution****Methods**

Expression mechanisms of hundreds and thousands of genes can be transformed by different environmental challenges as cleared by many microarray studies as these are correlative. The revolution of genomic research was marked by the arrival of NGS platform in mid 2000s that enabled many samples to be sequenced accurately at a greater depth. In view to incarcerate epigenetically modified genomic regions epigenetic community capitalizes this development (Meaburn and Schulz, 2012). NGS platforms have a capability to offer a wide-ranging and impartial interpretation of the epigenome and hence restricting the practice of content imperfect microarray platforms. Epigenomics heavily depends on bioinformatics that helps in understanding the concept at molecular level and enhances data generation that ultimately can be integrated into existing genomic database. The objective is to generate a definitive depiction of the epigenome assimilating DNA methylation, chromatin dynamics and accessibility and expression. Fluorescent in situ hybridization and chromosome conformation capture (3C15) are two new methods that may give spatial proximity evaluation and nuclear organization of specific genomic loci, allowing for thorough mapping of chromosomal interactions. Hi-C has opened up a whole new world of possibilities for researching chromatin connections and regulatory networks in 3D and recognizing the genome's architecture at high resolution.

**Conclusion and future perspective**

Understanding how the epigenome works in natural environments is becoming clearer as our awareness of essential ecological processes grows. Aside from determining the degree and distribution of epigenetic disparity in natural populations, important progress can be made in determining the ecological and evolutionary implications of such differences. However, since ecological epigenetics is still in its infancy, there are several issues that remain unanswered. Ecological epigenetics' future, like that of ecological genomics, would necessitate well-designed studies that account for genotype and environment impact. Future research may examine the activity of epialleles and interactions using experimental studies on genotypic replicates that are wide-open to different environments. To further improves the ability to detect duplicate or repeat sequences, Next-generation sequencing techniques can be utilized. From the preceding discussion, it can be revealed that the identical method could be employed in an experimental setting to relate replicates of similar genotype subjected to diverse environments, allowing a genome-wide investigation of methylation shifts.

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