



# Blinded by the lights? Re-examining the adaptive role of transposable elements in plants with population genomics

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Transposable elements (TEs) are ubiquitous components of the genome whose mobility can be triggered by environmental stress and influenced by genotype–environment interactions. In plants, TEs constitute a substantial proportion of the genome and frequently cause large-effect mutations that impact gene regulation, methylation, and phenotype expression. These characteristics have recently positioned TEs as potential drivers of rapid local adaptation. However, this perspective is not always integrated with the broader understanding of fitness effects and neutral processes. Despite numerous associations between TEs and fitness-related traits, clear cases directly linking TE insertion, phenotype, and fitness in natural populations—i.e., genuine examples of local adaptation—remain rare in plants. Emerging population-genomic evidence presents a more complex picture: while some TE insertions may facilitate adaptation or rapid responses to environmental change, most are selected against and act as deleterious, selfish elements. The evolutionary dynamics of TEs are further modulated by genome architecture, reproductive system, and ecological context, underscoring their system-specific behavior. In this opinion piece, I argue that generalizing about the significance of TEs in local adaptation in plants is fraught with complexity and risks oversimplification. As sequencing technologies advance, integrating theoretical population genetics with large-scale comparative analyses and simulations across a wider range of species will be essential to more fully characterize the dynamics of TEs.

## Addresses

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## TE activity generates diversity

Transposable elements (TEs) are a major component of plant genomes [1]. While stress can trigger their transposition in controlled experiments [2–4], genome-wide analyses of within-species polymorphism have also identified candidate genes involved in DNA methylation as genetic factors underlying recent TE activity [5–7]. It is now clear that the mobilization of TEs can evolve in a genotype × environment (G × E)-dependent manner [6]. Consequently, the insertional profile of TEs in a genome can vary at the intra-specific level [6–16], producing genetic diversity upon which selection can act.

Today, TEs are largely viewed as being more likely than classical single nucleotide polymorphisms (SNPs) to drive large-scale changes in gene expression [12,17–19], either through TE-induced epimutations [20] or independently of them, and to ultimately have large effects on phenotypes [21,22]. The spectacular observation that a few TE families, such as the heat-responsive TE *ONSEN* in *A. thaliana*, preferentially insert near genes and in H2A.Z-enriched regions associated with stress-responsive genes [22,23] has further fueled the hypothesis that TEs contribute directly to the stress response [19,21,23,24]. In this view, TEs are considered to provide a powerful mechanisms for plants to adapt more rapidly to new environmental conditions (for review [3,25–28]), thereby driving adaptation to both geographical and temporal environmental changes (Graphical summary – adaptive scenario). Collectively, the reviews and studies conveying this narrative have recently emphasized the potential regulatory and functional roles of transposable elements, positioning rapid or local adaptation [3,14,16,27–30], and even directed mutation [19,21,22,24,26], as central themes in TE biology, in line with a broader shift in population genomics toward adaptive explanations over nonadaptive ones [31].

However, as noted by Lisch more than a decade ago [32], these views are “inevitably subject to confirmation bias”. For instance, the genome-wide effects of TEs on methylation spreading and nearby gene expression observed in *A. thaliana* are clearly not consistent across

species [33,34] and only a handful of TE families are known to transpose *in planta* in response to stress. These nuances raise the question of how often and at what time scale transposition really occur in the wild, which natural conditions are needed to induce transpositions akin to laboratory-based observations and to what extent such events have functional consequences. In short, do TEs really provide plants with a powerful mechanism to adapt more rapidly to new environmental conditions? Despite popular claims, and in light of basic genetics and recent population genomics studies [7,9,11] building on pioneering work in *A. thaliana* [6,18,22,27], I argue that the broad role of TEs in rapid local adaptation in natural plant populations remains unclear and should be reconsidered within existing theoretical frameworks.

### TE-driven large effect mutations are not synonymous of adaptation

Historically, the impact of TEs on the genome structure and phenotypes has been largely investigated in crops. Because changes in shapes and colors are easier to spot than more quantitative changes [35], emblematic TE-driven phenotypes include Mendel pea seed shape [36] as well as cotyledon color and pod shape [37], kernel pigmentation in maize [38], the blood orange phenotype [39], grape skin color [40], tomato shape, color and aroma [41,42], melon streaks and spots [43], apple color [44], strawberry firmness [45], oil palm fruit abnormality [46] or rice grain width [47]. As large-effect loci underlie major domestication traits [48] (but see Ref. [49] for a more complete picture), these examples illustrate how TEs may have been targeted by artificial selection [12]. Yet, while such visible phenotypic changes in crops demonstrate the mutagenic properties of TEs and can be translated into market value (and, consequently, fitness), showing that TE insertions and mutations contribute to local adaptation in wild populations is rarely achieved.

TEs have typically larger effects than SNPs, as shown experimentally and through population genomics analyses [7,9,17,21,22]. This property makes TEs stand out in the way selection may act on them in comparison to SNPs, whose effects are generally more quantitative. However, large mutational effects do not necessarily translate into greater adaptive potential, contrary to what is sometimes assumed (e.g. Ref. [22]). For instance, many traits are polygenic. Whether selection acts on them by affecting many loci of small effect, few loci of large effect, or both, depends on various evolutionary forces and ecological factors. These include the distance from phenotypic optimum, selection strength, reproductive mode, genetic drift and hence, population size [50]. Genes also frequently act in a pleiotropic manner, leading to trade-offs between focal and non-focal traits.

Pleiotropy can reduce the likelihood that the mutation enhancing a focal trait will increase in frequency in the population, even though this also largely depends on the number of traits influenced by the gene considered [51]. Whether large-effect mutations such as those generated by TEs are favored by selection therefore depends on the specific system, population, and trait under consideration.

As an illustration of this distinction between mutational effect size and adaptive potential, Thieme et al. [21] showed that a specific insertion of the heat-activated *ONSEN* element in *A. thaliana* generated a drought-resistant phenotype via a loss-of-function mutation in Ribose-5-phosphate isomerase 2 (*RPI2*) by leading to reduced water consumption. However, due to the pleiotropic role of *RPI2*, this apparent fitness advantage was accompanied by reduced biomass and photosynthetic activity, which ultimately lower the survival probability under non-extreme drought conditions [21]. This underscores that measuring a mutation's effect on a functionally important phenotype is fundamentally different from assessing its overall fitness consequences in natural habitats [52]. Objectively, empirical cases fully demonstrating the adaptive role of TEs, i.e. linking TE insertion, phenotype and fitness in natural conditions, such as those on herbicide resistance [53] and flowering time [6] are extremely rare in plants. While such cases are important to understand the mechanisms underlying specific trait evolution, they remain of more limited value to devise a general model on the role of TEs in adaptation to rapid and local environmental changes.

### Quantifying TE fitness effect: lessons from population genomics

Population genomics offers a systematic alternative to labor-intensive, case-by-case studies for quantifying the fitness effects of TEs and assessing their evolutionary impact in natural populations. Numerous studies (Table 1) have examined genome-wide TE diversity at the intra-specific level in crops and wild species [6–11,13–16,18,54]. Across these studies, the site frequency spectra (SFS) of TE insertion polymorphisms (TIPs) is constantly skewed towards rare alleles (Graphical summary – purifying selection) for both retrotransposons and DNA-transposons. Although these studies portrayed purifying selection as a major factor shaping TE evolution, SFS can be misleading since TEs can evolve irregularly through bursts of transposition (but see Refs. [55,56] for a more nuanced view). Recent transposition activity can lead to an overrepresentation of young TEs in the population. Those will segregate at low frequency in the populations and mimic the effect of purifying selection. Accounting for TE insertion age and varying transposition rates is therefore crucial [15].

Table 1

## Population genomics studies of TEs.

Publication	year	Species	Clade		Sample size	Reproduction strategy	Cycle	Distribution	Genome size	Ploidy level	TE content
Baduel et al. [14]	2019	<i>ARABIDOPSIS ARENOSA</i>	Angiosperm	Eudicots	300	Outcrossing	Annual biennial	Central and Northern Europe	150 Mb	Diploid autotetraploid	NA
Padilla-García et al. [11]	2025	<i>Arabidopsis lyrata</i>	Angiosperm	Eudicots	810	Selfing outcrossing	Annual biennial	Central Europe North America	207 Mb	Diploid	25 %
Quadrana et al. [18]	2016	<i>Arabidopsis Thaliana</i>	Angiosperm	Eudicots	211	Selfing	Annual	Worldwide	120 MB	Diploid	20 %
Baduel et al. [6,27]	2021	<i>Arabidopsis Thaliana</i>	Angiosperm	Eudicots	1047	Selfing	Annual	Worldwide	120 Mb	Diploid	20 %
Jiang et al. 204 [7]	2024	<i>Arabidopsis Thaliana</i>	Angiosperm	Eudicots	1115	Selfing	Annual	Worldwide	120 Mb	Diploid	20 %
Stritt et al., 2018 [54]	2024	<i>Brachypodium distachyon</i>	Angiosperm	Monocots	54	Selfing	Annual	Mediterranean rim	230 Mb	Diploid	30 %
Horvath et al. [9]	2024	<i>Brachypodium distachyon</i>	Angiosperm	Monocots	330	Selfing	Annual	Mediterranean rim	230 Mb	Diploid	30 %
Horvath and Slotte [15]	2017	<i>Capsella grandiflora</i>	Angiosperm	Eudicots	166	Outcrossing	Annual	SE. Europe/ Turkey	220 Mb	Diploid	27 %
Carpentier et al. [8]	2019	<i>Oryza sativa (rice)</i>	Angiosperm	Monocots	3000	Selfing	Annual	Asia	430 Mb	Diploid	40 %
Castanera [13]	2021	<i>Oryza sativa (rice)</i>	Angiosperm	Monocots	738	Selfing	Annual	Asia	430 Mb	Diploid	40 %
Ren et al. [16]	2025	<i>Tetragymma hemsleyanum</i>	Angiosperm	Eudicots	139	Outcrossing	Perennial	China, Hainan and Taiwan	2.19 Gb	Diploid	73 %
Contreras-Garrido et al. [10]	2024	<i>Thlaspi arvense</i>	Angiosperm	Eudicots	280	Selfing	Annual	Worldwide	539 Mb	Diploid	61 %

Horvath et al. [57] addressed this issue by proposing an age-adjusted SFS, which compares TEs and neutral polymorphisms within the same age distribution. Applied to *A. thaliana* [7] and *B. distachyon* [9], this approach confirmed that purifying selection is the dominant force shaping TE insertions. Both studies also highlighted that TEs act as large-effect mutations, with impacts comparable to non-synonymous SNPs or LoF mutations. Interestingly, purifying selection in *B. distachyon* affects TEs regardless of their proximity to genes, suggesting that both cis- or trans-regulatory effects are visible to selection [9]. Conversely, in *A. thaliana*, purifying selection affects genic insertions more than intergenic ones [7], consistent with findings in other dicots [6,11,15]. This difference may reflect genome organization: in *B. distachyon*, genes are largely interspersed and intergenic TEs (>2 Kb away from genes) are rarer than in the highly compartmentalized genome of *A. thaliana* [34]. Interestingly, in maize, Liu et al. [58] interpreted a similar SFS skew as evidence for stabilizing selection: rare genic insertions preferentially affect genes with extreme expression, consistent with selection against alleles that push phenotypes away from the optimum. This pattern is indeed consistent with stabilizing selection, where the strength of selection scales with the phenotypic effect of an allele. Although SFS alone cannot reliably distinguish purifying from stabilizing selection [59], this later study highlights how incorporating different omics data can refine our understanding of the evolutionary forces acting on TEs.

While disentangling the effects of positive selection from hitchhiking on linked loci (Graphical summary – adaptive scenario) remains challenging (both for SNPs and TEs), the proportion of putatively adaptive TEs identified by environmental association analyses (GEA) or genome-wide scans of positive selection in both *A. thaliana* and *B. distachyon* ranges from approximately null to only about 100 putative candidates [6,7,9]. Similarly, in the substantially larger and TE-rich genome of *Tetragymma hemsleyanum* (Table 1), only 0.4% and 0.8% of TIPs show signatures of positive selection or association with climatic variables, respectively [16]. Notably, genes with adaptive TEs, whether under positive selection or correlated with environment-variables are far fewer than those associated with SNPs, indicating that TEs contribute only marginally to adaptive variation compared with SNPs in this species. However, detection methods based on short reads may differ in their false discovery rates for TIPs and SNPs because TE insertions are harder to map accurately, which complicates direct comparisons between the two variant types. Nevertheless, the overall limited evidence for adaptive TEs is consistent with the observation that TEs are predominantly selected against, constraining their evolution in natural populations – a consistent pattern across studies employing TE display [60], short-read [7,9], long-read [58], or reference-free mapping approaches [61].

Theory, however, predicts that large-effect mutations are favored primarily when populations are far from their optimum [50,62]. Therefore, TEs might be favored in extreme environments where drastically altered phenotypes could be advantageous [21] but remain at low frequencies in geographically diverse mapping panels typically used in population genomics studies. This illustrates that the evolutionary balance between adaptive and deleterious TE effects might be inherently time-scale dependent: short-term advantages may arise under extreme conditions, but long-term persistence is typically limited by purifying selection. In this context, local populations screens could change our perception of the temporal adaptive role of TEs. Moreover, large TE-mediated effects might facilitate rapid adaptation but are unlikely to persist over long timescales in fluctuating environments [21]. Such transient effects might of course be difficult to capture and link to causal selective constraints with population genomics data alone. How often local populations face such extreme scenarios remains debatable but gained a lot of interest in the context of global changes [6,26]. While these context-dependent adaptive processes likely apply to only a small fraction of TE insertions found in nature, temporal genomic surveys offer a promising avenue to reveal the short-lived yet potentially crucial contributions of TEs to rapid adaptation.

As a last illustration of how non-adaptive processes may further shape TE frequencies, changes in effective population size ( $N_e$ ) can affect selection efficacy, allowing deleterious TE insertions (or TE load, Graphical summary – demography), to rise in frequency in natural populations [60]. In *A. lyrata*, while purifying selection acts broadly against TE insertions in the ancestral European population, North American populations that underwent bottlenecks carry a higher TE load [11]. Similarly in *A. thaliana*, the TE load accumulated along front waves, especially in the expanded Yangtze River basin population where  $N_e$  explains 62% of the variance in TE load [7]. The increase of TE frequency up to fixation in such bottleneck populations [11,54] is expected to diminish the fitness of individuals in the extreme environments encountered at the edges of the distribution range, and actually limit adaptability potential [11]. These observations support the hypothesis that, in plants, variation in TE expansion may largely be driven by differences in demographic history and inherent factors such as effective population size, breeding systems, and domestication events [60], rather than adaptation.

Based on these studies, the broader picture emerging from population genomics data still supports the view that TEs mostly persist over long evolutionary time-scales [55] and proliferate primarily as selfish genetic elements, without benefiting the host or being functionally relevant [63]. This does not question their

central role in biological innovations and genome dynamics at the species level [64,65]. Despite, or rather because of their parasitic nature, TEs remain thus among the most fascinating genomic entities, revealing the subtle strategies that enable their persistence, even at low copy number [55], amid ongoing evolutionary conflict [66].

### Limitation of the current model and outstanding questions

Despite these advances, species in which TEs have been analyzed at the intra-specific level (Table 1), are mostly annual or short-lived perennial species with small, diploid genomes. An exception comes from the analyses of whole-genome re-sequencing data for 300 *A. arenosa* individuals, a species found as both diploid and autotetraploid. In this system purifying selection acts strongly in diploids but is relaxed in tetraploids, leading to TE over-accumulation particularly near environmentally responsive genes [14]. This pattern suggests that gene redundancy in polyploid species could relax selection constraints and thereby enhance the adaptive potential of TEs.

Selection can also act on standing genetic variation, without requiring new TE mobilization. In particular, pre-existing alleles maintained by processes such as balancing selection can facilitate faster adaptive responses than selection on newly arisen mutations [67]. Under such a scenario, one would expect more TIPs at intermediate frequencies, shared across populations, or with patchy geographic distributions, as observed by Ref. [53]. Yet, tests for balancing selection—using either genome–environment association (GEA), dedicated selection scans [9] or local population surveys [16,53] should be more routinely incorporated into TE studies to capture the full spectrum of evolutionary forces shaping TE variation.

Clearly, the forces shaping TE evolution are highly context-dependent, varying across species and populations, and even among organs, developmental stages, and TE families [11,32,68]. To reach unbiased conclusions on the matter, looking at plant species harboring not only different genome architectures but also various life-history traits, will be crucial. Key questions remain: What are the roles of standing variation and balancing selection in TE evolution? By influencing the expression of environmentally responsive genes, could TE promote phenotypic plasticity rather than adaptation? How do TEs evolve in larger, polyploid genomes? What is the dynamics of TEs in perennial, long-lived species, such as trees, where the interplay between local selection and gene flow may differ drastically? Has artificial selection,

#### Box1. Definition

**Directed mutation:** process by which individuals respond to an environmental challenge by an increased mutation rate in a target.

**Local adaptation:** occurs when a population evolves traits that provide a fitness advantage in its specific environment, often due to natural selection acting on genetic variation that is beneficial in that local context.

**Transposable element insertion polymorphisms (TIP):** TIPs are genetic variants where the presence or absence of a transposable element (TE) insertion at a specific genomic location varies among individuals in a population.

**Population genomics:** the study of genome-wide patterns of genetic variation within and between populations to understand evolutionary, demographic, and selective processes. It builds on classical population genetics, but uses high-throughput sequencing data to analyze thousands to millions of genetic markers across the genome.

**Selective sweep:** happens when a beneficial mutation rapidly increases in frequency and becomes fixed in a population, reducing genetic variation in surrounding genomic regions due to genetic hitchhiking (Graphical summary – adaptive scenario).

**Genetic load:** refers to the reduction in the average fitness of a population due to the accumulation of deleterious mutations relative to a hypothetical, optimal genotype (Graphical summary – demography).

**Site-frequency spectrum:** a summary of the distribution of allele frequencies at polymorphic sites in a sample of DNA sequences. It reflects the evolutionary history of the population and is used to infer demographic events and selection patterns (Graphical summary – purifying selection).

**Fitness effect:** refers to the magnitude of the mutation's impact on a trait or fitness. It quantifies how much a particular mutation changes the phenotype (observable characteristics) or affects an organism's survival and reproduction.

**Polyploidy:** the condition of having more than two complete sets of chromosomes in an organism. Instead of being diploid (2n, two sets), a polyploid organism might be triploid (3n), tetraploid (4n), hexaploid (6n).

**Balancing selection:** an umbrella term referring, for instance, to a form of natural selection that maintains genetic diversity in a population by favoring the persistence of multiple alleles at a locus over long periods of time.

**Life-history traits:** characteristics of an organism that influence its schedule for growth, reproduction, and survival. These traits shape how an organism allocates resources to various biological functions over its lifetime.

coupled with gene redundancy, really facilitated the emergence of TE-driven traits in crops? Addressing these questions will require moving beyond isolated case studies. Integrating simulations with empirical data and comparative analyses across diverse species offers the most promising path toward a predictive understanding of TE evolution and their contributions to plant adaptation (Box 1).

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There are no competing interests to disclose.

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## Data availability

No data was used for the research described in the article.

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