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Transposable elements: all mobile, all different, some stress responsive, some adaptive?

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Transposable elements (TEs) were first identified through the polymorphisms they induced in plants and animals. Genomic studies have later revealed that TEs were highly abundant in eukaryotic genomes. Recently, more precise single individual genomic analyses have unravelled the huge diversity of TE insertions in many plant and animal species. In most cases the stress conditions behind this diversity are not known and neither is the adaptive capacity of these natural TE-induced variants. Here, we review some of the most recent examples of TE-related impacts on gene expression at the locus or the genome level and discuss the rich diversity of the TE repertoire and its potential role in adaptive evolution.

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Introduction

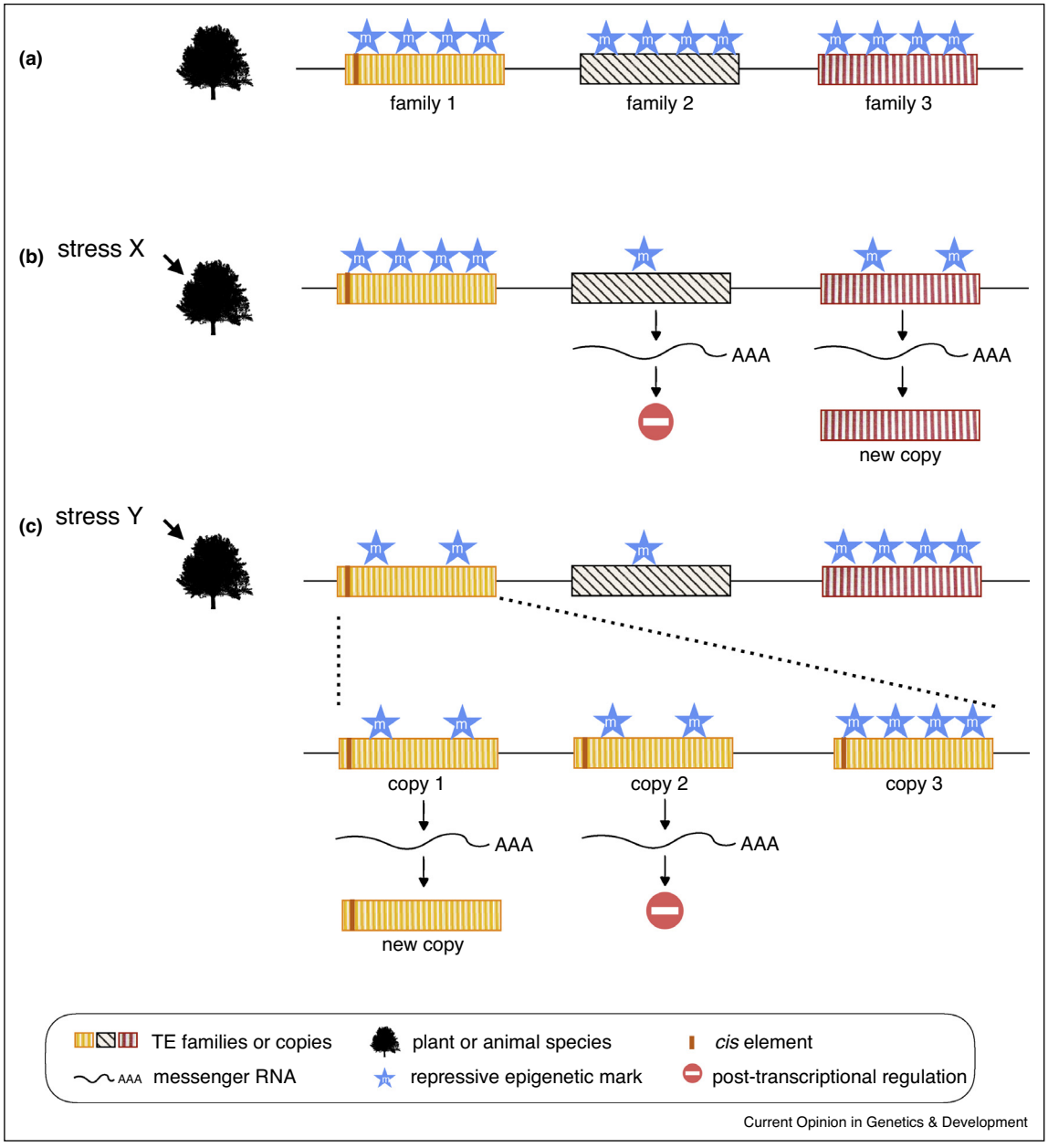
Transposable elements (TEs) are abundant in plant and animal genomes, and their role in genome evolution has been completely revisited in the last decade. Originally viewed as parasitic and/or mutagenic elements (although McClintock [1] and Britten and Davidson [2] had already envisioned in the 1950s their role as controlling elements), they are now considered as drivers in evolution and are the focus of numerous genomic studies. To better understand this paradigm shift, one should first acknowledge the fact that genomic studies have revealed the abundance and ubiquity of TEs. Their activation in response to stress was already noticed in the 1980s when the first retroelements have attracted the attention of scientists [3,4]. The presence of *cis* regulatory elements in their promoters have been intriguing suggesting that, far from junk DNA, TEs could also be involved in complex regulatory processes.

TEs are very diverse and differ in their relative representation in eukaryotic genomes as well as in their mechanisms of regulation and of activation (Figure 1). TEs comprise DNA transposons that move by a cut and paste mechanism and retrotransposons, that move by copy and paste, and these two classes are themselves divided into subclasses, each species containing a specific number of families representing the subclasses. The subclass of long terminal repeat (LTR) retrotransposons is predominant in plant genomes, while non-LTR retrotransposons make up the majority of animal genomes. Non-LTR retrotransposons can nevertheless be abundant in some plant genomes such as that of grapevine and the recently sequenced peanut genome [5], where they represent 10% of the genome. The origin of these species-specific differences is not understood.

TEs are silenced by epigenetic mechanisms, which explains why both the epigenomic landscape and the TE landscape vary between species [6]. Epigenetic regulations are also specific not only to subclasses but also to some TE families. In maize, for example, only some TE families are upregulated in RNA directed DNA Methylation mutants (RdDM, one of the silencing mechanisms controlling TE activity in plants) [7•]. Within these families some loci only can be overexpressed. In human cell lines, different subsets of the non-LTR LINE1 (L1) retrotransposon are active in different cell types [8•]. Epigenetic control might also depend on the age of the TE. Young TEs or intact full length ones seem to be under specific control as exemplified by the RdDM-controlled elements in maize and *Arabidopsis* [7•,9] or the young intronic L1 controlled by a newly identified silencing complex in human cell lines (HUB/MORC2) [10•]. In *Drosophila* hybrids, some TE families are upregulated while others are down regulated, suggesting a complex regulation that may depend on the TE family [11].

Recently, additional posttranscriptional controls such as the one exerted by small RNAs derived from tRNAs revealed in mouse and in *Arabidopsis* [12,13] or the alternative splicing shown in *Drosophila* [14] highlight the complexity of TE control. These examples further reinforce the idea that the transcription of TE families is far from reflecting their transpositional activity. While some geneticists tend to analyze TEs as a whole, it should

Figure 1



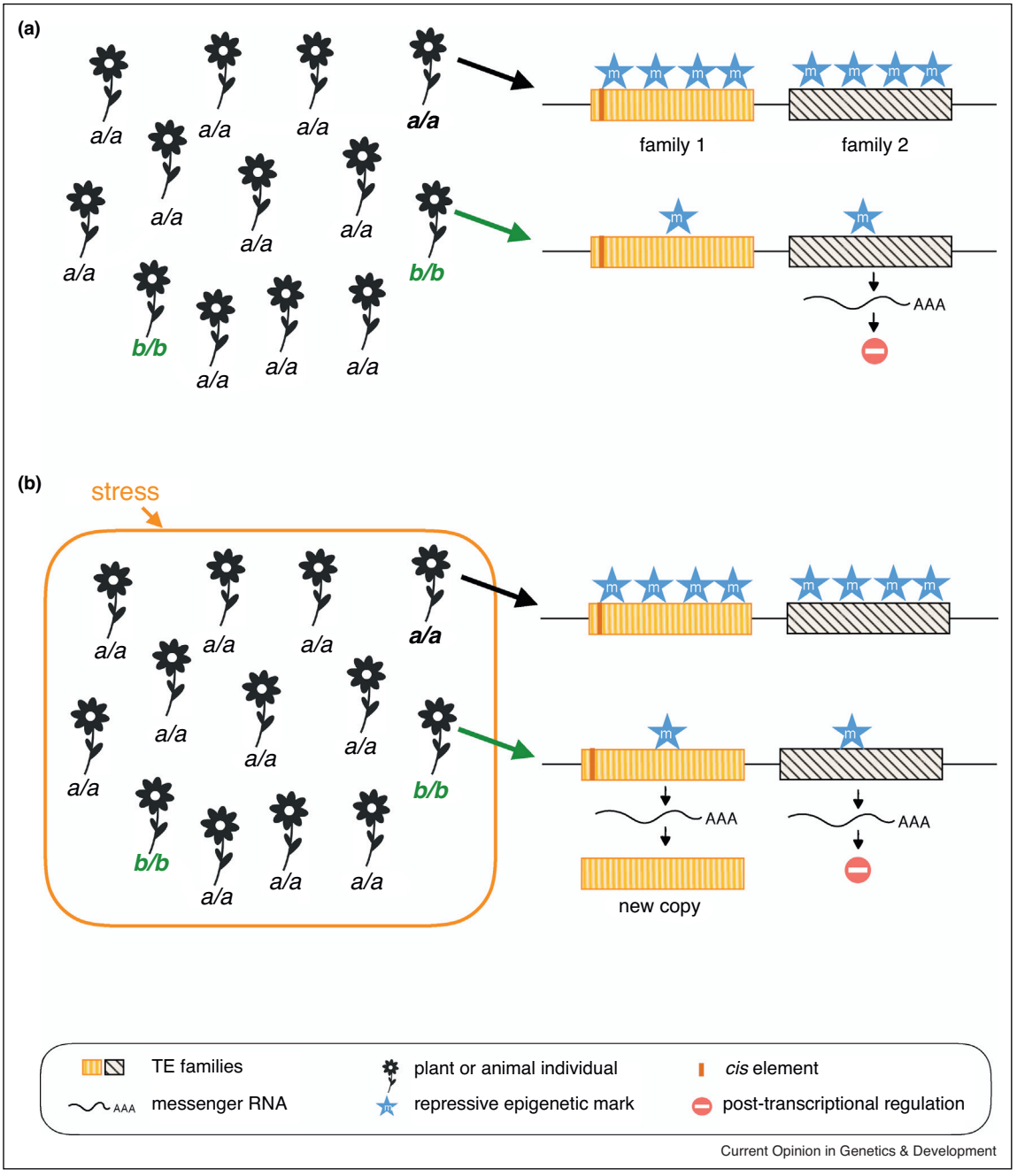
The stress response behaviour of TEs is family and copy dependent. **(a)** Example of three TE families repressed in normal conditions by epigenetic marks (e.g. DNA methylation). **(b)** A stress treatment can lead to TE derepression with some families generating new copies (family3) while others are still under posttranscriptional control (family2). **(c)** Here a different stress can lead to the activation of a distinct family (family1) and within this family of only some copies (copy1).

be emphasized that various stress or developmental stages can impact some copies of a particular family, specifically depending on their chromatin environment (Figure 2). The activity of some TEs thus appears to be the result of both a relaxation of the epigenetic control and the recruitment of specific regulatory factors binding to the promoter of the element [15,16,17•].

TEs as responsive elements to environmental stress

TE activation and transposition in response to stress have been dissected in great detail in excellent reviews [18–20]. As transcriptional units, TEs possess their own regulatory sequences that have likely evolved to contribute to their own fitness in their host genome. Interestingly,

Figure 2



A combination of stress and natural variation at epigenetic regulators can have an impact on TE activity in natural populations. **(a)** A natural population is depicted where a given epigenetic regulator can be found in two genotypes: *a/a* (major genotype) and *b/b* (rare genotype). On the right are shown the expression of 2 TE families for each genotype. While epigenetic control at TEs is released in *b/b* individuals, the expression of family2 TEs in silenced by posttranscriptional mechanisms. **(b)** The same population is subjected to an environmental stress (biotic or abiotic). The combination of release of epigenetic control and stress induces the expression of family1 in *b/b* individuals leading to new TE copies.

many examples suggest that TEs also provide a significant source of promoters and *cis* regulatory elements for eukaryotic genes [21••,22–25].

Consequently TEs can have an impact on gene expression in response to stress. We provide below some examples of their functional impact on a locus or on an entire regulatory network, as well as consider their structural impact.

Impact of TEs on the stress responsiveness of a locus

TEs can influence gene expression by adding a *cis* regulatory element or by modifying the epigenetic regulation

of a locus [20]. For example, a heat response element recognized by heat stress responsive factors has been identified in the promoter of the *ONSEN* LTR retrotransposon in *Arabidopsis thaliana* [15,26]. *ONSEN* insertions in genic regions can induce transcriptional upregulation of the neighbouring gene in response to heat stress [15]. Interestingly the heat responsiveness of this TE is conserved in different *Brassicaceae* species suggesting that it could be under positive selection [27]. There are numerous examples of TEs inserted near genes that affect their stress response. In plants with a high TE content, such as maize, transcriptional analyses showed that different TE families were associated with gene overexpression in response to abiotic stresses [28]. TEs can also contain *cis* elements involved in biotic stress response. In *A. thaliana*, a solo-LTR (harbouring the promoter of a LTR retrotransposon) was identified as a regulator of a pathogen response locus [29•].

TEs are thus emerging as a fertile substrate on which natural selection can act to evolve new *cis* regulatory elements and enhancers [25]. However the origin of these *cis* elements is not known. A recent observation of high rates of recombination between active extrachromosomal copies of the *ONSEN* retrotransposon family [30] could explain the fast evolving and rich genetic diversity of TEs and the acquisition of new regulatory sequences, although it has yet to be demonstrated.

TEs can also regulate gene expression by attracting repressive epigenetic marks. For example a DNA transposon (Miniature Inverted-repeat Transposable Element, MITE) insertion negatively regulates a gene involved in drought tolerance in maize through the RdDM pathway [31]. In rice and in response to inorganic phosphate starvation, TEs inserted in the vicinity of highly induced genes are hypermethylated [32]. Notably, the hypermethylation at TEs follows the upregulation of genes and is not inherited through mitosis or meiosis resulting in a fast but transient response. Here the causal relationships would have to be investigated further. Additional mechanisms by which TEs can mediate gene expression have been discovered recently. In mouse the chaperone heat-shock protein 90 (HSP90) represses the transcription activity of endogenous retroviruses (ERVs) elements thus decreasing nearby gene expression [33•]. As many environmental conditions result on HSP90 inhibition, this new mechanism is likely to play a role in stress response. In plants, TEs associated with long intergenic noncoding RNAs (TE-lincRNAs) are tissue specific and expressed under specific stress conditions suggesting they could be associated with the stress response [34]. New additional roles of TEs acting at the posttranscriptional level of gene control are also emerging. For instance in rice a DNA transposon named *MIKKI* is highly expressed in roots where it constitutes a target mimic that attracts the microRNA. By counteracting the effect of the microRNA, *MIKKI* leads to the root-specific expression of the *SCARECROW* gene normally targeted by this microRNA and important for root development [35•]. Given the high expression of some TEs in stress conditions, such role in depleting free microRNAs could be further explored in other systems.

Impact of TEs on gene regulatory networks

The comparison of transcription factor ChIP-seq data from different mammals has made it possible to define thousands of shared and lineage specific binding sites for the CTCF transcription factor [36]. The conservation of these motifs is inconsistent with neutral mutation. Interestingly the motifs are found in SINE and LINE non-LTR retrotransposons. More recently the analysis of ChIP-seq data from 26 transcription factors in human and mouse revealed that 2%–40% of their binding sites reside in TEs [37]. Using comparative ChIP-seq data during inflammation, Chuong *et al.* have shown that ERV are involved in the immune response [21••,38]. They further demonstrated that some ERV insertions are necessary to the interferon-induced expression of immune responsive genes in human cells. These examples highlight the potential impact of TEs in rewiring gene regulatory networks, which is only starting to be explored. In biological systems other than mammals, there are two difficulties that complicate this type of analyses. First, the TE half-life is much shorter in plants than in mammals (e.g. based on comparative genomic studies within the *Oryza* genus [39]), and the TE origin of the motifs might be difficult to establish in species with a high TE turnover. Second, for some species it could be challenging to obtain ChIP-seq data for transcription factors of interest.

Structural impact of TEs in stress responsive 'fast evolving' regions?

The interaction between pathogens and their hosts is a never-ending arms race and requires fast evolving genomic regions in both partners [40]. In filamentous fungi, the concept of 'two speed genomes' has emerged [41] to reflect this capacity of some subgenomic regions to evolve faster. Effector genes are inserted in these specific genomic compartments where they are strongly associated with TEs. Host specialization of the wheat pathogen *Zymoseptoria tritici* is for instance explained by a locus rearrangement provided by TEs [42•]. TEs are proposed to participate to the quick adaptive evolution of pathogen systems [40]. In the hosts these fast evolving regions have not yet been described as such. However a new reference genome sequence of the hot pepper has revealed the massive evolution of plant disease-resistance genes by retroduplication [43] suggesting a role for TEs in this process. Intriguingly stress response genes could also be hotspots for TE insertions. In *Drosophila* for instance, a cold responsive gene (*CG18446*) seems to be a hotspot for TE insertions of the *roo* family in different strains.

However only one insertion has an impact on the cold tolerant phenotype, in a strain where the TE provides an alternative transcription start site [44•]. This study highlights that TE polymorphisms *per se* do not systematically have an impact and that the functional impact of each TE insertion has to be investigated.

TE adaptive roles: the tip of the iceberg?

By regulating the transcriptional activity of genes, TEs can have a strong impact on the phenotype of host organisms [45,46], but to what extent can they be at the origin of adaptive traits? Already reported a decade ago, the insertion of a LINE retrotransposon in a *Drosophila* gene induces alternative splicing and the formation of a truncated functional protein conferring pesticide resistance [47] (Table 1). More recently, the dimorphism of the moth *Biston betularia* was explained by the presence of a TE in the first intron of *cortex*, a gene involved in the pigmentation pathway [48]. This TE induces the overexpression of the gene and consequently a gain of pigmentation. During the industrialization, black moths (with the TE insertion) were less visible to predators and the black moth population increased. Thus, the TE insertion has contributed to a selective advantage. Recent studies on *A. thaliana* natural populations.

Quadrana *et al.* and Stuart *et al.* [49••,50••] have revealed a huge diversity of TE insertions at the intraspecific level. Hotspots of TE insertions were identified with signatures of natural selection [49••]. One of these hotspots is located in the promoter region of the *FLC* gene involved in flowering time, a crucial developmental process for this annual plant. In these populations genome-wide TE insertion polymorphisms also explain a large part of differences in DNA methylation suggesting that epigenetic polymorphisms associated with structural variants might have been overlooked [50••]. A study of TE polymorphisms in the Asian tiger mosquito also illustrates recent adaptive evolution in European populations [51]. Looking for potential signatures of selection in recently adapted European populations and original populations from Vietnam, the authors performed a genomic scan and identified polymorphic TE insertions showing a high level of differentiation between temperate and tropical populations. Interestingly one of the neighbouring genes is encoding a hemolymphatic carrier of the juvenile hormone, an hormone involved in the maintenance of the diapause, a crucial phenomenon involved in adaptation to the environment.

How to explain the huge diversity of intraspecific TE polymorphisms despite numerous host mechanisms controlling TE silencing? Some TE families might evade silencing and undergo transpositional bursts as has been demonstrated in rice subjected to cold stress [52]. An important criterion to take into consideration could also be the natural variation at epigenetic regulators (Figure 2). For example in *A. thaliana*, a natural variant of the *MET2A* gene, encoding a DNA methyltransferase potentially involved in TE silencing, was associated with variations in the copy number of some TE families [49••]. Variations of DNA methylation levels have further been associated with natural alleles of an epigenetic regulator and with the geographical latitude of the accessions [53]. These variations can have an impact on TE activity. In *Drosophila simulans*, the copy number of *mos1*, a mariner DNA transposon, is correlated with the natural variation of the silencing machinery (piwiRNA genes) expression [54].

New approaches to study the role of TEs in the stress response

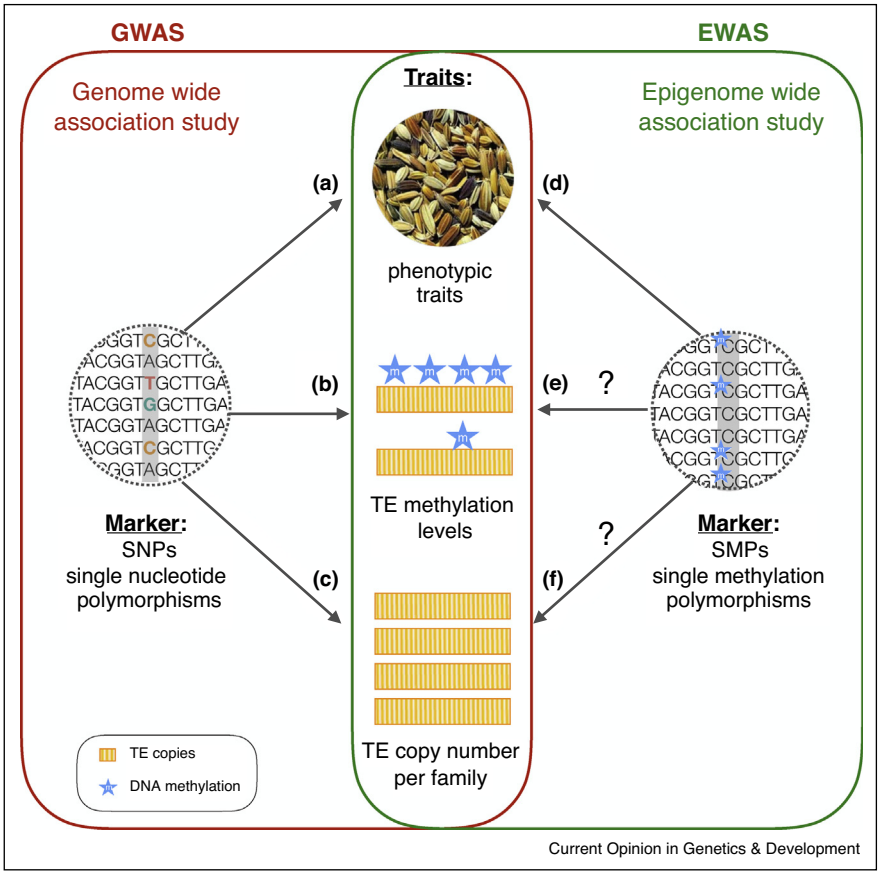
The vision of TEs and their impacts on eukaryotic genomes is constantly evolving. It is now clear that TEs have an impact on gene expression and participate to adaptive evolution. The examples cited above suggest that the roles of TEs in environmental adaptation could be much more prevalent than previously envisioned. One of the next steps is to evaluate the frequency of adaptive TE polymorphisms. New tools such as CRISPR-Cas9 may allow investigators to manipulate TE insertions,

Table 1

Examples of potentially adaptive TE insertions

Organism	TE type	TE family	Gene affected	Impact on the gene	Related phenotype	References
Drosophila melanogaster	Solo LTR	*Roo*	CG18446 (cold responsive gene)	Cotranscription (alternative TSS)	Increased viability (higher cold tolerance in some backgrounds)	[44•]
Drosophila melanogaster	LINE	Doc1420	CG10618 (CHKov-1)	Alternative splicing	Pesticide resistance	[47]
Biston betularia	Class II	*Carb-TE*	*Cortex*	Overexpression	*Carbonaria phenotype(dark pigmentation)*	[48]
Arabidopsis thaliana	LTR retrotransposon	*ATCOPIA4*, *ATCOPIA36*, *ATCOPIA63*, *ATCOPIA78*	*FLC (Flowering Locus C)*	Reduced expression	Early flowering	[49••]

Figure 3



New approaches to study TE activity in natural populations. **(a)** Classical GWAS where SNPs associated with a phenotypical trait (here rice seed colour) are identified. **(b)** GWAS-TE for SNPs associated with the copy number of a TE family [49••]. **(c)** GWAS for SNPs associated with the average methylation level of a TE family [61]. **(d)** EWAS for SNPs associated with a phenotypical trait [60]. **(e)** and **(f)** Possible EWAS that could be developed.

for instance by removing some TE insertions, to test their impact on the phenotype [21••]. One could also use drugs to promote the remobilization of TEs [55••]. All these new technological developments will certainly open new perspectives in our understanding of the adaptive potential of recent TE insertions.

Intraspecific genome-wide studies on TE polymorphisms have just begun and we have only a few indications of the extent of TE polymorphisms in natural populations. Future population genomic analyses using DNA capture or long read sequencing (such as PacBio or Nanopore technologies [56] to detect TE polymorphisms) could help addressing this burning question. Altogether, better assemblies and annotations of genomes improved by the use of optical mapping and chromatin conformation Hi-C should greatly facilitate the study of TE structural variation [57–59]. Using natural populations, genome-wide association studies will also help to identify genetic regulators of TEs (Figure 3). For example using the number of insertions per TE family as a phenotype can help to characterize the regions of the genome controlling the mobility of these families [49••]. Epigenome-wide association study is also an interesting approach to associate single methylation polymorphisms (used as marker) with a phenotype of interest [60]. However both identifying these variants within TEs and identifying TE insertion polymorphisms will be challenging because of the repetitive nature of TEs. In this regard, highly promising long read sequencing technologies will certainly be useful. Finally, sequencing the extrachromosomal circular forms of TEs could be used as a marker of ongoing transposition activity in stressed populations [17•]. With these exciting new tools, experiments on natural populations should help to identify how the mobilome might contribute to adaptation to environmental stress.

Conflict of interest statement

Nothing declared.

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