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REVIEW PAPER

The role of mobile DNA elements in the dynamics of plant genome plasticity

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Abstract

Plants host a range of DNA elements capable of self-replication. These molecules, usually associated with the activity of transposable elements or viruses, are found integrated in the genome or in the form of extrachromosomal DNA. The activity of these elements can impact genome plasticity by a variety of mechanisms, including the generation of structural variants, the shuffling of regulatory or coding DNA sequences across the genome, and DNA endoduplication. This plasticity can dynamically alter gene expression and genome stability, ultimately affecting plant development or the response to environmental changes. While the activation of these elements is often considered deleterious to the genome, their role in creating variation is important in adaptation and evolution. Moreover, the mechanisms by which mobile DNA proliferates have been exploited for plant engineering, or contributed to understand how desirable traits can be generated in crops. In this review, we discuss the origins and the roles of mobile DNA element activity on genome plasticity and plant biology, as well as their potential function and current application in plant biotechnology.

Keywords: Epigenetic regulation, exon shuffling, extrachromosomal DNA, genome plasticity, Pack-TIR, Pack-TYPE, plant viruses, transduplication, transposable elements.

Introduction

Mobile DNA elements are DNA sequences with the potential to replicate and integrate at several chromosomal locations of a host genome. They are often defined as 'selfish' because they primarily encode the factors to support their own replication and are normally not found under direct positive selection. These elements include transposable elements (TEs) which mostly originate from the host genome, and viral and viral-like elements, which are usually transmitted through infection (Box 1).

While originally associated with junk DNA and considered genetic 'parasites', the activity of mobile elements was later shown to contribute to the evolution of plant genomes (Fedoroff, 2000; Piacentini *et al.*, 2014; Vicient and Casacuberta, 2017) and, more recently, as a means for dynamic alterations to the genome in terms of both structure and function (Wicker *et al.*, 2018; Kalendar *et al.*, 2021). The insertion of these elements into new sites in the genome can have multiple consequences for the host (summarized in Fig. 1) and can contribute to increased diversity in a population (Chen *et al.*, 2020; Zhao *et al.*, 2022).

Mobile elements are found repeated and abundant in the genome of eukaryotic organisms and very often constitute the largest portion of nuclear DNA. In plants, the abundance of repetitive elements tends to correlate with the size of a genome, suggesting that their activity plays a direct role in genome

Box 1. Mechanisms of transposable element mobility

Transposable elements (TEs) were first characterized in maize, with transposition associated with kernel variegation due to insertion into anthocyanin-related genes (McClintock, 1950, 1953). Since this initial work, the structure, function, and consequences of TEs have been increasingly studied. What was originally thought of as 'junk DNA' is now seen to have functional regulatory roles in the genome (Lisch, 2013; Ariel and Manavella, 2021), with a range of consequences for genome plasticity. TEs can be broadly grouped, depending on their mode of transposition, into Class I and Class II. Class I TEs, also called retrotransposons, move via an RNA intermediate generated by transcription of the TE DNA locus, which is successively reverse transcribed into a DNA molecule and inserted into a new chromosomal location (Quesneville, 2020). Both the reverse transcriptase and the integrase enzymes necessary for the transposition are usually encoded by the transposon sequence. An abundant group of Class I TEs are characterized by long terminal repeats (LTRs) and closely resemble mammalian retroviruses in their replication mechanisms. For this reason, a common origin has been proposed among the two groups of elements (Hayward, 2017). While retroviruses infecting plants have not been formally observed, there is evidence of genome-integrated endogenous retrovirus (ERV) sequences which closely resemble active elements described in animals (Marco and Marin, 2005; Laten and Gaston, 2012). Moreover, antiviral drugs classically used to inhibit reverse transcriptase from mammal retrovirus can be also used to efficiently prevent the mobilization of active plant LTR retrotransposons (Brestovitsky *et al*., 2023).

Class II TEs transpose via excision and re-insertion into a new genomic location, a process that is mostly mediated by transposase enzymes encoded by the TE sequence (Quesneville, 2020). The TEs falling into each of these classes can then be further categorized based on their structures and exact modes of transposition (extensively reviewed in Quesneville, 2020). However, some Class II TEs do not conform to these groupings. For example, Helitron employs an entirely different mode of transposition (Fig. 2C). Instead of a 'cut-and-paste' mechanism, Helitrons are copied to form an ssDNA circle intermediate which is then inserted into the target site (Surzycki and Belknap, 1999; Grabundzija *et al.*, 2016). This mechanism closely resembles the rolling circle amplification which is observed occurring for geminiviruses, a large family of ssDNA viruses infecting plants, which are also often found integrated in plant genomes (Rogers *et al.*, 1986; Rizvi *et al.*, 2015; Sharma *et al.*, 2020).

Viral genomes are also considered to be mobile elements. Viruses share many common characteristics with TEs, and there is some evidence that TEs derived from viruses (Mustafin, 2018).

expansion (Tenaillon *et al.*, 2010). Despite the large number of mobile DNA elements found in plant genomes, most are in a quiescent state, with their activity controlled by both environmental and epigenetic mechanisms. Nonetheless, on an evolutionary scale, these elements are highly dynamic and are one of the main mechanisms for controlling the plasticity of the genome in its arrangement, structure, and function.

The ability of mobile elements to insert into new positions in the genome makes them an interesting source of genetic variation. Many transposition events result in random insertions in the genome, but there are multiple known examples of insertions consistently found in the same loci, some of which are discussed here. This consistency is an important trait if TEs are to be looked on as a potential means to alter gene expression. This review aims to discuss the developments in our understanding of how transposition impacts genome plasticity, and how these could potentially be used as a tool to alter gene expression in plants.

Structural variants with direct effects on gene expression

When TEs or other mobile DNA elements insert into new genome locations, their activity results in alterations to the local DNA structure, and they potentially interfere with genomic functions. The most known and studied effect of transposition is gene inactivation due to the integration interrupting the coding sequences or other critical regulatory DNA regions, with a mutagenic effect. In fact, an increase in the mutation rate in maize was the first documented effect of TE mobilization, observed in the pioneering experiments performed by Barbara McClintock and Donald Robertson (McClintock, 1950; Robertson, 1978). Such knockout capabilities have been harnessed to generate mutant lines of multiple species, with transposon insertions acting to disrupt coding genes by creating a frameshift or introducing premature stop codons (Thorneycroft *et al.*, 2001). This propriety of mobile elements has been applied to studying the function of mutated genes in plants, generating knockout lines in multiple species, including maize (May *et al.*, 2003), rice (Hirochika, 1997; Izawa *et al.*, 1997), and Arabidopsis (Wisman *et al.*, 1998).

Some groups of TEs show a preference to insert into genes or open chromatin (Ito *et al.*, 2011; Jiang *et al.*, 2011; Fu *et al.*, 2013). However, the insertion-targeting preference of mobile elements for genes could be underestimated due to potential negative selection against a high mutation rate with impacts on fitness. For example, the activation of the CACTA1 transposon

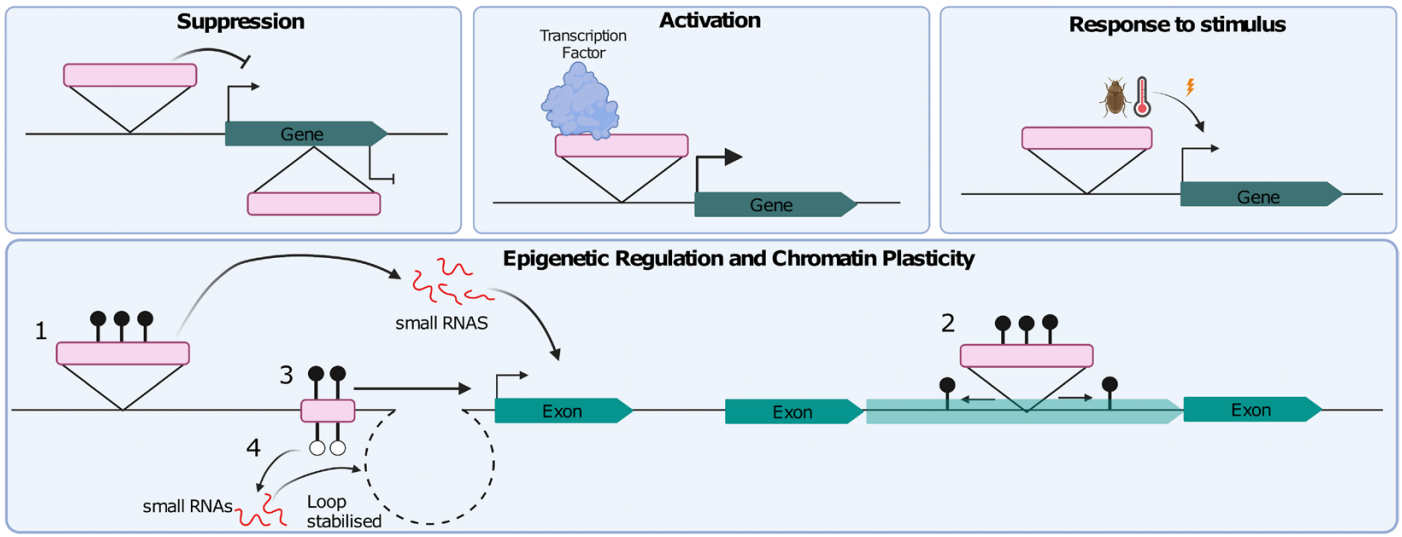

Fig. 1. Possible effects of gene expression of mobile elements during transposition. Insertion of the transposable element (pink) near to or within genes (dark green) can impact on transcription and gene regulation (three panels on top), inducing suppression, activation, or response to environmental conditions. The insertion can also lead to epigenetic regulation (bottom panel), resulting in the spread of suppression mediated by small RNAs (in red; 1) or DNA methylation (in black; 2, 3). Epigenetic modification can also alter splicing and lead to intron retention (faded shape; 2). Transposable elements can also regulate chromatin plasticity by influencing formation of chromatin loops (4).

in the *ddm1* Arabidopsis mutant, which is mostly located in the centromeric area of Arabidopsis chromosomes, leads to a much higher variability in the insertion sites compared with that suggested by the distribution of the CACTA1 family in wild-type plants (Kato *et al.*, 2004). Many studies have investigated the insertion bias of TEs and other genetic elements in plants, as well as the dynamic of their amplification mechanisms (Bourque *et al.*, 2018; Jiang *et al.*, 2018; Quadrana *et al.*, 2019; Quesneville, 2020; X. Zhang *et al.*, 2020; Ellison *et al.*, 2023; Pulido and Casacuberta, 2023; Huang *et al.*, 2024).

Today, we have multiple examples of TE mobilization events that can influence expression of surrounding genes, working as enhancers or repressors of transcription, or modifying splicing (Lisch, 2013; Ong-Abdullah *et al.*, 2015; Chuong *et al.*, 2017; Hirsch and Springer, 2017). Notable examples of TE insertions impacting expression are seen in domesticated crops, including grape (*Vitis vinifera*) (Kobayashi *et al.*, 2004; Carrier *et al.*, 2012) and maize (*Zea mays*) (Z. Zhang *et al.*, 2020). In a classic example, the insertion of the Class I TE *Gret1* (*grapevine retrotransposon 1*) into a Myb-related gene involved in anthocyanin biosynthesis of the commercial grape variety Pinot Noir resulted in the loss of colour in ancestral red grapes (Kobayashi *et al.*, 2004). In maize, insertion of a TE into the promoter of *stiff2*, a locus associated with decreased stem strength, was noted to repress *stiff2* transcription, thereby increasing stem strength (Z. Zhang *et al.*, 2020). These and other studies demonstrate that the inactivation of genes by TE activity is not necessary detrimental to plants, and can be responsible for agronomical traits (Lisch, 2013).

Transposon insertions can also increase gene expression by acting as enhancers. A key example of this was found in maize and has been associated with its domestication as a crop plant. Insertion of the *HOPSCOTCH* retrotransposon upstream of the promoter for the *teosinte branched1* (*tb1*) gene has been demonstrated to enhance gene expression, resulting in selection of increased branching during maize domestication (Studer *et al.*, 2011; Dong *et al.*, 2019). The TB1 protein also targets another domestication gene, *grassy tillers1* (*gt1*), which functions to promote branching and suppress tiller bud growth (Dong *et al.*, 2019). Similarly, transposons containing enhancer-like sequences have been noted in polyploid wheat (*Triticum aestivum*), with the presence of enhancer-like elements preferentially expressed in spikes associated with the B and D subgenomes (Xie *et al.*, 2023). Further examples are known in apple (Zhang *et al.*, 2019) and blood oranges (Butelli *et al.*, 2012), demonstrating that TE activity has been a determinant to generate agronomically important traits in crops.

A change in the response to environmental stimuli is another possible consequence of TE insertion, with several examples across model and crop plant species. The best characterized of these is the *ONSEN* TE, a long terminal repeat TE (LTR TE) also known as ATCOPIA78, which undergoes heat activation in Arabidopsis (Ito *et al.*, 2011). Following transition from 6 °C to 37 °C, *ONSEN* becomes transcriptionally active and is reverse transcribed (Cavrak *et al.*, 2014), indicating the ability to insert at new sites. This response has been attributed to the presence of a heat response element within the ONSEN LTR, conserved in *Brassicaceae* species, recognized by the heat shock factor A2 and able to promote *ONSEN* transcription subsequent to high temperature exposure (Cavrak *et al.*, 2014; Pietzenuk *et al.*, 2016). Following heat stress, *ONSEN* has been observed to transpose in Arabidopsis lines compromised

in the siRNA pathways (Ito *et al.*, 2016), or in plants exposed to chemical treatments which interfere with epigenetic regulation (Roquis *et al.*, 2021). Interestingly, genes surrounding new *ONSEN* insertions were reported to gain heat responsiveness (Ito *et al.*, 2016), with a range of effects on target loci, including constitutive expression and alteration of splicing resulting in exon skipping (Roquis *et al.*, 2021). This feature prompted the idea that TEs could facilitate adaptation to environmental changes (Fedoroff, 2012; Baduel and Quadrana, 2021), and indeed new insertions of *ONSEN* have been associated with emergence of new traits (Ito *et al.*, 2016; Thieme *et al.*, 2022). For example, a historical insertion occurred in the *Flowering Locus C* (*FLC*) gene in natural Arabidopsis accessions, and could be linked directly with a change in flowering time and adaptation to herbicide treatments (Raingeval *et al.*, 2024). Similar impacts in response to a variety of stressors have been noted in tomato (*Solanum lycopersicum*) (Benoit *et al.*, 2019), maize (Makarevitch *et al.*, 2015), and rice (*Oryza sativa*) (Yasuda *et al.*, 2013), indicating that TEs can aid the generation of more stress-tolerant plants, which could have implications for both crop systems and ecosystems.

TEs can contain transcription factor-binding sites (TFBSs), meaning that their activity has potential to increase and/or relocate the TFBSs present in the genome. Much of the evidence for this is from animals (Sundaram and Wysocka, 2020), but there are several examples of the evolutionary benefits of TFBS duplication by TEs in plants (Qiu and Köhler, 2020). Genome evolution of *Brassica* species has been related to TEs harbouring TFBSs, where consensus sequences of TFBSs for *Early region 2 binding factor* (*E2F*) transcription factor proteins were found within six TE families and have been amplified in five different *Brassica* species, including *Arabidopsis thaliana* and *Brassica rapa* (Hénaff *et al.*, 2014). Only a small proportion of sites were suggested to be functional, but were found to be capable of binding E2F and so were proposed to impact gene expression (Hénaff *et al.*, 2014). Similarly, differential expression of TFBSs in TEs of *Arabidopsis arenosa* alpine populations was associated with different levels of temperature and light tolerance, with stress resulting in TE activation and increased TFBS expression, typically along the alpine gradient (Wos *et al.*, 2021). This suggests evolutionary significance of TE activity for genome plasticity, where TFBS duplication confers a competitive advantage which has been maintained throughout selection.

Historical TE activity has also been associated with variation in splicing in maize, where a retrotransposon insertion into the *waxy* gene resulted in low *waxy* expression levels, attributed to disruption of splicing recognition sites and resulting in exon skipping (Varagona *et al.*, 1992). Furthermore, insertion of *Dissociation* (*Ds*), an Activator/Dissociation (Ac/Ds) TE classically associated with maize, produced a *de novo* intron, ultimately resulting in the production of novel exons (Giroux *et al.*, 1994). Since then, TE insertion has been found to impact splicing in multiple plant species. For example, in lettuce (*Lactuca sativa*), the insertion of a CACTA TE 10 bp downstream of the stop codon for *Golden2-like* reduced the number of wild-type transcripts to 6% that of plants lacking the insertion, leading to a pale leaf phenotype (Zhang *et al.*, 2022). Similarly, mobilization of the CACTA TE *Tgm-Express1* in soybean (*Glycine max*) produced novel exon combinations of the *up* allele associated with flower colour (Zabala and Vodkin, 2007). This mechanism has also been noted in *A. thaliana* in relation to the *ONSEN* TE (Roquis *et al.*, 2021), and has been implicated in the regulation of flowering time (Liu *et al.*, 2004). The diversity of plant species within which this occurs indicates a conserved mechanism, while also representing a possible natural mechanism to exploit in plant biotechnological applications.

Gene transduplication and exon shuffling

Gene transduplication is the process by which a gene or a gene fragment is duplicated and moved into a new chromosomal location. This activity is also often associated with exon shuffling, where coding DNA can be rearranged into new gene isoforms (Lisch, 2013; Bourque *et al.*, 2018). There are a range of examples in mammalian and bacterial systems (Ma *et al.*, 2023). In plants, there are multiple historical events of transduplication associated with the movement of TEs which have been described; however, most of these are considered the results of complex and unconventional transposition events that have been positively selected. Nonetheless, two groups of Class II TEs, Pack-TYPE and Helitrons, have been associated with constitutive events of transduplication (Zhao *et al.*, 2018; Catoni *et al.*, 2019; Gisby and Catoni, 2022).

The Pack-TYPE TEs (also known as Pack-TIR) are a group of non-autonomous TEs constituted by terminal inverted repeats (TIRs) compatible with different families of DNA transposases, which contain in their sequence portions of genomic DNA with potential coding capacity (Fig. 2A). Pack-TYPE TEs belonging to the Mutator-like transposable element) (MULE) TE superfamily (known as Pack-MULE) were first isolated in maize (Talbert and Chandler, 1988) and have since been reported in multiple plant species including *A. thaliana* and rice (Jiang *et al.*, 2004; Hanada *et al.*, 2009). The rice genome is reported to contain ~3000 Pack-MULE sequences, collectively containing fragments from >1000 coding gene sequences, with ~23% of the characterized Pack-MULEs containing two or more gene fragments (Jiang *et al.*, 2004). However, only 5% of these were found to be transcribed (Jiang *et al.*, 2004), indicating that the direct effects of Pack-MULEs on gene expression may be small, if compared with the number of loci affected by their mobilization. Since this study, further evidence indicates that up to 40% of Pack-MULEs are transcribed in rice, with 9% of these transcripts having an association with ribosomes and therefore indicating translation (Zhao *et al.*, 2018). Interestingly, tissue-specific expression of Pack-MULEs was noted, with preferential expression in the reproductive panicles (Zhao *et al.*, 2018). While

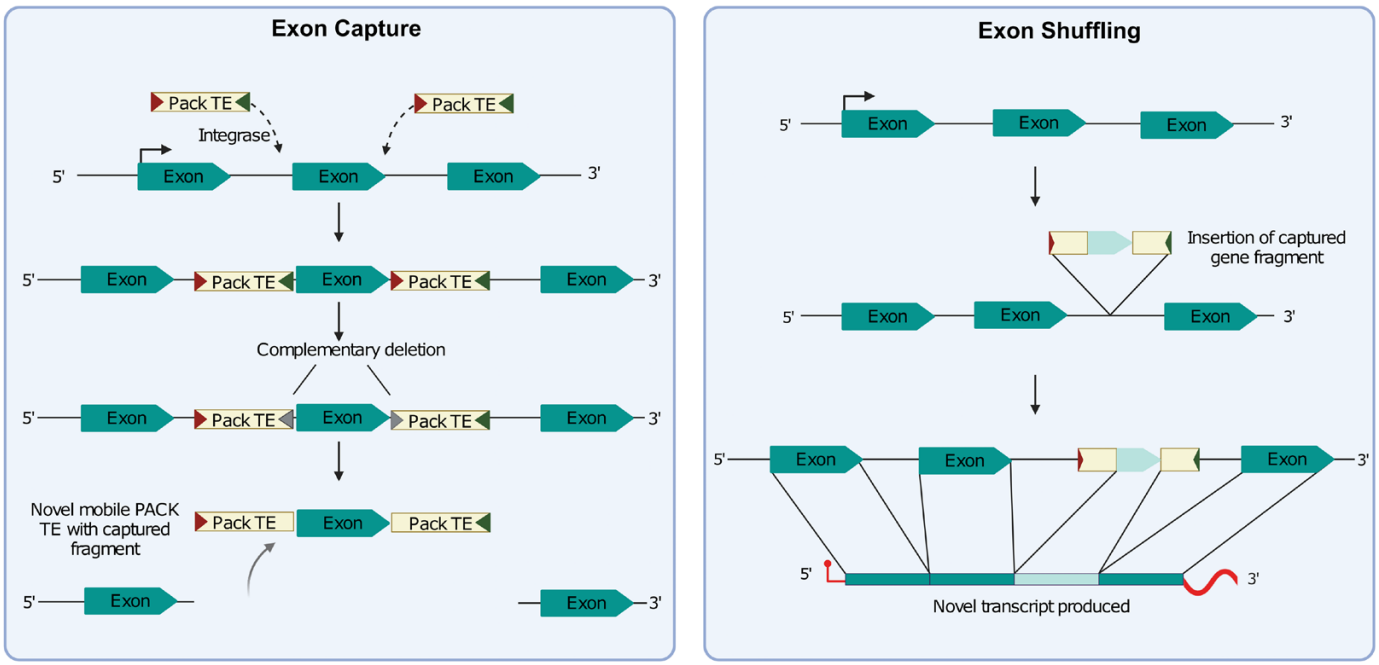

Fig. 2. Model for Pack-TYPE TE transduplication by exon shuffling. On the left, the insertions of two elements flanking an exon can lead to the mobilization of the entire coding sequence located between the two insertions. This can happen if complementary deletion or mutation will degrade the internal terminal inverted sequences (represented with triangles), necessary for the transposition. On the right, the transposition of a Pack-TYPE TE into an intron might result in the addition of coding DNA to an existing gene, allowing the generation of isoforms with new potential functions.

Pack-MULEs are the first discovered Pack-TYPE TEs, the information about their biology is derived from historical insertions because they are not transposing in real time. In contrast, mobile Pack-TYPE TE belonging to the CACTA family has been found in *A. thaliana* epigenetic recombinant inbred lines (epiRILs), a population of wild-type lines characterized by reduced DNA methylation in their genome (Reinders *et al.*, 2009; Catoni and Cortijo, 2018). With this finding, the concept of Pack-TYPE TEs was extended to other Class II DNA elements, and their exon shuffling activity was observed in real time (Fig. 1). The genomic rearrangements induced by Pack-CACTA mobilization were reported to be heritable (Catoni *et al.*, 2019), suggesting that genomic plasticity and TE insertion are not limited to somatic cells, confirming a similar conclusion reached in rice for Pack-MULE (Zhao *et al.*, 2018). Moreover, based on the study of Pack-CACTA mobilization, a model describing how these elements acquire new DNA has been proposed (Catoni *et al.*, 2019). Pack-CACTAs can capture gene sequences when two elements insert to flank a given sequence (Fig. 2), and then are excised together to give a single element (Catoni *et al.*, 2019). Therefore, in Arabidopsis, the activation of Pack-CACTAs is also contributing to increase the diversity of the TE family.

More recently, a significant number of Pack-TYPE TEs belonging to other TIR-containing DNA transposons superfamilies, such as *hAT*, *Harbinger-PIF*, and *Mariner*, have been found in different proportions in the rice and the maize genomes (Gisby and Catoni, 2022). This suggests that Pack-TYPE TEs are heterogeneous and can affect genome plasticity differently in various plant species. Interestingly, a similar survey performed on >100 animal reference genomes has identified only a few hundred Pack-TYPE TEs, in large part originating from transposition-independent recombination events (Tan *et al.*, 2021), suggesting that Pack-TYPE TEs could be much more abundant in plants than in other organisms.

Like Pack-TYPEs, Helitron TEs have been associated with gene fragment capture. Helitrons transpose via a rolling circle mechanism, and were first discovered in Arabidopsis, rice, and the nematode *Caenorhabditis elegans* via genome mining (Kapitonov and Jurka, 2001). However, their transduplication abilities were first reported in maize where, as in Pack-TYPEs, structures containing the Helitron terminal sequences were found to contain gene-derived fragments (Lal *et al.*, 2003; Morgante *et al.*, 2005). Loss of function of the *Shrunken2* (*Sh2*) gene was the first reported as a target of transduplication mediated by Helitron activity in maize, attributed to fusion of *Sh2* exons with those carried by the active Helitron and resulting in a novel transcript (Lal *et al.*, 2003). In two maize inbred lines, non-autonomous Helitrons were observed to carry one or more gene fragments and insert into multiple new locations (Morgante *et al*, 2005). It was also noted that the Helitrons were continually producing new non-autonomous elements, meaning that the maize genome could be undergoing continual change (Morgante

et al., 2005). Similar chimeric gene structures have also been reported in rice as a result of Helitron activity (Fan *et al.*, 2008); however, there has been little further investigation into their impacts and activity.

Helitrons able to carry coding DNA have also been identified in *A. thaliana*, with insertions of a non-autonomous form, known as *Basho*, found at 539 different loci (Hollister and Gaut, 2007). A total of 39% of these copies were noted to harbour sequences from other protein-coding genes, with the insertions also attributed to the divergence of *A. thaliana* and its close relative *Arabidopsis lyrata* (Hollister and Gaut, 2007). This demonstrates the possible evolutionary significance of transposon activity, suggesting that this mechanism could contribute to divergence from common ancestors.

Transduplication has also been associated with emergence of genome conflict. This occurs when siRNAs, which act in the establishment of silencing DNA methylation via the RNA-directed DNA methylation (RdDM) pathway, are generated against TE regions, thereby acting to silence the homologous sequence (Cuerda-Gil and Slotkin, 2016). Due to the capture of gene fragments by Pack-TYPEs and Helitrons, the siRNAs generated against them often display homology to coding sequences (Cuerda-Gil and Slotkin, 2016), meaning that silencing of coding genes can occur. If the captured gene is essential, then the individual is likely to be removed from the population via natural selection, or the silencing may be limited, introducing a conflict (Cuerda-Gil and Slotkin, 2016). This conflict can be resolved when the advantage of silencing the TE is balanced by the damage to gene function, but relatively few studies have investigated these effects. Observations of this balance have been reported in rice (Hanada *et al.*, 2009) and maize (Muyle *et al.*, 2021), with the activity of Pack-MULEs and Helitrons associated with production of siRNAs (Hanada *et al.*, 2009; Muyle *et al.*, 2021). Pack-MULEs in rice were noted to have homologous small RNAs (sRNAs), with 61% associated with siRNA generation, which ultimately resulted in both decreased Pack-MULE expression and decreased donor gene expression (Hanada *et al.*, 2009). In maize, transduplicated genes become the target of siRNAs generated against the carrier Pack-MULEs and Helitrons, a phenomenon not reflected in genes not subject to transduplication (Muyle *et al.*, 2021). This was accompanied by over-representation of repressive epigenetic markers in captured genes, particularly CG and CHG methylation (Muyle *et al.*, 2021). However, this was noted not to impact gene expression, supporting the hypothesis that silencing of genes is limited by the host (Muyle *et al.*, 2021).

Due to the relative abundance and activity of Pack-TYPEs and Helitrons, and the likelihood of other TEs with transduplication capabilities, it follows that genome plasticity is highly dynamic. With the capture, reshuffling, and combining of gene fragments in new locations, it is possible for the genome to be changing on a constant basis depending on the activity of the capturing TEs.

Epigenetic regulation and chromatin plasticity

Repetitive DNA sequences are the target of epigenetic regulation, and this regulation can be extended to neighbouring sequences or distant DNA with a similar sequence. Therefore, the activity of mobile elements can affect epigenetic plasticity of the host, providing epigenetic regulation at targeted genes.

One of the best known examples of epigenetic plasticity is related to the Karma TE, a long interspersed nuclear element (LINE) from the Class I superfamily found in oil palm trees. In oil palm agriculture, micropropagation of the elite hybrid oil palm trees is standard practice (Rao and Donough, 1990), which could generate somaclonal variation, resulting in some developmental alteration of fruit production in regenerated lines, negatively affecting palm oil production (Rao and Donough, 1990; Matthes *et al.*, 2001; Adam *et al.*, 2007). Early evidence attributed this to changes in DNA methylation, which was later associated with the Karma TE sequence inserted into intron 5 of the transcription factor gene *DEFICIENS* (Ong-Abdullah *et al.*, 2015). The hypomethylation of Karma induces an alteration in the splicing of the *DEFICIENS* gene, ultimately resulting in the production of a truncated transcript (Ong-Abdullah *et al.*, 2015).

Similar epigenetic plasticity has been reported in grapes, where the activity of Class I TEs has been associated with clonal polymorphisms (Carrier *et al.*, 2012). As with the oil palm, grape vines are clonally propagated, so comparison of the embryonic callus cultures and leaf tissue was performed to determine the degree of somatic variation generated by tissue culture propagation (Lizamore *et al.*, 2021). The authors of the work noticed, in embryonic callus, a significant increase of TE transcripts. If compared with leaf somatic tissue, this was associated with an overexpression of genes involved in epigenetic pathways, accumulation of sRNAs, and increased DNA methylation in the CHH context (H=A, T, or C) (Lizamore *et al.*, 2021). Altogether, these results indicate that genome-wide changes in epigenetic regulation occur in embryonic callus; however, the specific effects of the observed epigenetic variation on regenerated plants have not yet been described.

Both TEs and viruses are targeted by sRNAs which can modulate the suppression of expression of DNA of sequence complementarity, via a process known as RNA silencing (Baulcombe, 2004). Since early studies, RNA silencing has been associated with viral immunity (Covey *et al.*, 1997; Ratcliff *et al.*, 1997), as a consequence of the cleavage of viral RNA by Dicer-like (DCL) nucleases to form sRNAs, which can ultimately target the viral genome for silencing (Chen, 2009; Baulcombe, 2022). These sRNA molecules can also trigger transcriptional silencing of DNA sequences complementary to their sequence, in a process known as RdDM, whereby deposition of DNA methylation silencing marks is guided by sequence homology to the given sRNA (Gao *et al.*, 2010; McCue *et al.*, 2015). It has been shown that virus-induced gene silencing can be used to direct

RdDM-dependent changes in epigenetic regulation that are transgenerationally stable, such as the expression of the *FWA* gene which controls flowering time in *A. thaliana* (Bond and Baulcombe, 2015). Interestingly, RdDM appears also to target DNA viruses infecting plants by inducing DNA methylation of the viral genome, as observed for both Geminiviruses and Pararetroviruses (Noris and Catoni, 2020; Omae *et al.*, 2020). For both these groups of DNA viruses, a similar transcriptional silencing is also targeting endogenous virus-like copies integrated in the genome (Sharma *et al.*, 2020;Valli *et al.*, 2023).

In contrast to viruses, most TEs appear to be silenced in the Arabidopsis genome by a maintenance system which preserves their DNA methylation status across cell duplication independently of the presence of sRNAs (Zhang *et al.*, 2018). However, in the mutant of the chromatin remodeller Decreased DNA Methylation 1 (DDM1), this DNA methylation maintenance system is compromised, and many sRNAs are generated against activated TE transcripts by RDR6 and DCL2/4 (reviewed by Cho, 2018), as a compensatory silencing mechanism. While these sRNAs normally originate from TEs, if they have homology to coding or regulatory regions, this can impact gene expression (Li *et al.*, 2011; Zhang *et al.*, 2016). A range of these were found to interact with coding mRNAs, leading to degradation of the functional mRNA and therefore impacting gene expression (McCue *et al.*, 2012, 2013; Creasey *et al.*, 2014). This is a process often associated with genetic material recognized as 'non-self' as, for example, is happening with transgene silencing. Indeed, it has been observed for a long time that the increased methylation of a transgene locus results in decreased transgene expression (Van Houdt *et al.*, 1997). In fact, the propensity for a sequence to be targeted for transcriptional silencing appears to be fully determined by DNA features, such as the degree of repetition and the CG content (Catoni *et al.*, 2017; Sidorenko *et al.*, 2017).

Histone modifications have also been associated with TE regulation, with enrichment noted to be specific to the parent of origin in the endosperm (Moreno-Romero *et al.*, 2016). In crosses of Arabidopsis ecotypes Col-0 and Ler, >5000 TE regions had parental-specific patterns of H3 lysine 27 trimethylation (H3K27me3) in the endosperm, while relatively few were identified in the leaf. When assigned to TE families, Helitrons were noted to have significant enrichment of H3K27me3 in maternal tissues compared with paternal tissues linked to the activity of the Polycomb repressive complex 2 (PRC2), suggesting that silencing of mobile elements is parental specific and may ultimately contribute to diversity resulting from sexual reproduction (Barro-Trastoy and Köhler, 2024).

More recently, the epigenetic regulation of TEs has been directly associated with dynamic changes of genomic topology and transcription by affecting the formation and stability of chromatin loops in plants (Gagliardi and Manavella, 2020). In sunflower (*Helianthus annuus*), an inverted repeated (IR) element derived from a miniature inverted repeat TE (MITE), was found to regulate the expression of the nearby gene *HaWRKY6* through the dynamic formation of a chromatin loop (Gagliardi *et al.*, 2019). This is because a hairpin transcript produced by the TE locus upon loop formation promotes its own methylation via the formation of 24 nt sRNAs and the RdDM process, destabilizing the loop and reducing *HaWRKY6* expression (Gagliardi *et al.*, 2019). Interestingly, the abundance of loop formation was significantly higher in cotyledons than in the mature leaves, suggesting a role for TE activity throughout development. In Arabidopsis, a survey of IR elements associated with TEs has found that these produce sRNAs, trigger DNA methylation, and alter chromatin 3D organization similarly to the sunflower example (Arce *et al.*, 2023). The presence of insertional polymorphisms in a specific IR element has been found able to change the chromatin topology and expression of the associated gene, inducing variations in flowering time or in the response to light (Arce *et al.*, 2023). In a recent example, the IR element *Ea-IR* has been found to regulate the dynamic formation of a chromatin loop, which stabilizes the expression of the defence gene *EFR*, attenuating the immune response (Mencia *et al.*, 2024). These IR elements have been mostly found in MITEs, a group of TEs associated with regulation of gene expression also important in crops such as wheat (Yaakov *et al.*, 2012; Xi *et al.*, 2016) and rice (Avramova *et al.*, 1998; Lu *et al.*, 2012). Therefore, TE-containing regulatory elements could be exploited to control agronomically important traits, as for example demonstrated by the positive selection of TE insertion polymorphisms affecting gene expression which occurred during rice domestication (Castanera *et al.*, 2023).

Extrachromosomal DNA

Some mobile genetic elements can exist in the form of extrachromosomal DNA (ecDNA). Examples of this have been observed from both Class I and Class II TEs, particularly LTR retrotransposons and Helitrons, as well as DNA viruses. In plants, ecDNA copies have been found in both linear (eclDNAs) and circular (eccDNA) forms, and can originate from genetic elements present in the genome or derived from viral infection (Fig. 3).

Extrachromosomal DNA of viral origin

Viral elements with DNA genomes are normally replicated as ecDNA within the host and evolved highly efficient mechanisms of transmission among plants, which are often mediated by insect or animal vectors. There are two main groups of DNA viruses infecting plants. The first is constituted by viruses with an ssDNA circular genome, characterized by rolling circle amplification (RCA), including the families *Geminiviridae* and *Circoviridae*. The second group are constituted by the *Caulimoviridae*, which are pararetroviruses replicating by reverse transcription of RNA intermediates (Harper

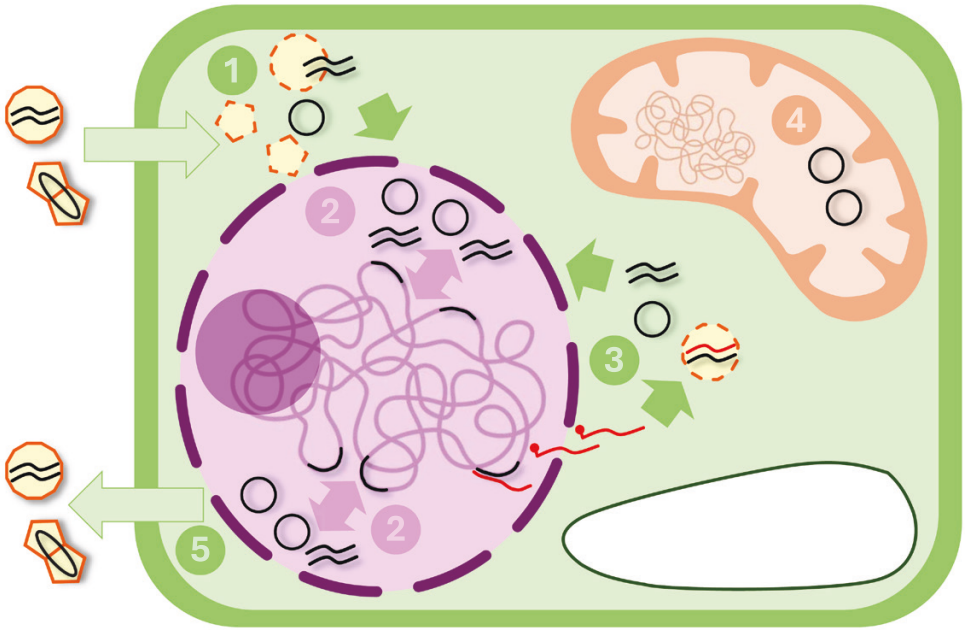

Fig. 3. Extrachromosomal DNA (ecDNA) in plant cells. Both circular (eccDNA, black circles) and linear (eclDNA, black lines) ecDNA of mobile elements can be found in plant cells. These molecules can enter the cell as viral forms (marked with 1) or be generated by endogenous DNA copies integrated into the genome, directly (2) or by reverse transcription into virus-like particles, starting from transcribed RNA molecules (3). Independently propagated eccDNA is also found associated with organelles (4). The ecDNA can leave the cell using viral carrier systems, in the presence of infections.

et al., 2002). Despite the replication cycles of these viruses not including a step of integration in the host genome, DNA fragments originating from viral genomes are abundant in several plant genomes (Chu *et al.*, 2014; Sharma *et al.*, 2020; Vassilieff *et al.*, 2023). Interestingly, there is also evidence of integrated elements originating from RNA viruses of non-retroviral groups (Chu *et al.*, 2014), suggesting the presence of multiple mechanisms of integration which are not necessarily linked to the viral replication cycle. In many cases, these insertions are associated with non-functional virus-derived sequences, but there are cases of endogenous Caulimoviruses transmitted only vertically through seeds or by grafting in banana (*Musa* spp.), *Nicotiana*, and Petunia (Harper *et al.* 2002).

On the other hand, it has been also proposed that viruses can potentially capture DNA of non-viral origin in their sequence, contributing to transfer DNA among plant species (Gilbert and Cordaux, 2017). However, while examples in prokaryotes and some mammalian models (e.g. retroviruses) are well studied, direct evidence of virus-mediated horizontal gene transfer events in plants is relatively scarce, despite the clear indications of gene flow occurring between plants and insect vectoring plant viruses (Sharma *et al.*, 2015; Lapadula *et al.*, 2020; Xia *et al.*, 2021).

A well-documented case of real-time generation of ecDNA induced by viral infection has been observed during infection of *Beta vulgaris* with the geminivirus beet curly top Iran virus (BCTIV) (Catoni *et al.*, 2018). In infected plants, several hybrid virus–host eccDNA molecules are formed from recombination of the viral genome and host DNA from different chromosomal locations. Such eccDNA has been found encapsidated in viral particles and is able to trans-replicate into other plant species if co-infected with the BCTIV (Catoni *et al.* 2018). It is plausible that such molecules can naturally spread across plants and replicate in other hosts using the viral transmission system, but the contribution of this mechanism to events of viral-mediated DNA horizontal transfer or viral genome evolution is still unknown.

Extrachromosomal DNA of TE origin

Beside viruses, LTR TEs can form both eclDNA and eccDNA by reverse transcription of RNA intermediates produced in a similar process to that which occurs for pararetrovirus. This process is necessary for their replication cycle, and ecDNAs are transported into the nucleus and integrate into a new chromosomal DNA location by the activity of the integrase enzyme (Cho *et al.*, 2019; Koo *et al.*, 2022). Given that the replication of LTR TEs is very similar to that of retroviruses, the International Committee on the Taxonomy of Viruses (ICTV) classify LTR TEs in the *Pseudoviridae* (Ty1/copia) and the *Metaviridae* (the Ty3/gypsy) families (Llorens *et al.*, 2020, 2021).

EclDNAs of LTR TE origin have been identified in multiple plant species, including Arabidopsis (Griffiths *et al.*, 2018), as well as in crop plants such as rice and tomato (Cho *et al.*, 2019), and some of these are noted to be induced as a stress response. For example, rice plants exposed to heat stress accumulate the

eclDNA of *Go-on*, an LTR TE containing a *cis*-acting regulatory element (Cho *et al.*, 2019). Furthermore, in tomato fruits, the FIRE retrotransposon produces eclDNA as a consequence of loss of DNA methylation and activation of the FIRE copies integrated in the genome (Cho *et al.*, 2019). However, whether these eclDNAs have undergone insertion in their respective genomes has not yet been reported, but a positive relationship between eclDNA production and genomic DNA (gDNA) insertion was observed, suggesting that some insertions have occurred.

LTRs can also form eccDNA. The presence of eccDNAs in higher plants was first reported in 1965 (Hotta and Bassel, 1965), and has since been reported in a range of plant species including *A. thaliana*, rice, wheat, and peas (*Lathyrus oleraceus*) (Navrátilová *et al.*, 2008), with increasing interest since the advent of high-throughput sequencing technology (Cohen *et al.*, 2008; Lanciano *et al.*, 2017; Peng *et al.*, 2022). Once reverse transcribed, LTR TEs are capable of forming eccDNAs by pairing of the terminal ssDNA LTR sequences (Rabson and Graves, 1997; Telesnitsky and Goff, 1997). Recent examples of these LTR eccDNAs have been reported in carrot (*Daucus carota*) cultures (Kwolek *et al.*, 2022) and potatoes (*Solanum tuberosum*) (Esposito *et al.*, 2019). In carrot, LTR eccDNAs were noted in material propagated in tissue culture, and appeared to be dependent on the genotype (Kwolek *et al.*, 2022). In potato, cold stress resulted in activation of LTRs capable of forming eccDNAs, and are thought to represent an important difference between domestic potato lines and their wild, cold-tolerant relative (Esposito *et al.*, 2019). By genome comparison, it has been identified that the eccDNA originated from *nightshade*, a Copia/Ale element which is inactive under cold conditions, but accumulates eccDNA in non-stressed plants (Esposito *et al.*, 2019). These finding suggest a role for TEs in generating genome plasticity in response to stress, although the consequences of LTR-derived eccDNA production are currently not well understood. In addition, the stress-related production of eccDNAs is often not consistent. For example, in *Brachypodium distachyon*, the formation of eccDNAs was not found to be related to a particular stress response in a screening involving 320 accessions, but was instead associated with loss of RNA polymerase IV activity (Thieme *et al.*, 2024). Therefore, the triggers for eccDNA production may be dependent on both the specific regulatory activation system of a TE and the presence of a particular epigenetic allele.

The presence of ecDNA has been linked to epigenetic alterations and the generation of structural variations in plants. The mutations of a combination of epigenetic factors have been associated with generation of ecDNA and structural variants in Arabidopsis (Peng *et al.*, 2022; Zhang *et al.*, 2023). Interestingly, this DNA variations was not only observed at TE sequences, but was also found at level of clusters of highly repeated pathogen response genes, suggesting a role in altering their copy number.

Another attractive hypothesis could be related to ecDNA acting as a 'sponge' for transcription factors or other DNA-binding molecules, by changing the ratio of protein and target DNA motifs in the cell environment. Recently, the eccDNA produced by activation of the LTR TE *PopRice*, which contains abscisic acid- (ABA) responsive regulatory elements and gibberellin- (GA) responsive sequence motifs, has been found to bind the ABA-responsive transcription factor OsABI5 (Chu *et al.*, 2023, 2024). When *PopRice* generation was inhibited, seed germination was delayed, attributed to reduced expression of α-amylase (Brestovitsky *et al.*, 2023; Chu *et al.*, 2023), indicating the first functional evidence for TE-derived ecDNA in plants.

In some organisms such as insects and yeast, LTR TEs have been found to produce viral-like particles and are able to be horizontally transmitted (Song *et al.*, 1994; Curcio *et al.*, 2015; Mérel *et al.*, 2020). In vertebrates, several examples of past events of horizontal transfer of TEs among species has been reported (H.H. Zhang *et al.*, 2020). While in plants there is no direct observation of transmission of LTR TEs, genome comparison studies of the genus *Oryza* have provided evidence of horizontal transfer of RIRE1 elements (Roulin *et al.*, 2008). Although currently the horizontal transmission of TEs is considered a rare event in nature (Fortune *et al.*, 2008), the clarification of a potential role for ecDNA in this movement could help to better understand the process of plant genome evolution and the acquisition of new gene functions.

Extrachromosomal DNA of unknown origin

Not all ecDNAs found in plants have a clear TE origin. For example, Helitrons (Class II TEs), abundant in both plant and insect genomes, are known to produce eccDNA copies during their replication (Yang and Bennetzen, 2009). These elements are phylogenetically linked to geminiviruses and share the same replication mechanisms, which is based on RCA (Murad *et al.*, 2004). Considering that many endogenous geminiviral sequences have also been observed to be integrated in plant genomes (Sharma *et al.*, 2020), it could be that Geminiviruses and Helitrons might not have such a clear boundary to separate them.

Moreover, ecDNA can be also found to contain DNA that is not associated with either a virus or a TE. For example, mitochondrial-derived eccDNA molecules (Fig. 3) have been found naturally replicating in *Beta vulgaris* (Hansen and Marcker, 1984; Mann *et al.*, 2022), and recently fully sequenced with high-throughput approaches (Mann *et al.*, 2022, 2024). These molecules are polymorphic in multiple *B. vulgaris* accessions, and their variation has been associated with cytoplasmic male sterility in this species (Thomas, 1986; Halldén *et al.*, 1989). Interestingly, similar molecules have also been found in *Vicia faba* (Flamand *et al.*, 1992), suggesting that these elements are common to multiple plant species.

Another remarkable example is also related to the endoduplication of the *5-enolpyruvylshikimate-3-phosphate synthase* (*EPSPS*) gene occurring in the weed *Amaranthus palmeri*, which induces natural resistance to the herbicide glyphosate. It has been reported that this resistance is associated with mitotically and meiotically transmissible eccDNA molecules containing copies of the *EPSPS* gene (Koo *et al.*, 2018). The presence of the *EPSPS* gene has been also found at multiple chromosome locations, suggesting the presence of transposition-mediated amplification mechanisms, but classic TE-derived structures have not been found associated with *EPSPS*-containing eccDNA molecules (Gaines *et al.*, 2010).

Conclusions and perspectives

As explained above, the consequences of mobile DNA elements on genome plasticity are diverse. While many studies report the detrimental effects of TE and viral genome insertion on plant fitness (Cosby *et al.*, 2019), their activity has also been associated with evolution (Anderson *et al.*, 2019; Huang *et al.*, 2021), genetic adaptation (Catoni, 2024; Raingeval *et al.*, 2024), species divergence (Reineke *et al.*, 2011), and crop domestication (Studer *et al.*, 2011; Dong *et al.*, 2019; Huang *et al.*, 2021). The possibility to use TE activation mechanisms to accelerate breeding has previously been discussed (Paszkowski, 2015), and the mechanisms of transposition have been exploited in genetic engineering. Good examples are the recent development of a plant transposase-assisted target site integration system (Liu *et al.*, 2024), or the use of a geminiviral-based vector as donor of DNA to obtain gene targeting in plants (Wang *et al.*, 2017).

TE insertion impacting genome plasticity could also have ecological consequences. Global or specific activation of TEs in response to stress is well documented (Wessler, 1996; Negi *et al.*, 2016), as is the heritability of the resulting insertions (Matsunaga *et al.*, 2015) and changes to DNA methylation (Hofmeister *et al.*, 2017). If new TE insertions or the formation of ecDNA can directly improve the fitness of the host in a determined condition, the presence of mobile elements in a particular genome will be an advantage for the host, perhaps suggesting that the activation of these elements may play a critical role in adaptive responses and underlie genetic adaptation in plants as in other eukaryotic organisms, as has been more convincingly proposed recently (Schrader and Schmitz, 2019; Godden and Immler, 2023; Catoni, 2024).

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Author contributions

RE: prepared the initial manuscript and Figs 1 and 2; MC: reviewed the manuscript, provided perspectives on viral contributions, and prepared Fig. 3. Both authors contributed equally to revisions and approved the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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