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Transposable element evolution in plant genome ecosystems

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Abstract

The relationship of transposable elements (TEs) with their host genomes has usually been seen as an arms race between TEs and their host genomes. Consequently, TEs are supposed to amplify by bursts of transposition, when the TE escapes host surveillance, followed by long periods of TE quiescence and efficient host control. Recent data obtained from an increasing number of assembled plant genomes and resequencing population datasets show that TE dynamics is more complex and varies among TE families and their host genomes. This variation ranges from large genomes that accommodate large TE populations to genomes that are very active in TE elimination, and from inconspicuous elements with very low activity to elements with high transposition and elimination rates. The dynamics of each TE family results from a long history of interaction with the host in a genome populated by many other TE families, very much like an evolving ecosystem.

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Introduction

More than twenty years ago, the first draft of a plant genome, *Arabidopsis thaliana*, was published [1]. However, it was not until very recently that this first plant genome sequence was finally completely assembled, from telomere to telomere including the centromeres [2]. This highlights the difficulty of fully understanding what a genome is, both at a technical and conceptual level. One of the questions that the sequence of the genomes of plants and animals has opened is why genes occupy only a fraction, very small in most cases, of the genome space, whereas a major fraction of the non-genic part of genomes of both plants and animals is composed by transposable elements (TEs). The role of these elements in genomes has been controversial ever since the proposal of their existence by Barbara McClintock. Whereas her view was that these elements endow genomes with the capacity to restructure when facing stressful conditions [3], others considered that the only reason explaining their maintenance was their capacity to replicate [4]. It is now well established that although TE insertions can lead to deleterious mutations, most of them are almost neutral and a few of them can become adaptive under certain conditions [5,6], and it is now clear that TEs, together with polyploidization, are a major driver of plant genome evolution [7,8]. On the other hand, we also know that TE activity is tightly controlled and that epigenetic mechanisms are key in their regulation [9]. However, we are still far from a complete understanding of how TEs are controlled and how they impact the structure and evolution of plant genomes. Here we review recent data from an increasing number of analyses of assembled plant genomes and resequencing population datasets that shed new light on the dynamics of TEs in plants.

Increasing and decreasing TE copy number in plant genomes

TEs are a heterogeneous group of mobile genetic elements that can be divided into two major classes, depending on the intermediate of transposition, RNA for class I (retrotransposons), and DNA for class II (DNA TEs). In general, class I elements are more prevalent in genomes as their 'copy and paste' replicative transposition leads to an increase in copy number as they transpose. Among them, Long Terminal Repeat Retrotransposons (LTR-RTs) are the most abundant in plant genomes, frequently representing up to 90% of the total TE content, as for example in the case of maize [10]. LTR-RT amplification can strongly impact genome size, and in fact, LTR-RT copy number is strongly correlated with genome size for small and medium size genomes. Although this relationship is not maintained for genomes larger than 10 Gb, this is not the

consequence of a lower TE activity but rather of a reduced rate of elimination leading to the accumulation of very old TE insertions that become less repetitive through repeated mutation [11].

Most class II TEs transpose by a 'cut and paste' mechanism that, in principle, does not lead to an increase in TE copy number. A moderate increase could, however, be achieved, for example, by linking transposition and DNA replication from a donor site already replicated to a target site still to be replicated, as it is frequently the case for the Ac/Ds elements [12]. However, this cannot be compared with the increase in copy number achieved by the replicative transposition of class I elements. For that reason, class II elements usually represent a smaller fraction of the TE content in plant genomes. There are, however, two types of class II TEs that can achieve high copy numbers in plant genomes: *Helitrons* and MITEs. *Helitrons* are a unique type of eukaryotic DNA transposon probably transposing via a rolling-circle mechanism [13], which would explain why they can reach high copy numbers in some genomes. Miniature inverted-repeat transposable elements (MITEs), on the contrary, mainly arise as deletion derivatives of autonomous TIR TEs [14], and it is not clear why they reach much higher copy numbers than their autonomous counterparts (see Box 1 for a discussion) and are among the most prevalent TEs in plant genomes in terms of copy number [15].

Although for some time it was assumed that the impact of TE activity should inflate genomes irreversibly, it is now clear that both the amplification and the elimination of TEs are highly dynamic processes in plant genome evolution [7]. Recombination between different TE copies or between repeated sequences within TEs, such as the two LTRs of LTR-RTs, is probably the main active mechanism for reducing TE load and genome size. There is actually a direct relationship between genome size, retrotransposon content, and genome recombination rate, with small genomes such as Arabidopsis showing signs of more and larger deletions than larger genomes such as that of barley [16]. But deleting genome regions between repeated TEs is not without risk for the genome, as important genes may be lost in the process. For this reason, recombination is frequently suppressed in repetitive TE-rich regions, such as the pericentromeric regions, which on the other hand favors the accumulation of TEs in these regions as they are more difficult to purge [17]. On the other hand, recombination efficiency depends on the size and the distance of the homologous sequences. Therefore, with respect to the intra-element recombination, elements with long repeated sequences will tend to recombine more and more frequently generate defective elements. For example, the *Brachypodium distachyon* genome contains many copies of very young *Angela* LTR-RTs consisting mostly of solo-LTRs, suggesting that their long LTRs and short internal sequence trigger their fast removal shortly after transposition [18]. Still, the same genome contains a high number of Retand elements characterized by long internal sequences and short LTRs, which are much older because they are not frequently eliminated by recombination [18]. On the other hand, the elimination rate will also depend on the TE location in the genome, with a more difficult elimination of the TE insertions located close to genes, due to the risk of losing important genic information, as shown, for example in *Arabidopsis halleri* and *Arabidopsis lyrata* [19].

Finally, selection and drift will be important mechanisms to eliminate TE copies. Their relative contribution will greatly depend on the population size and, more generally, on the demographic history of the species or the population in question [20]. On the other hand, as already mentioned, the efficiency in eliminating TEs

Box 1. The elusive MITE amplification mechanism.

MITEs, together with LTR-RTs, are the most prevalent type of TEs in plant genomes and can attain very high copy numbers [15]. However, MITEs are deletion derivatives of Class II TIR TEs and are mobilized by a "cut and paste" mechanism by transposases encoded by their autonomous counterparts [33], which does not easily explain their high copy numbers. MITEs seems to be highly promiscuous in using transposases of related elements, which has been proposed as a possible explanation for their high copy numbers [33]. Small differences in the transposase of related elements that give rise to a small number of class II elements or to a high number of MITEs in different genomes suggested that particular characteristics of the transposase could explain the ability to generate MITE families [55]. On the other hand, it has also been proposed that MITEs could be more efficiently mobilized than their autonomous counterparts, and this could allow them to reach higher copy numbers [58]. Recent analyses of the *Ping/mPing* system, one of the best known MITE/TIR TE families, suggested that the number and the presence of particular copies of the autonomous *Ping* element could be linked to the high amplification of the rice *mPing* MITE [59,60], linking again the ability to generate MITEs to particular characteristics of the related transposase. A recent Genome-Wide Association Study (GWAS) looked for genetic factors linked to MITE amplification in rice failed to detect associations with their autonomous counterparts [47], although this result may not be conclusive as MITEs can use different transposase sources and the mobile nature of the autonomous elements may make them difficult to detect by GWAS. However, this analysis [47] did show associations between the presence of particular MITE copies and MITE amplification, suggesting that MITE amplification depends on certain characteristics of the copy to be amplified. This may be due to the presence in most copies of sequences inhibiting transposition by the related transposases, as recently shown for *mPing* elements [61], but could also suggest that few elements can amplify by a replicative mechanism. The fact that phylogenetic studies of MITE populations in different plants are compatible with the replicative amplification of single or very few elements suggests a replicative mechanism of transposition not necessarily linked to its transposition (see Ref. [47] and references therein), as proposed long time ago [62].

will also depend on the recombination frequency of the region where the TE is sitting [17].

TE strategies to persist in genomes

Although some TE insertions can be adaptive and therefore be selectively maintained, this will not be the case of most insertions. Some TE insertions will be strongly deleterious and most of them are considered neutral or slightly deleterious [5]. Thus, there will be a selective pressure to eliminate the deleterious insertions and mechanisms in place to limit their amplification and their potential mutagenic effect. The main mechanism to control transposition in plants is the suppression of their expression by different layers of epigenetic silencing [9], although all and every step of transposition, from the expression to the integration, can be an object of control. TE impact greatly depends on how much and when transposition occurs and where the TE is inserted. For this reason, TEs have evolved mechanisms to limit their activity and select specific regions of the genome for integration. With respect to the latter, TEs as a whole tend to accumulate in heterochromatic regions. This is both the result of a reduced elimination rate from these regions, as discussed above, and of a target preference for these regions of some TEs (see Table 1 for some examples), which in some cases target these regions by means of specific protein domains in their integrases [21]. On the other hand, targeting gene-rich regions can also be a strategy to be maintained, and many TEs target genic regions for integration, which may somehow protect them from host silencing. They can do it through general (e.g. preference for open chromatin) or specific (e.g. interacting with proteins co-localizing with genes) mechanisms, and many do it in a way that may minimize their negative effect on host fitness (see Table 1 for examples).

With respect to the regulation of TE activity, and in line with the seminal proposals of Barbara McClintock, the expression of many TEs is associated with stress situations, which are circumscribed in time and space, limiting the impact of transposition (see Table 1 for examples). This association of TE expression and stress may be due to the presence of stress-inducible promoters, as is the case for example of the tobacco Tnt1 and Arabidopsis *ONSEN* LTR-RTs (see Table 1), or to a weakening of the silencing of TEs associated in stress situations, as it has been shown that stress alters the distribution of epigenetic marks and, in particular, DNA methylation [22]. The relationship of stress with TEs is a complex one, with TEs being induced by stress and, in turn, modifying the stress responses of the plant by inserting within or near stress-responsive genes [23–27]. An interesting example are the Arabidopsis *ATCOPIA93* and *ONSEN* LTR-RTs, which seem to target regions enriched in nucleosomes containing the histone variant H2A.Z, which typically correspond to stress-responsive genes [23,24]. Targeting stress-responsive genes for integration could help both TEs to be maintained and plants to evolve new stress responses, as it has been proposed [27].

TEs, together with RNA viruses, are the main target of host silencing mechanisms, which efficiently suppress their expression. Similar to what happens with viruses, TEs have evolved mechanisms to escape silencing. A simple strategy could be to insert very close to genes that need to be maintained active, which is what was proposed to explain the lack of silencing of Arabidopsis AtMu1 elements inserted within the 3′ untranslated region of genes [28]. But in other cases, there are hundreds of elements actively transcribed and not being silenced even when the silencing machinery actively targets their sequence, as it has been shown for the

Table 1

Strategies employed by TEs to persist in plant genomes.

Strategy		TE family/lineage	TE superfamily	Plant species	References
Targeting	Centromere	*CRs*	*Ty3/Gypsy*	*Poaceae* spp.	[63]
		Tal1	*Ty1/Copia*	*A. lyrata*	[54]
	Gene 3′ UTR	*AtMU1*	*Mutator*	*A. thaliana*	[28]
	Transcription Start Site	*Mu*	*Mutator*	*Z. mays*	[64]
	Gene upstream region	MITEs	*PIF-Harbringer*	-	[25]
Activation by stress	Environmental response	*ATCOPIA93*	Ty1/Copia	*A. thaliana*	[24]
	Heat stress	*ONSEN*	Ty1/Copia	*A. thaliana*	[23,65]
	Pathogen response	*Tnt1*	Ty1/Copia	*N. tabacum*	[66]
	Cell culture	*Tos17*	Ty1/Copia	*O. sativa*	[67]
TE structure	Mobile unit/protein donor split	MITEs	*PIF-Harbringer*	*O. sativa*	[33]
		Dasheng/RIRE2	*Ty3/Gypsy*	*O. sativa*	[68]
	Low LTR/internal region ratio	*Retand* lineage	Ty3/Gypsy	*B. distachyon*	[18]
Silencing interference	Anti-silencing RNA	*CACTA mir820*	*CACTA*	*O. sativa*	[30]
	Anti-silencing proteins	*VANDAL21/VANDAL6*	*Mutator*	*A. thaliana*	[31,32]

tobacco Tnt1 element [29], suggesting that TEs can actively interfere with their silencing. This has been shown to be the case for different class II TEs that encode a microRNA targeting silencing machinery components [30], or antisilencing proteins [31,32] (see Table 1 for examples).

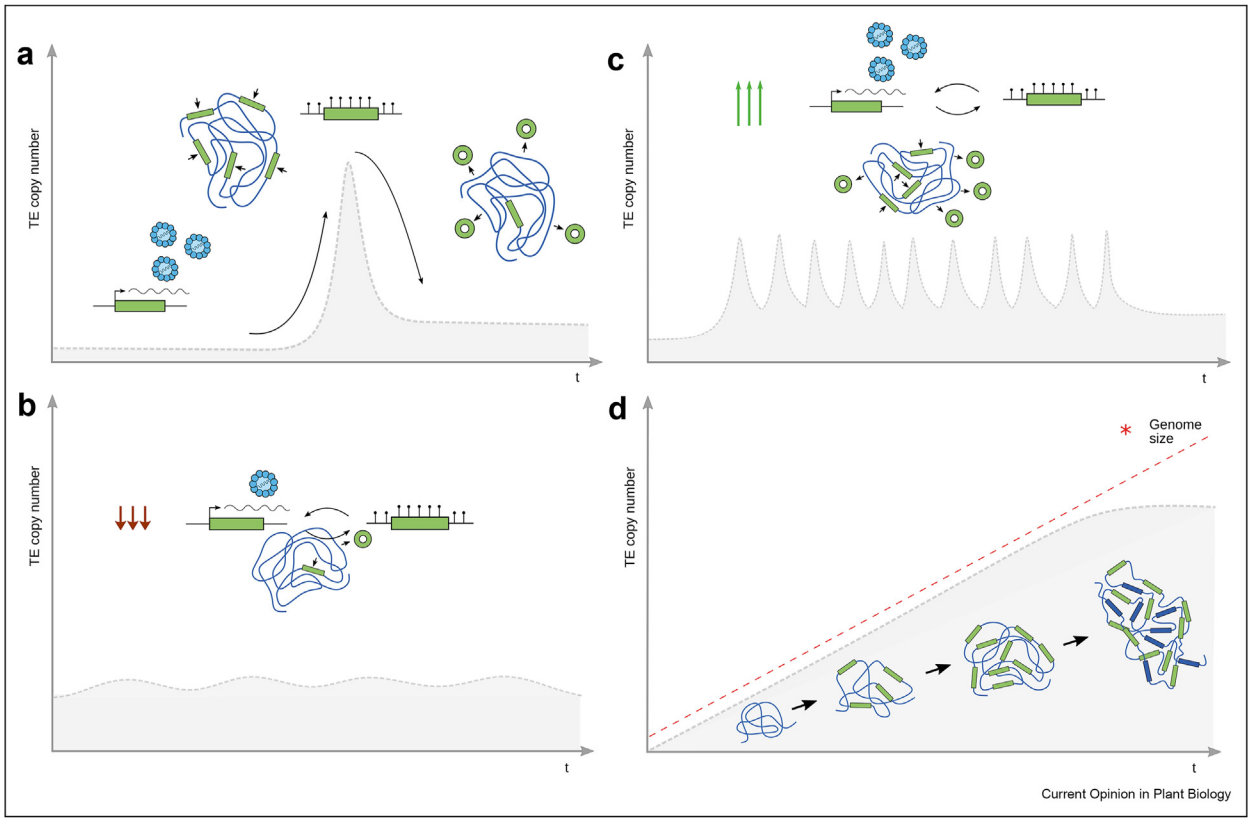
Although the transposition of class II elements depends on the expression of the transposase, as well as additional proteins in some cases, these proteins can be provided in *trans* and transposition does not require the expression of the copy to be mobilized. This is probably one of the reasons explaining the success of MITEs in reaching high-copy numbers. MITEs do not encode for the proteins needed for transposition that are encoded by related autonomous class II elements [33]. In most cases, the autonomous elements are maintained at low copy numbers, and, therefore, may not trigger their silencing, whereas the related MITEs are not expressed and their methylation appears to have no impact on their amplification [34]. The proliferation of non-coding or defective elements is not exclusive to class II TEs and mobile defective LTR-RTs also exist (see Table 1 for examples). A particular case is when the different proteins needed for transposition are encoded by different elements, as it is the case of the LTR-RTs Cinful and Zeon, with the former encoding the enzymatic polyprotein domains, and the latter encoding for the structural GAG protein [35]. Splitting the coding capacity in two LTR-RTs may limit the activity of these elements, a strategy that seems to have been successful in some genomes such as maize, which contains more than 25 LTR-RT families where gag and pol genes are mostly found in separate TE copies [10].

TE dynamics in plant genomes

The interaction of TEs and genomes has been frequently viewed as an arms race between TEs attempting to colonize the genome and the host trying to control transposition and to eliminate TEs, and it is generally assumed that this leads to long periods of time where TEs are quiescent punctuated by bursts of amplification, frequently of one or very few families [36]. These bursts could result from the activation of one or few copies by stress, the transient weakening of the TE silencing mechanisms or the horizontal transfer (HT) of a TE from another host, a phenomenon now recognized as being more frequent during evolution than previously thought [37–39]. The first steps of the burst would lead to the amplification of the TE family until it becomes silenced again when stress has passed, the silencing efficiency is recovered or, in the case of HT, until the new TE family amplifies over a threshold that drives its recognition by the silencing machinery (Figure 1a). Clear examples of these bursts are the amplification of three LTR-RTs in *Oryza australiensis* to reach 90,000 copies and doubling the genome size in just three million years [40] and the massive amplification of the *mPing* MITE in some rice varieties [25]. TE bursts can be associated to genomic changes that could be considered as a genome stress, such as interspecific crosses and polyploidization events [41], but they could also be associated to environmental changes such as domestication, as it has been recently proposed for olive trees [42]. Interestingly, many of the plant domestication traits result from the insertion of TEs [43].

However, even in species with small genomes assumed to hold few active TEs, such as Arabidopsis, recent analyses of more than 1000 accessions suggest a much higher and constant transposition rate than previously assumed, with the TE polymorphism rate approaching that of SNPs [44]. Purifying selection rapidly eliminates most new TE insertions, but the few adaptive insertions have the opportunity to remain. Recent population analyses across hundreds of accessions of tomato [45] and rice [46,47] show that, indeed, there seems to be a high level of ongoing transposition in plants. Most TE insertion polymorphisms detected in these analyses are present at very low frequencies, suggesting a high turnover of TE insertions, with high activity coupled with a high elimination rate (Figure 1b). This is also what has been shown for some Copia LTR-RT families of *B. distachyon*, which seem to be not only highly active but also rapidly removed through LTR–LTR intraelement recombination [18]. Therefore, although TEs can amplify dramatically in some genomes in particular moments followed by periods of time of apparent TE stability, this does not necessarily mean TE quiescence, as in many cases, there is a high TE activity coupled with the rapid elimination. On the other hand, it has also been reported that TE families with a low transposition rate can be maintained in evolution. This is the case of several lineages of *Copia* LTR-RTs, such as Ale, that are present at low copy numbers throughout the phylogeny of angiosperms [48], which shows that some TEs can maintain a certain degree of activity with no apparent cost for the host genome (Figure 1c). Actually, analyses in different genomes have indeed shown that an important fraction of TE insertions, even when close to genes, seem to be well tolerated by the host and can remain for long periods of time unfixed. This is, for example, the case of many polymorphic TE insertions in almond that are older than its evolutionary split from peach [49], or many of the recently described polymorphic TE insertions close to genes in rice, that predate its domestication from *O. rufipogon* [50]. Interestingly, it has also been shown that some of these old insertions in rice are associated with changes of gene expression and are positively selected in particular rice populations, suggesting that they become adaptive under particular agroecological conditions [50]. This suggests that the modular nature of promoters may tolerate the insertions of TEs, which may have a minor effect on transcription and be phenotypically almost neutral in normal conditions but, in

Figure 1



Different TE amplification and elimination dynamics. (**a**) Burst of amplification of a TE family. The activation of one or few TE copies by horizontal transfer (HT), stress activation or transient weakening of TE silencing starts an amplification burst that generates new insertions increasing the TE family copy number until it becomes silenced. This is followed by a period of TE elimination through recombination, selection or drift, reducing the TE load. (**b**) Dynamic equilibrium reached by a TE family with constant insertions and eliminations maintained through low TE activity (self-regulation). (**c**) Cyclical TE amplification dynamic. After a first burst of amplification, silencing and TE elimination, the remaining copies reactivate and generate a second burst, followed again by silencing and TE elimination. (**d**) The uncontrolled amplification of a TE family directly contributes to genomic expansion. Through the accumulation of mutations, older copies of the family become fossilized non-repetitive sequences and are no longer recognized as copies of their former TE family.

particular cases, may become adaptive in a changing environment. This may explain the increasingly recognized role of TEs in the evolution of transcription networks in plants [51], which may be particularly relevant for MITEs, whose small size would allow their insertions to be less deleterious when inserting close to genes. The more difficult elimination of insertions close to genes and their potential adaptive effect under certain conditions may explain why their association with genes increases as they get older, as it has been shown in rice [47]. All this data suggests that not all TEs elicit a strong defensive reaction from the host genome and that, in many cases, their activity can be well tolerated. Finally, the need to control and eliminate TEs seems to vary from genome to genome, and it seems now clear that some plants do not eliminate TEs efficiently, letting them slowly degenerate by mutations while the genome increases, as it is the case for gymnosperms (Figure 1d) [11].

The picture that emerges is that even if general trends for the whole TE population or even for superfamilies can be drawn, within the same superfamily of TEs, different families may have different TE dynamics. This probably reflects the very old but dynamic association of TEs with genomes, with some old adaptation strategies shared by most members of a superfamily within most genomes, and more recent TE/host arrangements specific for particular families in a genome. For example, whereas gypsy LTR-RTs tend to concentrate in heterochromatic regions and copia LTR-RTs are frequently enriched in gene-rich regions in most flowering plants, in *Physcomitrella patens* gypsy and copia LTR-RTs have an opposite distribution. Indeed, in *P. patens*, a copia LTR-RT is almost exclusively located in a single location in the chromosome, proposed to coincide with the centromere, and gypsy LTR-RTs are distributed along chromosome arms [52]. The lack of gypsy LTR-RT in the centromere

is shared by *Marchantia polymorpha* [53], suggesting that gypsy LTR-RTs evolved to target the centromere in flowering plants. However, not all gypsy LTR-RT families in flowering plants accumulate in pericentromeric regions. For example, in maize, in spite of the pericentromeric accumulation of gypsy LTR-RTs as a whole, the second and the third largest gypsy LTR-RT families are enriched in chromosome arms or distributed evenly in the chromosomes of this species [10]. This suggests that the adaptation of TE families to the host is dynamic and that some gypsy LTR-RT families have more recently evolved different strategies to be maintained during evolution. Similarly, there are examples of TE families that evolve very differently in different genomes. For example, the related COPIA93 and Tal1 elements from *A. thaliana* and *A. lyrata*, respectively, are found at low copy numbers in gene-rich regions in *A. thaliana*, whereas in *A. lyrata*, they reach high copy numbers and target the centromere [54]. Interestingly, Tal1 also targets the centromere when introduced in *A. thaliana* [54], suggesting that the difference in targeting is an intrinsic characteristic of the elements that evolved different strategies to be maintained in the two genomes. Similar examples can also be found for TIR-TE elements. As an example, the *Lemi*1 element, a pogo-like TIR-TE, reaches a moderate number of copies and does not generate MITEs in *M. truncatula* whereas it is maintained at one or two copies in Arabidopsis and generates hundreds of related MITEs [55].

The reasons for a differential evolution among genomes can be manifold. Differences in selective pressure due, for example, to different environmental constraints, reproductive systems, or population sizes, could definitely influence TE evolution. On the other hand, the size and organization of the genome could be a key factor. For example, the ploidy level and the history of interspecific crossings are known to influence TE activity [41,56]. But an important factor that will influence the evolution of a particular TE is the evolution of all the other TE families that coexist in the same genome.

Conclusions

With many possible strategies to be followed, even within a single TE superfamily or lineage, and an important interplay with the environment, the life of a TE family will be constrained by the dynamics of the other TE families with which it coexists in the genome. Therefore, the dynamics of TE families very much resembles that of the different players in an evolving ecosystem, as proposed quite a long time ago [57]. Under this scenario, TE dynamics appears as a diverse and rich collection of evolutionary histories that cannot be summarized just as a simple arms race between an invasive parasite and a defensive host.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

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

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