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Article *in* Journal of Evolutionary Biology · October 2014

DOI: 10.1111/jeb.12513

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JOURNAL OF Evolutionary Biology

doi: 10.1111/jeb.12513

REVIEW

Bursts of transposable elements as an evolutionary driving force

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Keywords:

evolution;
genome;
marginal populations;
speciation;
transposable elements.

Abstract

A burst of transposable elements (TEs) is a massive outbreak that may cause radical genomic rebuilding. This phenomenon has been reported in connection with the formation of taxonomic groups and species and has therefore been associated with major evolutionary events in the past. Over the past few years, several research groups have discovered recent stress-induced bursts of different TEs. The events for which bursts of TEs have been recorded include domestication, polyploidy, changes in mating systems, interspecific and intergeneric hybridization and abiotic stress. Cases involving abiotic stress, particularly bursts of TEs in natural populations driven by environmental change, are of special interest because this phenomenon may underlie micro- and macro-evolutionary events and ultimately support the maintenance and generation of biological diversity. This study reviews the known cases of bursts of TEs and their possible consequences, with particular emphasis on the speciation process.

Perpetual generators of genomic conversion

Changes in genomes occur constantly in nature, and very often as a response to changing environments. Genetic/epigenetic plasticity is the only way to avoid the extinction of populations under increasing ecological stress (Lindsey *et al.*, 2013). Evolutionary rescue occurs when natural selection enriches a population with more stress-tolerant genetic variants. Among the internal sources for genotypic population change, transposable elements (TEs) are of high importance as a result of their ability to create mutations, alter gene expression and promote chromosomal aberrations (Bennetzen, 1996, Bennetzen, 2000a,b). Since the discovery of TEs by Barbara McClintock, the genome is seen as a mobile, rapidly changing entity. Although current knowledge of the mechanisms of activation of TEs appears far from complete, it is fairly clear that changing environmental conditions may play an important role in this process (McClintock, 1984; Wessler, 1996; Capy *et al.*, 2000; Slotkin & Martienssen, 2007; Hosid *et al.*, 2012).

The majority of TEs and their derivatives are located in heterochromatin (Heslop-Harrison *et al.*, 1997; Belyayev *et al.*, 2001; Saunders & Houben, 2001; Slotkin & Martienssen, 2007; Raskina *et al.*, 2008), but a small percentage of transpositionally active TEs may actually be inserted at novel locations either near (Bohne *et al.*, 2008) or directly into regulatory and coding sequences (Lowe *et al.*, 2007) (Fig. 1). TEs show certain patterns of insertion preferences (Dietrich *et al.*, 2002; Liang *et al.*, 2009; Jianga *et al.*, 2011; Green *et al.*, 2012), and these patterns have definite implications. Insertions close to genes may potentially involve TEs in transcriptional regulation, thereby shaping and specializing the landscape of gene regulation. In vertebrate evolution, for example, mobile DNA has contributed at least 5.5% of highly conserved mammalian-specific nonexonic sequences involved in the regulation of gene expression (Lowe *et al.*, 2007). The insertion of TEs directly into coding sequences may simply disrupt the functioning of the gene. Most likely, this process represents a mechanism of formation of pseudogenes (Pavliček *et al.*, 2002). In addition to the disruption of the gene, the insertion of TEs into a functional copy of a gene can cause exon skipping, alternative splicing or transcription alteration (Bernstein *et al.*, 1995;

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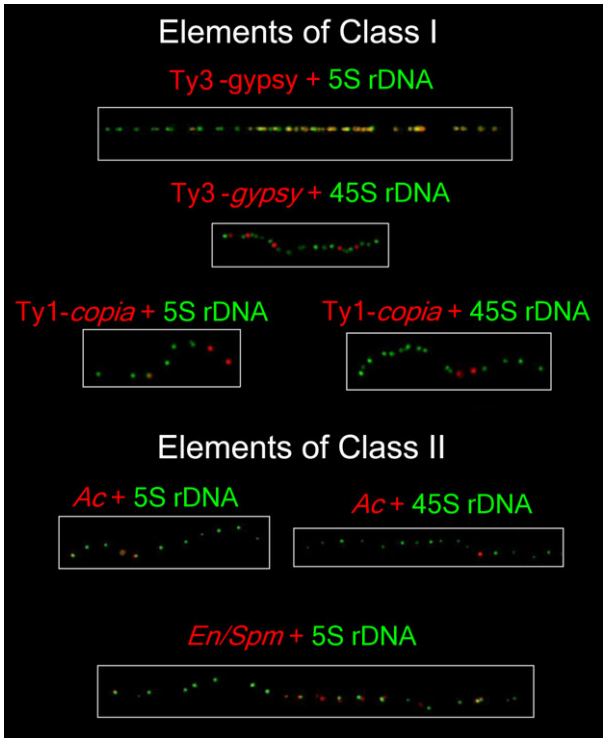


Fig. 1 Example of transposable elements insertions in the ribosomal gene regions. In situ hybridization (FISH) on the DNA fibres of *Aegilops speltoides and Triticum dicoccoides*. Class I and Class II transposable elements (red) and 5S and 45S rDNA probes (green) (Raskina *et al.*, 2008).

Stewart *et al.*, 1997; Musova *et al.*, 2006; Gray *et al.*, 2012). For example, 25% of human promoter regions contain TE-derived sequences, including experimentally verified *cis*-regulatory elements (reviewed in Jordan *et al.*, 2003; Biémont & Vieira, 2006); cryptic TEs might contribute to the regulatory regions of many genes. The insertion of transposed elements into introns can also lead to their activation as alternatively spliced cassette exons, an event termed exonization (Sela *et al.*, 2010; Schmitz & Brosius, 2011; Stower, 2013). The formation of new genes and genetic regulatory networks from TEs (domestication) such, for example, as HERV-W that seems to be intimately involved in diversification of placental mammals through its role in syncytiotrophoblast formation (Mi *et al.*, 2000) has also been documented (Jordan *et al.*, 2003; Jurka *et al.*, 2007).

Another consequence of the activation of TEs is TE-induced epigenetic alterations (depend on organism). DNA methylation is required for the epigenetic silencing of TEs, but environmental changes can lead to physiological, and therefore, epigenetic stress, which disrupts the tight control of TEs. The resulting TE mobilization drives genomic restructuring that may sometimes provide the host with an innovative genetic escape route (Slotkin & Martienssen, 2007; Martienssen, 2008; Rebollo *et al.*, 2010). Epigenetic regulation is known to be a widespread way of achieving a balance between TE multiplication and minimal damage to the host, quieting transposition on one hand, yet reversible on the other (Weil & Martienssen, 2008).

In 1946, Barbara McClintock suggested that TEs could cause chromosomal breakages. Subsequent findings suggested that TEs could promote chromosomal aberrations such as translocations, inversions, deletions, duplications and the formation of fragments (Danilevskaya *et al.*, 1994; Kunze *et al.*, 1997; Bennetzen, 2000a, b; Gray, 2000; Kidwell & Holyoake, 2001) (Fig. 2). Natural populations are known to be enriched with chromosomal rearrangements that generally occur in the heterozygous state (White, 1978; Rieseberg, 2001; Levin, 2002). The effect of chromosomal rearrangements is the suppression of recombination within rearranged regions (inversions), the disruption of existing linkage groups and the creation of new ones (translocations), which may produce changes in gene expression and in the interactions between genes (Rieseberg, 2001; Strasburg *et al.*, 2009; Brown & O'Neill, 2010). Certain chromosomal aberrations may become fixed in the population by positive selection if they are associated with the emergence of an adaptive combination of traits, especially in a changing environment (Kirkpatrick & Barton, 1997, 2006; Hoffmann *et al.*, 2004; Coghlan *et al.*, 2005; Orr, 2006; Rieseberg & Willis, 2007; Charlesworth, 2009).

Based on all of these strands of evidence, it is apparent that mobilized TEs can restructure the genome, providing an escape from stasis and generating genetic innovations required for rapid diversification (Oliver & Greene, 2009; Zeh *et al.*, 2009). This observation, in

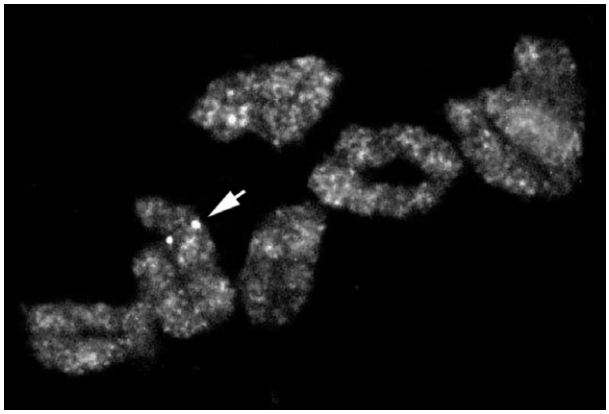


Fig. 2 Example of the presence of large transposable elements clusters in the regions of major chromosomal rearrangements. Clusters of *En/Spm* elements in the regions of translocation are shown by arrow (Raskina *et al.*, 2004a).

turn, raises the question of the level of TE activity in natural populations under abiotic stress and the tempo of population transformation.

Genomic explosion events

It follows from the above considerations that single insertions of TEs can definitely induce genomic and phenotypic variations (Matsubara *et al.*, 2005; Akagi *et al.*, 2013); however, a massive outbreak – bursts of TEs when rapid multiplication of one or several TEs occurs – provokes radical genomic rebuilding. This phenomenon is usually associated with the genesis of new phylogenetic groups. For example, a mass insertion of SINE elements occurred during the formation of the Primates at the boundary of the Mesozoic and the Cenozoic (Pace & Feschotte, 2007). A total of 74 000 to 93 500 insertions occurred during this period. The early radiation of the *Vespertilionidae*, the most species-rich bat family, also coincides with a burst in activity of TEs, particularly with the Helitron element (Pritham & Feschotte, 2007). In addition, a major episode of diversification in *Myotis*, the most species-rich mammalian genus, corresponds to a period of intense activity of Tc1-like elements 12–13 Mya (Ray *et al.*, 2008). In fish, many bursts of TEs are potentially associated with speciation (Volff *et al.*, 2000, 2001; De Boer *et al.*, 2007). Thus, bursts of TEs have been connected with significant events in evolution. However, whether this genomic explosion is a relatively rare event resulting from major natural disasters or a congenital response mechanism of the genome to a rapid change in different external factors remains to be determined. The speed for the old amplifications also cannot be evaluated: any amplification that happened 1 Myr ago will be considered as burst, even if real transposition rate was low and the process took thousands of generations because dating of the TEs' insertions is rather approximate. In such conditions, it seems very difficult to distinguish a signal in co-occurrences of speciation/TEs' bursts.

In the past few years, several research groups have discovered recent stress-induced bursts of TEs belonging to different families (Naito *et al.*, 2006, 2009; De Boer *et al.*, 2007; Tsukahara *et al.*, 2009; Belyayev *et al.*, 2010). For example, the DNA transposon mPing has increased its copy number by 40 per plant per generation during recent rice domestication (Naito *et al.*, 2006). Insertions have been detected in 59 flanking sequences of genes generating new regulatory networks (Naito *et al.*, 2009). *Ty3/gypsy*-like LTR retrotransposons independently experienced massive proliferation in three ancient hybrid sunflower species following their origins (Ungerer *et al.*, 2009). In *Arabidopsis thaliana* self-pollinated ddm1 mutant lines, an increase in the copy number of gypsy and copia retrotransposon families and an increase in the copy number of a Mutator family DNA transposon have been detected (Tsukahara *et al.*, 2009). Bursts of various TEs have also been detected in several genotypes from a small marginal population of *Aegilops speltoides*, a wild relative of cultivated wheat (Belyayev *et al.*, 2010). Among the processes that may cause bursts of TEs are domestication (Naito *et al.*, 2006), polyploidy (De Boer *et al.*, 2007; Kraitshtein *et al.*, 2010; Kenan-Eichler *et al.*, 2011), interspecific and intergeneric hybridization (Ungerer *et al.*, 2009; Kenan-Eichler *et al.*, 2011), changes in mating systems (Belyayev *et al.*, 2010; Boutin *et al.*, 2012) and changes in the external environment (Belyayev *et al.*, 2010). These examples point out that the TEs' bursts could occur not as a gradual process but in several cases happen suddenly, leading to rapid changes in the genome. In natural populations under the influence of an unusual ecology, bursts of TEs are of special interest because this phenomenon may underlie micro- and macro-evolutionary events leading, ultimately, to the maintenance and generation of biological diversity, but is there a causal link between TEs and speciation involving adaptation?

It is generally accepted that genomes respond to variations in environmental conditions and that the large-scale features of plant systems (such as yield and sustainability) depend on interactions between individual organisms and environmental factors (Yin & Struik, 2007; Martienssen, 2008). It has been shown that TEs are sensitive to prominent changes in the external environment (McClintock, 1984; Wessler, 1996; Kashkush *et al.*, 2003; Grandbastien *et al.*, 2005; Ansari *et al.*, 2007; Martienssen, 2008; Laudencia-Chingcuanco & Fowler, 2012). The environment can have a decisive influence on the structure of the genome, changing it in a certain direction that could be heritable (Martienssen, 2008).

Recently, we published the data from our long-term study of the dynamics of TEs in natural populations of *Ae. speltoides* (Belyayev *et al.*, 2010; Hosid *et al.*, 2012). The results of the study showed that the TE fraction has undergone major changes in the genomes of plants from marginal populations. After the transition of the majority of plants to self-pollination, considered a powerful defence mechanism under critical external conditions (Darwin, 1859; Lewis, 1953; Stebbins, 1970; Moeller & Geber, 2005), several investigated TEs from the various families varied substantially in copy number between individuals from the same population and selfed progenies. The fluctuations in TE copy numbers were genotype and TE family specific. The latter observation is consistent with data from other research groups (Brookfield & Badge, 1997; Tsukahara *et al.*, 2009; Jurka *et al.*, 2011; Boutin *et al.*, 2012; Laudencia-Chingcuanco & Fowler, 2012; Lu *et al.*, 2012). The data on temporal dynamics showed that TE copy numbers have decreased and increased significantly in an oscillatory fashion, with an increase in one generation followed by a decrease in the next and vice versa. These

oscillations displayed much higher amplitudes in reproductive tissue (Belyayev *et al.*, 2010).

Modelling of the temporal dynamics of TE copy number showed that in gametophytes, the actual number of retroelements detected in the progeny of a single genotype requires the presence of mechanisms in addition to simple chromosomal inheritance. Therefore, at least part of the observed variation in TE abundance can be explained by TE activation and subsequent insertion of new copies and by the specific loss of integrated TEs. Inter-retrotransposon amplified polymorphism (IRAP) data and cloning of novel unique IRAP bands that appear in the S1–S3 generations support the proposal that a small percentage of TEs that increase in copy number are transpositionally active and can actually be inserted at novel locations, serving as a bona fide mutagen (Belyayev *et al.*, 2010). We have observed chromosomal abnormalities and changes in plant morphology in parallel with TE bursts (Fig. 3). The latter observation is particularly important when considering that it was shown how morphological changes in plants may be caused by TEs insertions (reviewed in Lisch, 2013). Thus, we hypothesize that TE activation could promote or intensify morphological and karyotypical changes, some of which may be potentially important for the process of microevolution, and allow species with plastic genomes to survive as new forms or even as species in times of rapid climatic change. The phenomenon mirrors Barbara McClintock's (1984) view of TEs as an evolutionary driving force.

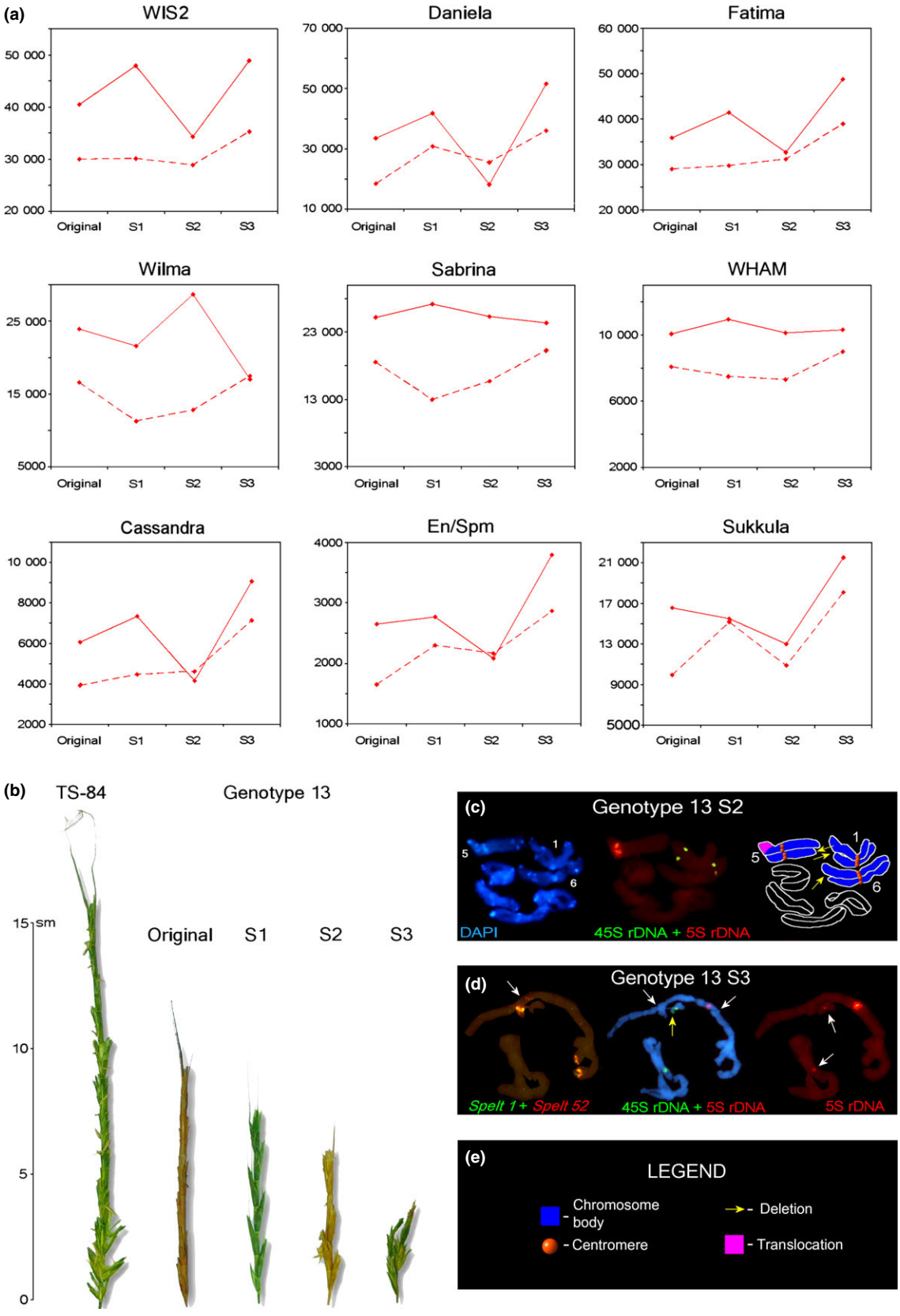
Nursery for biodiversity

Theory predicts that it is difficult for a novel genetic variant to become fixed except in small, inbred populations (Husband, 2004). Thus, the above-mentioned bursts of TEs in small marginal populations may have significant implications. Small marginal populations are expected to exhibit lower genetic diversity and higher genetic differentiation than central populations, and small population sizes might have played a major role in the fixation of nonadaptive DNA in eukaryotes, including TEs (Charlesworth & Charlesworth, 1983; Lynch & Conery, 2003; Husband, 2004; Jurka *et al.*, 2007, 2011). Indeed, our IRAP data on the intraspecific variability of LTR retrotransposons in *Ae. speltoides* show that various genotypes from the 13 populations studied differ significantly with respect to the patterns of the four explored LTR retrotransposons (*WIS2, Wilma, Daniela* and *Fatima*) (Hosid *et al.*, 2012).

This diversity indicates a constant ongoing process of LTR retrotransposon fraction restructuring in populations of *Ae. speltoides* throughout the species' range and within single populations in time. The maximum changes were recorded in genotypes from small stressed populations. The most striking example is presented by the *Fatima* element. The similarity of IRAP patterns in several closely related species indicates the stability of the *Fatima* retrotransposon over time. This stability may result from complete silencing of the element for a long period and/or from the relatively short LTRs of *Fatima*, that is a poor template for recombination. Violations of this pattern may indicate the movement of the retrotransposon in the genome. This movement may be a movement of the element itself by a copy-and-paste mechanism, indicating the activity of *Fatima* elements in certain genotypes, and/or the rebuilding of blocks enriched with *Fatima* retrotransposons. In any case, this movement can be regarded as a significant microevolutionary event in the genome, especially if inherited. Obviously, 96% of the genotypes with the unusual *Fatima* IRAP-pattern are from stressed, critically endangered micropopulations. The passive accumulation of TE insertions may be facilitated by small population sizes (Flowers & Purugganan, 2008). Moreover, population size reduction will increase the probability of fixation of deleterious mutations (Ohta, 2002), leading to genomic diversification via the accumulation of molecular changes (Lynch & Conery, 2003) and changes in TE copy numbers (Brookfield & Badge, 1997).

In addition to the major alterations in the landscape of TE fractions, it has been assumed that the fixation of

Fig. 3 Example of TEs stress-induced burst of TEs in individual genotypes from a small, marginal population of *Aegilops speltoides*. In the experiments, the progeny from each genotype were obtained in three rounds of selfing. Thus, we simulated the situation in nature where, in marginal populations under critical external conditions, outcrossing plants very often transit to self-pollination. (a) Significant temporal fluctuation in the copy number of TEs was observed. Solid line denotes the fluctuations in the TE copy number in generative tissues. The dotted line represents the fluctuations in the TE copy number in vegetative tissues. It is therefore tempting to hypothesize that the TE activation we observed may be a primary or secondary effect of the mating system change, although substantiating evidence is still lacking. (b) Changes in spike morphology in three self-pollinated generations of genotype 13 from the marginal population of *Ae. speltoides*. Normal spike morphology of plants from the area distribution centre is shown on the left. (c, d) In situ hybridization (FISH) and differential staining with DAPI on somatic and meiotic chromosomes of *Ae. speltoides* displaying the major chromosomal rearrangements in the selfed progenies. (c) The meiotic chromosomes in diakinesis stage. A scheme of the main chromosomal rearrangements is on the right (see LEGEND). (d) Paracentric inversion in the long arm of the chromosome 5 marked by a small cluster of tribe-specific tandem repeat *Spelt 52* is shown with an arrow. Two points of heterologous synapses involving both short and long arms of chromosome 5 are shown by two white arrows; heterozygous deletion of the satellite of chromosome 6 is shown by the yellow arrow. On the right: additional 5S rDNA clusters on chromosomes 1 and 6 in the NOR regions (arrowed). (e) Legend for (c) (for details, see Belyayev *et al.*, 2010).


(a)
WIS2
Daniela
Fatima
Wilma
Sabrina
WHAM
Cassandra
En/Spm
Sukkula
Original
S1
S2
S3
(b)
TS-84
Genotype 13
15 sm
10
5
0
Original
S1
S2
S3
(c)
Genotype 13 S2
DAPI
45S rDNA + 5S rDNA
(d)
Genotype 13 S3
Spelt 1 + Spelt 52
45S rDNA + 5S rDNA
5S rDNA
(e)
LEGEND
Chromosome body
Centromere
Deletion
Translocation

individual TE families may occur in small marginal populations (Jurka *et al.*, 2011). This process has been proposed to be linked to bursts of TEs (Jurka *et al.*, 2011; Lu *et al.*, 2012). For example, pairwise nucleotide diversity and phylogenetic tree analysis have indicated that individual MITE families resulted from one or multiple rounds of amplification bursts (Lu *et al.*, 2012). Most eukaryotic populations include individuals who carry a variety of active TEs that are not fully suppressed by the silencing mechanisms (Belyayev *et al.*, 2010; Jurka *et al.*, 2011). Most likely, active TEs that survive the silencing are outliers in terms of their structure or sequence divergence, and a small population can 'incubate' multiple repetitive families (Jurka *et al.*, 2007, 2011). The number of TEs fixed in small populations is determined primarily by the rate of transposition and the time during which the elements were active, and it has been noted that only a few TEs can reach such bursts of activity (Tsukahara *et al.*, 2009; Jurka *et al.*, 2011).

Facing consequences

The possible consequences of TE bursts are an additional important topic. In small marginal populations under the influence of stress factors, bursts of TEs are apparently rather frequent but occur asynchronously in different genotypes of the population (Tsukahara *et al.*, 2009; Belyayev *et al.*, 2010). It has also been noted that only a few TEs can reach bursts of activity, whereas the majority of the elements remain silent (Volff *et al.*, 2000, 2001; De Boer *et al.*, 2007; Jurka *et al.*, 2007; Pace & Feschotte, 2007; Pritham & Feschotte, 2007; Ray *et al.*, 2008). Nevertheless, bursts of even single or several TEs may cause significant genomic rebuilding, including the rebuilding of regulatory systems, proposed to represent major evolutionary events (King & Wilson, 1975; Jurka *et al.*, 2007). However, even in the case of stress-induced transposition, bursts of transposition have never been associated with demonstrated adaptive effects. On the contrary, deleterious effects have been already clearly identified (in hybrid dysgenesis, for example). There is evidence of burst associated with evolutionary transitions, but without any demonstration of a role of such burst in the transition. This is important to consider, because within a burst, the number of insertions with negative effect is expected to be much higher than the number of rare beneficial insertions.

Any insertion of TEs may reflect propagation without fixation. For a new insertion to be heritable, it must occur clonally in a cell, giving rise to a germ cell. Even if a new TE insertion arises in a germ cell, that cell may not produce viable embryos. Nevertheless, it has been repeatedly shown that certain insertions can be heritable (Liu *et al.*, 2004), and this principle is supported by our data on the inheritance of the novel unique IRAP bands (Belyayev *et al.*, 2010) (Fig. 4). Moreover, it has repeatedly been shown that TE activity alters the epigenetic landscape (Martienssen, 2008; Weil & Martienssen, 2008; Michalak, 2009) and that epigenetic status can also be inherited (Morgan *et al.*, 1999; Henderson & Jacobsen, 2000; Rakyan *et al.*, 2002; Lippman *et al.*, 2003; Wallace & Orr-Weaver, 2005; Slotkin & Martienssen, 2007). Environmental stimuli might affect the siRNA population in accessory cells and establish the epigenetic state of the progeny, creating a transgenerational 'memory' of the environment to which the parents were exposed (Molinier *et al.*, 2006; Chinnusamy & Zhu, 2009). Thus, the effects of TE bursts influence subsequent generations, resulting in mutations, alterations of the epigenetic landscape, and quantitative and qualitative changes in the TE fraction.

These changes in the TE fraction can be explained by the occurrence of purifying selection as a response to an increase in TE copy numbers (Charlesworth *et al.*, 1994; Nuzhdin, 1999; Le Rouzic *et al.*, 2007; Lowe *et al.*, 2007; Jurka *et al.*, 2011). Enhanced amounts of TEs successfully enhance ectopic recombination, which has been proposed as the principal driving force behind decreases in genomic size (Langley *et al.*, 1988; Capy *et al.*, 1997; Devos *et al.*, 2002). It has been proposed that after a first-invasion stage, the appearance of new copies is roughly balanced by the losses, and TE families could be maintained in the long term through transposition-selection equilibrium (Charlesworth *et al.*, 1994; Shirasu *et al.*, 2000; Le Rouzic & Deceliere, 2005; Le Rouzic *et al.*, 2007). This pattern was observed in our experiments on stress-induced temporal changes in the TE fraction. After the burst, the TE copy numbers decrease in the next generation (Belyayev *et al.*, 2010). Several cycles of burst purification have been observed

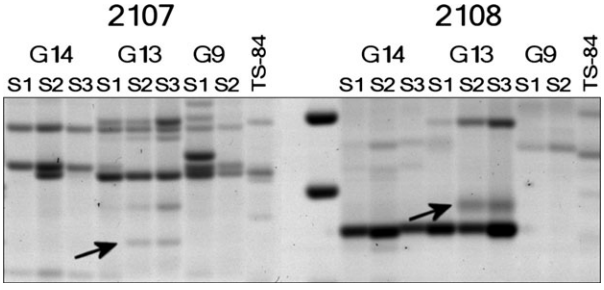


Fig. 4 Example of possible transposable element (TE) transposition. Inter-retrotransposon amplified polymorphism fingerprinting revealed unique bands for *Wilma* retrotransposon that appear in S2 and are inherited in S3 generation (shown by arrows) in the selfed progenies of genotype from a small, marginal population. The appearance of unique novel bands is consistent with TE activation, and it is possible to propose that a small percentage of TEs that increase in copy number can actually insert at novel locations (Belyayev *et al.*, 2010).

in successive generations after a single impact of a stress factor (in our experiments, a change in the mating system) faded over time (Liu & Wendel, 2000). However, bursts of TEs could occur permanently in natural, small marginal populations under constant stress impact.

Burst-purification cycles equilibrate TE copy numbers by 'cleaning' a certain number of TE copies from the genome (for review see Le Rouzic & Deceliere, 2005). Apparently, ectopic recombination encompasses not only a TE fraction but also the entire amount of highly repetitive DNA. The majority of the TEs are located in heterochromatin (Heslop-Harrison *et al.*, 1997; Belyayev *et al.*, 2001; Saunders & Houben, 2001), and closely located sequences of other types could also be eliminated. The phenomenon of the depletion of species-specific tandem repeats in marginal populations discovered by us is most likely a result of burst-purification cycles (Raskina *et al.*, 2011). In the analysed marginal populations of *Ae. speltoides*, the number of species-specific *Spelt 1* chromosomal blocks can be 12–14 times lower than that in the centre of the species distribution (Fig. 5). Evidently, a stable equilibrium of copy number is not observed, and there is constant depletion of various elements of the repetitive DNA fraction, primarily in heterochromatic regions. This assumption is supported by data that the recent burst of retrotransposition in natural population is targeted to centromeric repeats and heterochromatin (Tsukahara *et al.*, 2009). Thus, genome is de-heterochromatinized (juvenilized, if you will, as genome of old stabilized species usually possesses high content of heterochromatin) and a depleted population-specific chromosomal pattern is formed, which may cause the formation of reproductive isolation between populations by altering chromosome segregation (Ferree & Barbash, 2009; Ferree & Prasad, 2012). At the same time, it becomes a possible conjugation of homeologous chromosomes if the hybridization event between individuals from the marginal colocated populations of the related species occurs, thus providing a case of hybrid speciation (Wendel & Doyle, 1998; Rieseberg *et al.*, 2003; Linder & Rieseberg, 2004) (Fig. 6).

The 'stress-induced' hypothesis states that environmental disruption by some means caused direct activation of TEs (McClintock, 1984). Experimental evidences for this phenomenon are growing (Maumus *et al.*, 2009; Castrillo *et al.*, 2013). Alternatively, 'selectionist' hypothesis argues that organisms with initial increased TEs activity are selected when species is under intensive

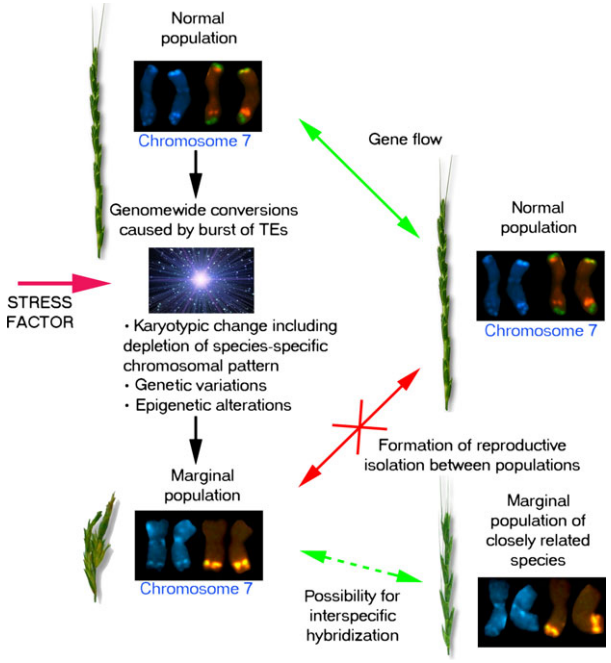


Fig. 6 Scheme of the proposed scenario for events driving to rapid speciation.

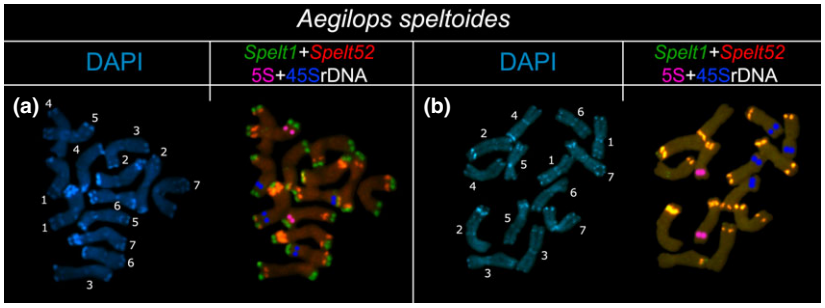


Fig. 5 Example of the formation of depleted population-specific chromosomal pattern in small marginal population. Fluorescence in situ hybridization (FISH) and differential staining with DAPI on somatic chromosomes of *Aegilops speltoides*. (a) Central population; (b) marginal population. Decay of almost all terminal *Spelt 1* blocks in marginal population was observed. The DNA probes: species-specific tandem repeat *Spelt 1* in green, tribe-specific tandem repeat *Spelt 52* in red, 5S rDNA in pink pseudocolor and 45S rDNA in blue pseudocolor (Raskina *et al.*, 2011).

selective pressure (Schaack *et al.*, 2010). Thus, two possible mechanisms can account for the TE-related transformations of the genome. In any case, the presence of multiple-mutant genotypes in the population leads to rapid genetic drift (Jurka *et al.*, 2007, 2011). As a result, the small marginal population develops a unique structure. With constant exposure to stress factors and, consequently, increased activity of TEs, the population can become extinct due to fitness loss and purifying selection against deleterious mutations. However, another outcome, although rare, is that an increase in the number of genomic variants exposed to natural selection (Grant, 1981; Raskina *et al.*, 2004b; Belyayev *et al.*, 2010) may allow a population with enhanced TE activity to escape from stasis (McFadden & Knowles, 1997; Zeh *et al.*, 2009) and to survive as a new form or even a new species during environmental fluctuations. Thus, genome explosion events in a small population can be regarded as a possible mechanism for punctuational change (Eldredge & Gould, 1997) that could produce rapid evolution. Unfortunately, the existence of such a possible mechanism does not answer the long-debated question of how frequently this model of evolutionary change occurs – is it the norm, or only an exception?

McClintock (1984) predicted the possible connection between speciation and the activity of TEs when species could originate due to sudden TE-induced chromosomal reorganizations followed by a complex genomic response. Gene rearrangements, particularly those leading to changes in regulatory regions, may account for the principal organismal differences (Jurka *et al.*, 2007). Multiple bursts of TEs in a small population that are caused by stressful abiotic factors and followed by enhanced ectopic exchanges provide an escape channel for the genome. Apparently, this mechanism represents a common response of organisms to climate fluctuations, which may happen quite rapidly. For example, the transition to the onset of the Younger Dryas cooling occurred in 1 year, according to subannual records of varve microfacies and geochemistry from Lake Meerfelder Maar in western Germany (Brauer *et al.*, 2008), and the abrupt termination of the Younger Dryas climate event, according to ice core records from Greenland, was completed in approximately 50 years, during which the average temperatures increased 7 °C (Dansgaard *et al.*, 1989; Steffensen *et al.*, 2008). Such rapid changes in the external environment force populations to choose between extinction and rapid transformation (Jurka *et al.*, 2007).

The scenario of events preceding speciation by different models in small marginal populations could be as follows: under the influence of unusual ecological conditions, TEs become active; the mobilization of TEs produces genetic variations, epigenetic alterations (an important source of phenotypic variability) and high rates of karyotypic change (including changes in species-specific chromosomal pattern). Some of these mutations could be heritable. As a result of these genomewide conversions, genetically based barriers to gene flow between populations (i.e. reproductive isolation) may form (Fig. 6).

During the formation of a species, new species-specific assortments of diverse repetitive families are formed (Jurka *et al.*, 2011), and species-specific sequences accumulate, creating a novel chromosomal pattern. It can be reasonably hypothesized that arrays of species-specific repeats may derive from the active TEs (from solo LTRs, for instance) because the replicative proliferation of a single, active TE copy generates a population of closely related sequences, with most copies sharing high genetic similarity within a genome (Casacuberta *et al.*, 1997).

Conclusions

Bursts of TE have been reported in connection with the formation of taxonomic groups and species. Accordingly, such bursts are associated with major evolutionary events. However, at the moment, there is a lack of evidence for a specific role of burst in the evolutionary transitions.

Recently discovered stress-induced bursts of TEs in natural populations suggest that these bursts may represent a habitual reaction of the genome to rapid changes in external environments.

Bursts of TEs provoke radical genomic rebuilding, and some of these changes may be hereditable. Burst-purification cycles under a constant environmental stress factor can lead to the emergence in a population of lineage-specific genotypes with differences in important aspects of genomic function, regulation and chromosome structure.

Transposable elements burst-purification cycles most probably affect colocated sequences that lead to constant depletion of various elements of the repetitive DNA fraction (primarily in heterochromatic regions). Thus, a depleted population-specific chromosomal pattern is formed, which may cause the formation of reproductive isolation between populations by altering chromosome segregation.

The presence of multiple-mutant genotypes in a small marginal population leads to rapid genetic drift. As a result, the population develops a unique structure. The ongoing production of an extended number of genomic variants as a substrate for natural selection may allow a population with enhanced TE activity to escape from stasis and to survive as a new form or even a new species during climate fluctuations.

Burst of TEs may have pleiotropic effects on the genome, and it is likely that unambiguous answer what sequence of events lead to reproductive isolation will not be found. In certain taxonomic groups under the influence of certain external conditions, it may be a specific combination of speciation driving forces.

Acknowledgments

The author is most grateful to reviewers for helpful comments. The research was partly supported by the long-term research development project no. RVO 67985939 from the Academy of Sciences of the Czech Republic.

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Received 4 July 2014; revised 17 September 2014; accepted 17 September 2014