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Transposable elements in vertebrates: species evolution and environmental adaptation

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Abstract

The evolutionary success of species is strictly related to their genome in terms of composition and functionality. Transposable elements (TEs) represent a considerable fraction of the nuclear DNA content, and given to their ability to spread throughout the genome, they are able to create genetic diversity at sequence, gene structure, and chromosome level. Vertebrates represent a highly successful taxon and its lineages are characterized by a variable TE content suggesting a different impact on the genome. In this manuscript, we highlight the importance of TEs in creating new regulatory sequences and genetic innovations extremely useful for diversification of vertebrates. Moreover, an increasing number of evidence suggests a link between TEs and environment. Indeed, given the richness of species adapted to a wide range of habitats and conditions, vertebrates are exposed to several ecological pressures with consequent effects on evolutionary adaptation.

Keywords: *Transposable elements, vertebrate, evolution, environment*

Introduction

The evolutionary success of species is strictly related to their genome in terms of composition and functionality. The coding gene component represents a small fraction of the nuclear DNA content that on the contrary is mostly composed of repetitive DNA and in particular of transposable elements (TEs) (Box 1). These mobile elements are considered as the main drivers of genome shaping given their ability to spread throughout the genome, to generate new coding genes or regulatory elements, to contribute to genome size, and to influence chromosomal rearrangements (López-Flores & Garrido-Ramos 2012; Canapa et al. 2015; Sotero-Caio et al. 2017; Biscotti et al. 2019).

Vertebrates present a very high diversity of species that colonized numerous habitats, from water to land, from temperate to extreme environments. Analysing the genome of these organisms emerges that the TE content varies among vertebrate lineages suggesting a different impact on their genomes (Figure 1). If in many cases the activity of TEs can lead to evolutionary

advantages for host in others can be deleterious in particular into germline cells in which changes are transmitted to progeny. Thus, several mechanisms for silencing TEs such as DNA methylation or RNA interfering by piRNA were adopted by organisms (Deniz et al. 2019). However, during evolution and/or in particular environmental conditions, these mechanisms might not be efficient and consequently burst of TEs can occur creating a deep genome reshaping and speeding up genetic variability (Casacuberta & González 2013; Stapley et al. 2015). These observations open up a series of questions about how the environment influence TEs, acting on their activity or on their sequence selecting specific variants that spread and are fixed into a population. An increasing number of reports evidences a correlation between TE and environment trying to get more insights on which factors and mechanisms are involved. This manuscript aims to highlight the importance of TEs in the evolution of vertebrate genome, adapted to a wide range of ecological conditions, focusing on the recent findings linking TEs and environment.

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Box 1. Transposable elements classification based on their mechanism of transposition.

Transposable elements (TEs) are sequences repeated hundreds of times in the genome and able to insert themselves into a novel genomic position represents the so-called repetitive fraction of DNA. They are the major accountable in provoking sensible variations in genome size (Garrido-Ramos 2017). Up to date, an accepted classification of TEs can be given considering their mechanism of transposition. Thus, two main classes can be distinguished: Class I retroelements characterized by the *copy* and *paste* mechanism of transposition; Class II DNA transposons characterized by the *cut* and *paste* mechanism of transposition, exception made for *Helitron* and *Maverick/Polinton*.

Class I elements use a RNA intermediate, reverse transcribed into its complementary DNA. Long Terminal Repeat (LTR) and non-LTR (non-LTR) retrotransposons are the major representative of Class I elements. The ability of LTR retrotransposons to transcribe themselves and consequently insert into the host genome, is conferred by the presence of direct flanking sequences (250–600 bp length on average) and some indispensable genes such as for reverse transcriptase, RNase H, and integrase. After the synthesis of cDNA mediated by reverse transcriptase, the integrase inserts the cDNA into a new position of the genome. Unlike retroviruses, LTR are not able to move between cells and to infect them (Malik et al. 2000; Ribet et al. 2008). The sub-classification of LTR retrotransposons includes three main TE superfamilies in vertebrates: *Ty1/Copia* (Pseudoviridae), *Ty3-gypsy-like* (Metaviridae) and *BEL/Pao* (Chalopin et al. 2015).

Non-LTR retroelements are mainly represented by Long Interspersed Nuclear Elements (LINEs) and Short Interspersed Nuclear Elements (SINEs). LINEs can be defined as autonomous retrotransposons thanks to the presence of one or two open reading frames (ORFs) that encode for a reverse transcriptase and an endonuclease protein (Wicker et al. 2007), while SINEs need reverse transcriptase encoded by autonomous elements to be transposed (Kramerov & Vassetzky 2011).

Differently from retroelements, DNA transposons are able to transpose themselves without any RNA intermediates (Bourque et al. 2018; Goerner-Potvin & Bourque 2018). Each element grouped in Class II follows a different strategy to move their genomic DNA copies. On one hand, *Crypton* and *Terminal Inverted Repeats (TIR)* DNA strands are cleaved and transposed following the canonical *cut* and *paste* mechanism while both *Helitron* and *Maverick/Polinton* use the *copy* and *paste* mechanism. Finally MITEs, also grouped in Class II, do not encode for a transposase and therefore they exploit transposase encoded by autonomous elements to move throughout the genome (Feschotte et al. 2003).

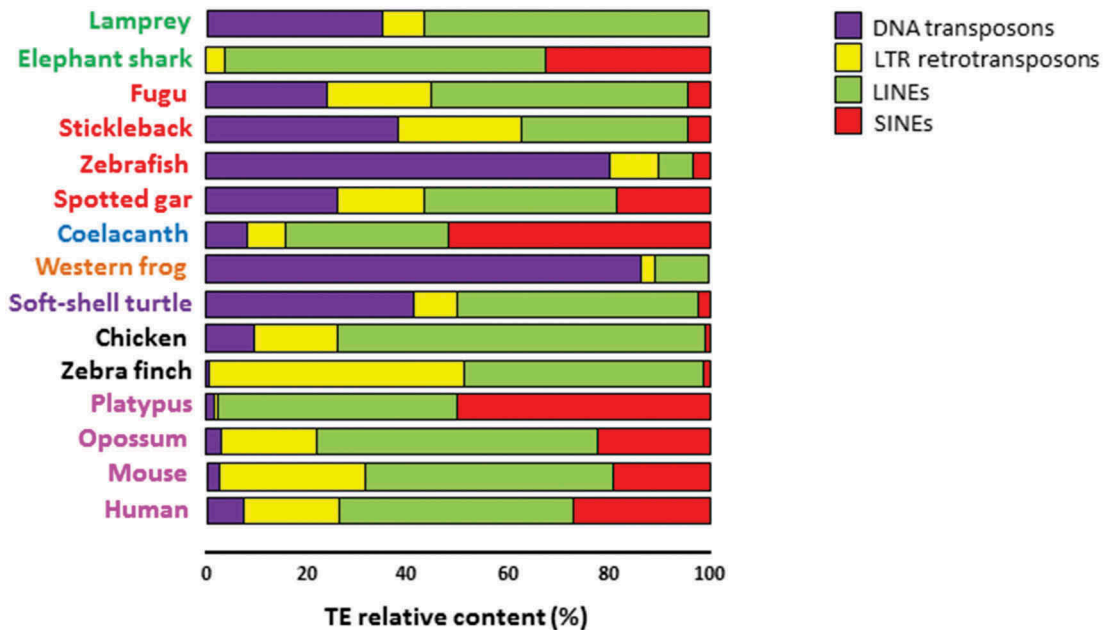
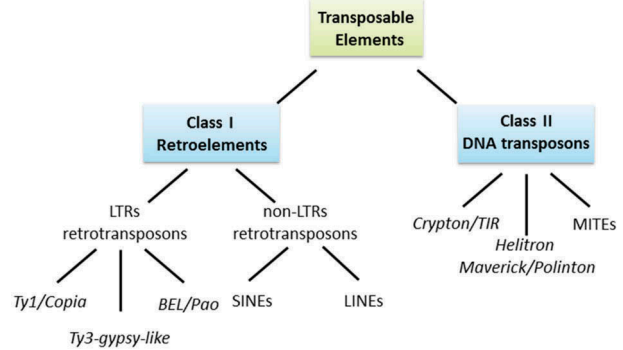


Figure 1. Transposable element relative content in vertebrates. Common names have been coloured based on vertebrate classification: nonbony vertebrates are reported in green, actinopterygians in red, lobe-finned fish in blue, amphibian in orange, nonbird reptile in purple, birds in black, and mammals in pink. Modified from Chalopin et al. (2015).

Transposons as drivers of evolution

The evolutionary success of vertebrates lies in the functional and structural complexity of their genomes. One of the components of major interest is represented by transposable elements (TEs). The advent of genome sequencing allowed to evidence that transposon content varies considerably between lineages: birds and some fish as *Tetraodon* present low amounts of TEs while in mammal, non-bird reptile, shark, lamprey, and some fish genomes mobile elements are widely represented. Moreover, all types of TEs are present in vertebrate genomes, but TE diversity, copy number, and age differ between vertebrate lineages in relation to various factors as rate of transposition, rate of DNA elimination, horizontal transfer, and host defence mechanisms (Biscotti et al. 2019). These observations suggest that the impact of TEs on genome evolution might be different in vertebrate lineages. TEs are considered the major drivers of genomic and biological diversity and thus of speciation and evolution. Indeed, the activity of transposons has been found to be responsible for genome expansion and chromosomal rearrangements (Rebollo et al. 2010; Zhang et al. 2011; Auvinet et al. 2018), but also to generate, through co-optation and exaptation, regulatory sequences, coding exons, or entirely new genes that represented evolutionary advantages for the host (Sundaram et al. 2014; Chalopin et al. 2015; Warren et al. 2015; Sotero-Caio et al. 2017).

Bursts of TEs have accompanied the genesis of new phylogenetic groups. For example, the origin of primates between Mesozoic and Cenozoic occurred in parallel with a massive insertion of SINE elements (Pace & Feschotte 2007), while an increase of *Helitron* activity was associated with the radiation of the Vespertilionidae, a bat family (Pritham & Feschotte 2007). Similarly, about 12–13 Mya, a burst of activity of *Tc1*-like elements determined an explosion of species in the mammalian genus, *Myotis* (Ray et al. 2008).

The evolution of vertebrates has been characterized by significant transitions and severe ecosystem changes that have led to species extinction or radiation. The colonization of new environments has been possible thanks to changes in the genomes that allowed organisms to adapt to new conditions. One of the most important step in the vertebrate history was the transition from water to land. In lungfish and salamanders, this event was accompanied by a high proliferation of TEs leading to organisms with giant genomes (Metcalf et al. 2012; Sun et al. 2012; Canapa et al. 2015; Biscotti et al. 2016).

The activity of TEs may also affect chromosomal diversity and thus karyotype (Kehrer-Sawatzki & Cooper 2007; Raskina et al. 2008; Kraaijeveld 2010). This aspect is extremely interesting since chromosomal rearrangements may drive lineage-specific diversification (Biscotti et al. 2015a, 2015b; Warren et al. 2015). Recently Auvinet et al. (2018) have reported the location of *DIRS1* (*DI*ctyostelium *R*epetitive *S*equence 1) in “hot spots” of insertion along chromosomes. This event likely facilitated non-homologous recombinations responsible for the high chromosomal diversity observed in the Antarctic teleost genus *Trematomus*. Overall an extensive review published by our group underlined the key role of *Rex* retroelements in the differentiation of sex chromosomes, in the formation of supernumerary chromosomes, and in the evolution of karyotype in this extremely diversified taxon (Carducci et al. 2018).

During the evolutionary history, TEs can be co-opted to influence the expression of the nearby genes or to give rise to new protein-coding genes. In mammals, the expression of placenta-specific genes is altered by TE-derived regulatory sequences (Chuong et al. 2013). Moreover, in these organisms, Franchini et al. (2011) reported a paleogenomic study in which the expression of the proopiomelanocortin gene (*POMC*) is regulated by two enhancers derived by the independent exaptation of two unrelated TE retrotransposons. Due to the key role of this gene in food intake, the acquisition of two overlapping enhancers could have increased the ability in mammals to avoid foraging behavior during risky environmental conditions (e.g. escaping from predators). Instead, a LF-SINE (Lobe-Finned fish or Living Fossil SINE) isolated in the Indonesian coelacanth *Latimeria menadoensis* was co-opted to generate the enhancer responsible for the expression of the neurodevelopmental gene *ISL LIM homeobox 1* (*ISL1*) encoding a transcription factor required for motor neurone differentiation in the common ancestor of tetrapods (Bejerano et al. 2006).

Alu elements are the most abundant repetitive elements in human genome and it has been reported the insertion of these transposons within mature mRNAs. Sela et al. (2010) have evidenced that exonization events of *Alu* elements occur preferentially near the 5' end of protein-coding sequences. Moreover, TE-derived exons are prone to accumulate single nucleotide polymorphisms (SNPs) that in turn can provoke divergence and thus leading to speciation. Also, LTR retrotransposons, and in particular their flanking regions, have been found in exons contributing significantly to human proteome (Piriyapongsa et al. 2007).

The LAP2alpha domain present in *TMPO* and *ZNF451* genes derives from a *DIRS1*-like transposon. Although these two genes are present in all vertebrate lineages, the isoforms containing the LAP2alpha domain are exclusive to mammals for *TMPO* and to eutherians for *ZNF451*. The purifying selection characterizing *TMPO* and *ZNF451* strongly supports the functional relevance in mammalian lineage (Abascal et al. 2015).

In jawed vertebrates, the wide repertoire of antibodies is guaranteed by the genes *RAG1* and *RAG2* encoding recombinase which catalyzes the V(D)J recombination. These two genes are derived from a *Transib* superfamily DNA transposon about 500 Mya and their onset has led to an important functional advantage for the adaptive immune system of gnathostomes (Kapitonov & Jurka 2005; Schatz & Swanson 2011).

Overall, given the contribution of TEs to coding regions and thus their ability to directly influence the proteome of a species and its phenotype, mobile elements are of particular interests. The effects of TE activity can be deleterious, neutral or even enhance fitness through the generation of genetic innovations extremely useful for rapid diversification, strongly contributing to the evolution process.

The relationship between TEs and environmental conditions

Since Barbara McClintock (1984) reported about the possible helpful role of mutations induced by the activation of TEs in response to stress, their definition as “selfish” has been progressively abandoned (Fedoroff 2012).

Environmental stressors represent a daily challenge for each living organism (Casacuberta & González 2013). Thus, an organism must adapt to survive to these continuously changing environmental conditions. Variations can occur such as in chemical and nutrients concentrations, in temperature, and humidity, provoking a consequent acceleration on evolutionary rates and increase in selective pressures. As a consequence, the onset of new genetic variants that increase in frequency in the population leads to advantages in terms of survival and reproduction (Chénais et al. 2012). As summarized in the review of Casacuberta and González (2013) TEs might play positive role conferring to organisms the ability to be responsive to the continuously changing environment since they are responsible for genetic diversification (Yuan et al. 2018). Recently an increasing number of studies reported a link between TE activity and their responsiveness to environmental conditions (Fujino

et al. 2011; Hua-Van et al. 2011; Makarevitch et al. 2015; Carducci et al. 2019).

Vertebrates represent a highly successful lineage and it is recognized that transposable elements fulfil a key role in the evolution of species belonging to this taxon (Warren et al. 2015; Sotero-Caio et al. 2017; Biscotti et al. 2019). Intriguingly, the wide range of habitats colonized by vertebrates suggests their exposure to several ecological pressures with consequent effects on evolutionary adaptation. The relationship between TEs and environmental conditions and the comprehension of involved mechanisms are representing an attractive challenge for the scientific community. Recently, besides to mixed mating strategy, a putative correlation between TE diversity and ecological pressure has been suggested to explain the high genetic diversity of *Kryptolebias marmoratus* (mangrove killifish) genome compared to other killifish species (Rhee et al. 2017).

An exhaustive work on 52 fish species suggests a positive correlation between abundance in repetitive elements and genome size and a preferential distribution of TE specific classes depending on their living environments: Class II transposons (see Box 1) in freshwater fish species, Class I retrotransposons (see Box 1) in primitive fishes (e.g. cartilaginous fishes and lampreys); on the contrary in marine bony fishes has been evidenced an abundance of satellite DNA, in particular of microsatellites (Yuan et al. 2018). Overall, these findings and more recent evidences strengthen the hypothesis of a correlation between TEs and environmental conditions. In particular, the presence of Class I retrotransposons in cartilaginous fishes and lampreys may be due to the internal fertilization. In this case, exposure of gametes and embryos to horizontal transfer of Class II transposons is minimized. On the other side, the prevalence of Class II transposable elements in freshwater species may be due to an environment more prone to the spreading of DNA transposons. Indeed, in freshwater environment stress events such as droughts and floods might accelerate transposition providing new genetic variants and thus an advantage to species. For the Antarctic teleost genus *Trematomus* (Notothenioidei: Nototheniidae) TE mobilization has been proposed as possible responsible for chromosomal diversification and consequent rapid speciation in this taxon. As mentioned in the previous paragraph Auvinet et al. (2018) performed an extensive phylogenetic and cytogenetic analyses evidencing a preferential accumulation of four families of *DIRS1* in pericentromeric and centromeric regions in species of this genus but not in outgroups. This difference was attributed to the multiple glacial-interglacial cycles that occurred in Antarctic continental shelf. According to the authors, the repetitive temperature changes determined a breakdown in

epigenetic regulation leading to TE bursts. Recently, a work published by our group (Carducci et al. 2019) evidenced an intriguing behavior of *Rex3* elements analysed in 39 teleost species. The performed phylogenetic analysis evidenced, independently from taxonomy relationships, an unexpected clusterization of *Rex3* retroelement isolated from species living in cold waters (Arctic and Antarctic regions and cold waters of temperate regions) compared with those isolated from species living in warm waters suggesting a selective role of temperature on a specific TE sequence variant.

Within vertebrates, *Anolis* lizards is a classic example of adaptive radiation. In particular, Feiner (2016) has reported a high number of TEs within *Hox* clusters due to a preferential insertion in open chromatin during early developmental stages. Given the involvement of *Hox* genes in determining phenotypic variations, the high number of mobile elements in this marker region contributed to the adaptive diversification in the extant *Anolis* lizards. Author suggested two possible explanations to justify the positive correlation observed between TE proliferation and the rapid speciation of lizards: TE activity can cause both phenotypic innovations and structural changes in the genome leading to reproductive isolation; TEs proliferate in species having small population size and weak natural selection. However, the latter is not suitable for lizards, characterized by larger population size, and Feiner speculated that environmental factors such as temperature and humidity might be the responsible for TE activity.

TEs have been proposed also to be involved in the rapid adaptation of invasive species to new environments. In this context mobile elements contribute to increase genetic diversity, allowing organisms to better adapt to new conditions (Stapley et al. 2015). The colonization of new habitats represents a stress condition that affects the epigenetic control of mobile elements adopted by host genome with consequent mobilization. The main mechanisms (Table I) involved in TE silencing both at transcriptional and post-transcriptional level were brilliantly reviewed by Deniz and colleagues in the early 2019: (i) *via* small-RNA, PIWI interacting RNAs (piRNA) (Molaro & Malik 2016), (ii) TE binding proteins that lead to

their silencing *via* repressive-chromatin formation; (iii) ATP-dependent chromatin remodellers and (iv) the use of 5-methylcytosine (5mC). The latter remains the most widespread mechanism used to silence mobile elements and strongly differs moving throughout the different evolutionary lineages (Lechner et al. 2013). The potential synergistic action between transposable elements and epigenetic components in speeding up genetic variability is always increasing agreement to be at the “heart of eukaryotic evolvability” (Fedoroff 2012; Rey et al. 2016).

To date, the world of transposable elements has been characterized by continuous changes in what was originally thought about this fascinating portion of DNA. The progressive abandon of TEs improper attributions as (i) “selfish” and (ii) deleterious, led to the inexorable increase in the availability of genomic and epigenomic data. Thanks to Next-Generation Sequencing and more sophisticated annotation workflows, more precise and complete maps of TEs and DNA modifications have been provided to the scientific community. This led to the uncovering of the relationships between DNA modifying factors, TE evolution, and their sensitivity to environmental stressors, endorsing the key role of mobile elements in rapid adaptation to global changes (Deniz et al. 2019).

Conclusions

Each living organism is continuously exposed to environmental changes and its ability to adapt resides within genome. Certainly, transposons are elective candidates since they are capable to generate genetic innovations extremely useful for rapid adaptability. Intriguingly, as highlighted in this manuscript, an increasing number of studies reports a link between TE and their responsiveness to environmental conditions whose changes induce the inactivation of TE silencing mechanisms leading to their mobilization. Therefore, mobile elements may generate genetic and/or chromosomal diversifications that represent a barrier to gene flow with consequent reproductive isolation and speciation. In other cases, TE activity may give rise to an increase in genetic

Table I. Main silencing mechanisms of transposable elements.

Small RNAs (piRNA)	TEs are degraded post transcriptionally into piRNAs
Krüppel-associated box Zinc Finger Protein (KRAB-ZFPs)	Transcriptionally inducing the deposition of epigenetic modifications
ATP-dependent chromatin remodellers	The interaction of TE and KRAB-ZFPs determines the recruitment of the KRAB-associated protein 1 (KAP1) which is involved in the formation of repressive chromatin
5-methyl cytosine (5mC)	Allow DNA methyl transferases (DNMTs) to confer repressive DNA and chromatin modifications
	Deposition of 5-methylcytosine for maintaining TEs in a repressive state




diversity that allows invasive species to rapidly adapt to new environments. In addition to TE activity, abiotic factors may also act at sequence level, selecting a specific variant that may confer a better TE functionality.

These are probably only some of the examples on how TE and environment interact and might represent only the tip of the iceberg. Further studies have to be focused on a better comprehension of mechanisms and factors involved in this extremely fascinating relationship. New insights on this issue will be useful to increase our knowledge on adaptability of organisms to global changes.

Disclosure statement

No potential conflict of interest was reported by the authors.

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