Taming, Domestication and Exaptation

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Contributor: Pierre Capy

During evolution, several types of sequences pass through genomes. Along with mutations and internal genetic tinkering, they are a useful source of genetic variability for adaptation and evolution. Most of these sequences are acquired by horizontal transfers (HT), but some of them may come from the genomes themselves. If they are not lost or eliminated quickly, they can be tamed, domesticated, or even exapted.

transposable elements domestication exaptation taming

1. Introduction

Transposable elements (TE), frequently called "*selfish genes*" [1], "*selfish DNA*" [2], or junk or garbage DNA, according to the categories defined by Graur et al. [3], present several genetic characteristics that allow them to rapidly invade genomes and populations, as well as to sometime to settle there permanently. Generally, after their arrival in a naïve genome and an invasion phase, their overall activity decreases drastically, leading to the maintenance of very few autonomous copies. However, several non-autonomous or dead copies, or even pieces of TE, can be preserved with non-neutral effects on individual fitness, due to their particular insertion site or the acquisition of new characteristics after a more or less lengthy coevolution with genomes.

During this coevolution process between TE and genomes, various interactions and trajectories can lead to the emergence of relatively stable evolutionary states, usually described as taming, domestication, or exaptation. Although these different terms seem to be closely related, they cover different phenomena, as briefly described below.

Taming. This interaction tends to rapidly reduce and limit the negative fitness impact of an excessively high transposition rate of a new invading TE on both genome structure and function. This is not an irreversible phenomenon because, sometimes, it must be reset at each generation, especially if it is due to non-transgenerational epigenetic marks. Moreover, in stressful conditions, an element can escape and have an intensive transposition activity. This can be illustrated by the regulation of TE activity, with occasional wake-up and bursts [4][5][6][7][8][9]. In this respect, the epigenetic regulation of TE activity plays an important role, and a few autonomous and silenced copies present in the genome can be reactivated occasionally by biotic, abiotic, genomic, or demographic stress. At the populational level, this is crucial for creating new genetic variability to cope with stress and adapt to new environmental conditions.

Domestication. The general definition of domestication is: a sustainable interaction, maintained over generations, resulting from a hierarchical relationship, based on a directional transformation of one entity by another for its own benefit. This leads to deep modifications of genetic material of the domesticated entities, like acquisition, loss, or transformation of one or several traits. In a genomic context, TEs are the domesticated entities and genomes of the “hierarchical superior”. Moreover, while there is no emergence of a new function, they can have an impact on the genome’s functioning. Indeed, a copy, through its genomic insertion site, can impact individual fitness and rapidly invade and settle in the population if it provides an advantage. In this respect, work based on populational analyses has reported many examples [10][11][12][13].

Exaptation. This term, introduced by Gould and Vbra in 1982 [14], refers to the emergence of a new function that enhances the fitness of individuals. More precisely, it (in Table 1 of their publication) suggests two different processes: “*1—character, previously shaped by natural selection for a particular function (an adaptation), is coopted for a new use-cooptation; 2—A character whose origin cannot be ascribed to the direct action of natural selection (a nonaptation), is coopted for a current use-cooptation*”. It is, therefore, a sequential evolution of a trait that was initially shaped (or not) by natural selection to a trait today shaped by natural selection and adapted to a new function.

Numerous biological examples, at the morphological, physiological, and molecular levels, can illustrate such an evolutionary trajectory, such as the feathers of birds originally “designed” for thermoregulation and today exapted in flight. At the molecular level and, more particularly, in the TE world, several examples will be detailed below.

During evolution, genetic tinkering is a major source for the emergence of new regulation systems, genome reorganization, and new functions [15][16][17]. Within species, this tinkering may be due to the shuffling and association of different parts of a genome by ectopic recombination, transposition, gene duplication, frameshift mutation, translocation, or, again, autopolyploidy in plants. However, this dynamic can also be fueled by the acquisition of external genetic material, as a result, for example, of interspecific hybridizations or horizontal transfers (HT). Such phenomena are responsible for the emergence of genetic novelties, as, for instance, the acquisition of new genes, paralogs of existing genes, and xenologous gene displacement [18]. In addition, they can occur in distantly related species, from different kingdoms within eukaryotes, or even between prokaryotes and eukaryotes. Many example of adaptive horizontal transfers are reviewed by Crisp et al. [19]. According to these authors, 2% of the foreign genes of primates come from archaea, 25% from bacteria, 57.6% from protists, 5.4% from plants, and 10% from fungi.

Based on all genome analyses during the last decade, it has been evidenced that the exchange of genetic material between closely or distantly related species is probably much more frequent than previously assumed. Concerning TE, HT are possible both after an interspecific hybridization or between distantly related species. Nowadays, such transfers do not appear to be rare evolutionary events, and the number of descriptions or suspicions continues to increase [20][21][22][23]. For instance, in insects, Peccoud et al. [22] found that out of 195 genomes, 4500 HT can be detected.

More precisely, inter-specific hybridizations occur between closely related species, which can hybridize and are able to produce fertile offspring. In plants, such a phenomenon is frequent and leads to the emergence of allopolyploids [24]. This favors the addition of genetic material in both species and the introduction of new variants, which can become the raw material for new genetic tinkering. In animals, inter-specific hybridization can also be observed between species with sexual reproduction. In such a case, and according to Haldane's rule, only the homogametic sex is fertile (for instance, XX females in the XY system and ZZ males in the ZW system). The fertile sex can then be backcrossed with individuals (males XY or females ZW) of one of the two parental species, leading to the transfer of genetic material of one species to the other (introgression).

On the other hand, horizontal transfers also occur between distantly related species when no sexual reproduction is possible. They were probably very frequent during the early steps of life [25] and were at the origin of important evolutionary steps, such as the exchanges between prokaryotes and eukaryotes or between bacteria/archaea and extremophilic eukaryotes [26][27]. This also occurs during the endosymbioses of proteobacteria and cyanobacteria, leading to the emergence of mitochondria and chloroplasts [28] or between prokaryotes (see for instance the numerous examples in Escudero et al. [29], or San Millan et al. [30]), where they frequently promote the exchange of resistance to environmental stress via conjugation, transduction, and transformation, whether or not they use TE as vectors [31][32].

2. Short-Term Co-Evolution of Transposable Elements and Genomes: Taming

While in prokaryotes, the HT mechanisms are known and responsible for rapid diffusion of resistance to environmental stresses [30], the transfer mechanisms remain unknown in eukaryotes, and several scenarios have been proposed [21][33][34]. However, it is likely that the arrival of a new TE in a eukaryotic genome probably occurs in most cases by horizontal transfer [21][35]. At this point in the TE life cycle, there is only one copy in a single individual. Therefore, the probability of losing this copy through genetic drift is very high. To maintain it and allow genome and populational invasion, the impact on fitness must be positive and very high or more likely, TEs have to adopt a parasitic strategy, i.e., a low phenotypic effect, with a relatively high transposition rate [36]. In addition, it seems that several TE, among which some members of the Tc1-mariner superfamily, such as Bari1, Bari3, and Sleeping Beauty would facilitate their genomic diffusion after a horizontal transfer, might have evolved as “blurry promoters” [37][38].

After this more or less lengthy invasion phase, a plateau is reached, during which the number of copies is stabilized. Few copies of this element will then remain autonomous, while the others will become non-autonomous but *trans*-mobilizable, with the remaining copies degenerating. In this context, it is interesting to observe that a competition can take place between the different types of copies from the same family (between autonomous vs. non-autonomous but *trans*-mobilizable copies), leading to a dynamic similar to that described by Lokta [39] and Volterra [40] for the prey-predator relationship in population biology [41][42].

This basic TE life cycle can be viewed as a parasitic strategy in the invaded genome. However, the golden rule of many parasitic entities is to be as “silent” as possible. In other words, to be maintained over long evolutionary periods, the TE copy number must be neither too low to avoid elimination by genetic drift or ectopic recombination nor too high to avoid a negative impact on individual fitness.

In this phase, TE silencing may be promoted by epigenetic regulation. The term “epigenetics” generally refers to several mechanisms, such as cytosine methylation in *Arabidopsis thaliana*, where most copies are methylated and inactivated [43]; small RNA (*si*RNA and *pi*RNA), as described in different tissues in *D. melanogaster* (in germline to control *I* and *P* element transposition [44], testes and ovaries [45][46][47][48]), and somatic and germinal tissues of arthropods [49] (as a stress response in *A. thaliana* [50]), as well as long non-coding RNA in plants with differential expression in tissue and depending on environmental conditions [51]. While the epigenetic regulation seems to be dominant, other mechanisms of TE-silencing can be evoked, such as those involving a self-encoded repressor (such as the internally deleted KP element, derived from the *P* element), [52] or to splicing events, such as for the Bari1 element [53].

One of the evolutionary interests of such silencing is its reversibility. This has two main effects. First, when epigenetic marks are removed, a transposition burst can be observed [54][55] and second, genes located near the TE insertion site can also be reactivated because the methylated area may be larger than the TE itself and can encompass neighboring sequences [56][57][58][59]. Therefore, this type of reversible interaction between TE and genomes can be useful for the genome, insofar as it allows it to maintain a functional “genetic toolbox”, which can be reactivated when necessary to generate new genetic variability and evolve rapidly in a changing environment.

3. Long Term Co-Evolution of Transposable Elements and Genomes: Domestication and Exaptation

Two common characteristics are shared by the processes of domestication and exaptation. The first is the “capture” of a copy in a specific genomic location, and the second its maintenance, which can go as far as fixing itself in a population or a species. Regarding the genomic location, this raises the question of the distribution of TE copies in a genome. Is there a random distribution or a patchy distribution with hot insertion regions?

For more than 30 years, it has been observed that TE distribution is patchy [60]. On a coarse scale, this distribution can vary from one chromosome to another, but also within a chromosome, and again among the main TE Classes. For instance, in the human genome, the *Alu* distribution is not similar between chromosomes 21 and 22 [61], and L1 elements are not randomly distributed, although they seem able to target all genomic regions [62]. A similar distribution bias is also observed in *Drosophila* [63], catfish [64], and woodpeckers [65], among others. All these results suggest that even if TEs are potentially capable of jumping everywhere in the genomes, purifying selection against new insertion and ectopic recombination can remove several of them and reshape distribution [66][67]. However, the alternative hypothesis, assuming that TEs insert into peculiar regions, cannot be ruled out.

With the accumulation of complete genome sequences and the new molecular tools recently developed to explore them, it is now clear that this distribution is patchy. In addition to the evolutionary forces previously mentioned, new parameters must be taken into account, such as the status (condensation vs. decondensation) of chromatin [68] or "DNA sequence, chromatin and nuclear context and cellular proteins" because they are also involved in TE integration [69], showing that peculiar genomic territories are more prone to TE insertions than others.

More precisely, several results show that regions with a specific chromatin structure seem to be more "attractive", such as the regulatory regions of genes or heterochromatin, whether they are centromeric, telomeric or interspersed in euchromatin [70][71][72][73][74]. Insertions of TEs in gene-rich regions have also been frequently described in numerous species, such as *Drosophila* for retrotransposons [75], for the retroposon *Accord* in 5′ of a gene involved in resistance to insecticides [76][77][78], and, more recently, for diverse TE families, frequently associated with stress-related genes [79]. Similar observations have been reported in mice [80] and wheat [81]. Moreover, the existence of nested accumulation of TEs in euchromatin [82], useful for TE "paleontology" [83], must also be considered. Especially, since they could be at the origin of Pi clusters, involved in regulation of TE activity by small RNA [48][84][85][86][87].

Some regions are the main targets of TEs, probably because of their accessibility [88][89][90]. In addition, patchy distribution due to the accessibility effect could be reinforced by the existence of low recombination rates, leading us to consider some of these regions as TE graveyards [91][92][93][94].

Therefore, patchy TE distribution is the result of multiple factors, and two steps must be considered: first, an insertion phase with random or non-random insertions, and second, a differential elimination or maintenance phase, due to selection against deleterious insertions, positive selection on insertion with beneficial host impact and elimination in regions with a high recombination rate.

In this review, I will differentiate *domestication* and *exaptation*. Can an insertion close to a gene and modifying its expression profile not be considered as an exaptation? Although such insertions have an impact on the host genome, as illustrated by many examples such as Mendel's wrinkled pea [95], the industrial melanism of *Biston betularia* [96], the resistance to insecticides [77][97][98] or to xenobiotics [78] in *D. melanogaster*. Their frequency may increase in natural populations more or less rapidly, depending on their effect on host fitness [99] and/or the genetic drift, due to the effective population size (*Ne*). Domestication applies to a whole TE copy or a part of it, and frequently a copy is completely domesticated as soon as its mobility and its capacity to encode a functional transposition machinery is lost. Whatever the situation, these copies have an impact on the expression profile of the surrounding genes, but they are not initially the source of new functions or new genes. However, domestication can be a step towards exaptation.

On the other hand, in an exaptation process, all or part of the sequence of a copy is fixed in the population or species. This is the source of new functions and sometimes new genes, which significantly increase host fitness. Such novelties are present in a single species when exaptation is recent or in a group of phylogenetically related species for an older exaptation that occurred before the speciation events. Several examples detailed later will illustrate such a phenomenon, such as the telomeric element in arthropods [100], the vertebrate immune system [101], or placenta development in mammals [102].

Domestication and *exaptation* can be detected from analysis of the evolution of polymorphism along the chromosome by the existence of regions with low variability due to the effect of selective sweep or background selection. As recently suggested in very interesting articles [103][104], these phenomena require several successive stages. Here, I would just like to summarize this process and add several considerations.

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