Retrotransposable Elements, Retrotransposition and Genome Evolution

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Hybrid genome evolution by transposition

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Abstract. Species hybridization is reviewed focusing on its role as a source of evolutionary novelties. Contrary to the view that hybrids are lineages devoid of evolutionary value, a number of case studies are given that show how hybrids are responsible for reticulate evolution that may lead to the origin of new species. Hybrid evolution is mediated by extensive genome repatterning followed by rapid stabilization and fixation of highly adapted genotypes. Some well-documented cases demonstrate that bursts of transposition follow hybridization and may contribute to the genetic instability observed after hybridization. The mechanism that triggers transposition in hybrids is largely unknown, but coupling of hybrid transposition and demethylation has been observed in mammals and plants. A natural scenario is proposed in which marginal small hybrid populations undergo transposition mediated genome reorganizations accompanied by exogenous and endogenous selection that, in concert with drift, lead to rapid fixation of high fitness hybrid genotypes. These genotypes may represent parental introgressed species or be entirely new species.

Hybrids have been stigmatized as low fitness genotypes without evolutionary value since the advent of the biological species concept (BSC) (Dobzhansky, 1937). This species definition requires a highly effective reproductive isolation among species, mediated, in most cases, by hybrid inviability or sterility. Yet, this view of hybrids as lineages devoid of evolutionary significance was not shared by some early naturalists, Linnaeus among them, and several neodarwinian naturalists, such as Anderson and Stebbins (1954) and Grant (1971), who considered hybridization a mechanism of speciation. The present availability of genome-wide molecular markers has allowed documenting a large number of unsuspected cases of historical interspecies crossing that leads, in many cases, to species of hybrid origin (see Arnold, 1997, for a review). Moreover, the use of those markers has unveiled a guild of natural instances where true divergent species share genes due to historical interspecific crossing. Surprisingly, this natural reticulate evolution has been experimentally reproduced in part, demonstrating that the process of genome repatterning after hybridization is rapid and fertility is restored in a few generations (see Rieseberg et al., 1996 for a documented case). This paper is aimed, first, to analyse the putative causes of the genome reorganization that follows hybridization and vindicate hybrids as a positive source of evolutionary innovations. This paper is also devoted to describe how transposable elements (TEs) may play a decisive role in hybrid genome evolution, focusing on bursts of transposition that occur during hybridization.

Hybrids as a source of evolutionary novelties

Traditionally, species hybridization has been taken as an exception to the BSC by neodarwinists. Yet, not all evolutionists have dismissed "hybridizing morphs" as perfect species, this being especially true for botanists, who are very familiar with plant hybridization in nature. Most importantly, plant species do not lose their species integrity in spite of their gene exchanging due to hybridization. Recently, natural hybridization among animal species is being frequently reported, increasing the view that hybridization is a common event not only in plants but also in animals, contradicting the reproductive isolation tenet of the BSC (see Arnold, 1997, for a general review and Kaneshiro, 1990, for a review of *Drosophila*).

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Table 1. Hybrid fitness in some genera known to hybridize in nature[a]

Genus	Measured fitness component in hybrids	Comparative hybrid fitness[b]
Plants		
Quercus	Fruit maturation	L (L-E)
Artemisia	Developmental stability, herbivore attack	E
	Seed production and germination	E
Iris	Shade tolerance	I (I-H); I (I-E)
	Viability of mature seeds	E, L
Eucalyptus	Reproductive value	I (I-H); I(L-H); L
Carpobrotus	Recruitment (seeds per plant)	I
	Seed germination (after gut passage)	H
Animals		
Hyla	Developmental stability	E
Sceloporus	Chromosome segregation in males	E (E-L)
	Female fecundity	E; L
Colaptes	Clutch and brood size	E
Geospiza	Survivorship, recruitment, breeding success	H
Allonemobius	Survivorship	I(L-I)
Mercenaria	Survivorship	L; E(E-H)
Notropis	Survivorship	L(L-E)
Bombina	Viability	L; E
Apis	Metabolic capacity	L
Gasterosteus	Foraging efficiency	I
Gambusia	Development	H; I

[a] Adapted from Arnold (1997), where all work references are found, except for *Carpobrotus* (Vilà and D'Antonio, 1998).

[b] Fitness estimates are relative to both parents: L = lowest fitness; I = intermediate; E = equivalent; H = highest fitness. Most common fitness is given followed by range of fitness values in parenthesis.

The fundamental tenet of the BSC that hybrids are low fitness genotypes is also contradicted by measuring fitness components. Often, detailed studies have demonstrated that overall fitness is not more inferior in hybrids than in their parental species. Table 1 shows that the range of hybrid fitness is wide, from low to high values relative to parent species, and that these values depend on the fitness component. This makes it elusive to compute accurately the overall hybrid fitness as the resultant of a set of components in which fertility is just one component, although an important one. As an example, hybrids of *Carpobrotus* plant species owe their invasive advantage to the higher resistance of hybrid seeds to the passage through the digestive gut of mammal herbivores, showing that decreased fertility does not guarantee low overall fitness (Vilà and D'Antonio, 1998).

The above paragraphs provide a sound background for the evolutionary potential that may lead hybrids to species formation. Recently, several cases of hybrid speciation have been reported in detail, mainly in plants but also in animals. The plant *Iris nelsonni* has been known to be of hybrid origin for a long time, due to chromosomal studies and morphology; later molecular markers have supported this view. Experiments with hybrids between the three parental species *(I. fulva, I. hexagona* and *I. brevicaulis)* have shown post-pollination barriers, making F_1 hybrids very rare, but not impossible. Some of these rare hybrids, however, show higher fitness in certain environments such as new transitional habitats (ecotones), where they can outcompete the parental species (Arnold and Bennett, 1993). The occupation of new habitats by hybrid genotypes is a common observation not only in plants but also in animals, such as in the finches of the genus *Geospiza* (Grant and Grant, 1996).

In some instances, hybrid speciation has been thoroughly studied, ecologically and genetically. The genus *Helianthus* comprises a set of self-incompatible annual plants (sunflowers), living in a variety of habitats. *H. annuus* and *H. petiolaris* produce hybrid swarms in sympatry, with semisterile F_1 hybrids and F_2 progeny showing a wide range of fitness fertility (13–97 % of pollen viability). Repeated hybridization allows for the origin of new species, such as *H. anomalus*, a hybrid species invasive of xeric habitats. The hybrid origin of this species is based on molecular studies that show reticulate evolution for ribosomal DNA combining variants from *H. annuus* and *H. petiolaris*, the two originating parental species (Rieseberg and Noyes, 1998). There are similar cases in animals. The whole fish genus *Gila* (Cyprinidae, minnows) is now recognized to evolve via reticulate introgressive processes due to the extreme mitochondrial DNA (mtDNA) similarity among *Gila* species (Dowling and DeMarais, 1993). Introgression or hybrid speciation in animals has also been described in species of *Drosophila* (Kaneshiro, 1990), *Sorex* (Searle, 1984), *Felis* (O'Brien et al., 1990), *Canis* (Lehman et al., 1991; Roy et al., 1994) and others.

Hybrids as promotors of rapid genome reorganizations

Detailed genomic analyses have shown not only that hybrid genomes are common in phyletic reticulate studies but also that genome reorganizations are rapid after hybridization experiments. This new genomic repatterning affects the overall fitness of the organism, in particular the recovery of fertility. Genetic map comparisons between *H. anomalus* and its parental species reveals an extensive repatterning in gene order, requiring at least three chromosomal breakages, three fusions and one duplication to explain the differences between hybrid and parental species. Rieseberg et al. (1996) have mimicked this natural hybridization in the laboratory, obtaining, after five generations of selfing and/or backcrossing, three fertile, synthetic hybrid lineages that showed a high concordance in genomic composition using 197 RAPD markers. Most surprisingly, this repatterned genome was statistically concordant with that of *H. anomalus*, the natural hybrid species, suggesting that natural genomic reorganization is not only rapid but also repeatable. Causes of repeatability are not known but the rapid increase in fertility of the synthetic lines, from 4 % to more than 90 % in only five generations, suggests the action of endogenous selection for gene blocks that increase fertility rather than the operation of ecological (exogenous) selection, irrelevant under laboratory conditions. As far as I know no similar studies have been performed with other homoploid species of hybrid origin, but it is reasonable to think that this may be a general process.

Rapid genome reorganization following hybridization is also expected under the formation of alloploid species if this process were ubiquitous. Surprisingly, although alloploidy is perhaps the single universally accepted mechanism of hybrid speciation, little is known about the evolution of the polyploid genome immediately after its formation. Yet, experiments with

Table 2. Genetic instability in *D. buzzatii* (db)/*D. koepferae* (dk) hybrids

A) Rate (R) of new rearrangements in progenies of male introgressed hybrids and *D.buzzatii* lines[a]

Line/Hybrid	Number of parental individuals	Number of progeny larvae (N)	Number of new rearrangements (nr)	Rate per gamete per generation (R = nr/N)
Db line	62	1382	0	$< 10^{-3}$
Db/Dk hybrid	59	1668	35	2.1×10^{-2}

[a] Adapted from Naveira and Fontdevila (1985).

B) Transposition rates (TR) of Osvaldo in *D.buzzatii* and in *D.buzzatii* /*D.koepferae* hybrids[a]

Line/Hybrid	N	LNI	NI	TO	TR = NI/TO
Db line	301	15	36	4224	8.5×10^{-3}
Hybrid with Ko-2.6 Dk line	163	15	29	1836	1.5×10^{-2}
Hybrid with Ko-SL Dk line	174	39	87	2230	3.9×10^{-2}

[a] Adapted from Labrador et al. (1999).

Note: N, LNI and NI stand for number of analysed larvae, number of larvae with new insertions and number of new insertions, respectively. Transposition rate (TR) is defined as the number of transpositions per element per generation. Transposition opportunities (TO) are the grand total of number of times that each element has passed through a chromosomal generation. If a position is fixed, TO is simply the number of fixed sites times the number of analyzed larvae times the number of genomes contributing to the offspring (i.e. one diploid genome for each parental sex). When a position is polymorphic TO must be estimated from offspring segregation numbers of each cross. Results are reported for two experiments with two *D. koepferae* lines.

the genus *Brassica* are very illustrative (Song et al., 1995). Thus, synthetic *Brassica* allotetraploids were self-fertilized and extensive genomic changes were observed, involving loss or/and gain of parental and novel DNA fragments, across five generations of selfing.

Summarizing, these and other similar studies strongly suggest that genomic reorganization of hybrid species, be they homoploid or alloploid, may be practically fixed in a few generations after hybridization and stay practically static thereafter. Yet, these results do not provide evidence for responsible mechanisms. However, studies with the recently formed allotetraploid cotton *Gossypium barbadense*, show not only that both parental genomes differ in gene order in the hybrid, but also that some DNA dispersed repeats from one parental genome have spread to the other. Four of these repetitive DNA probes correspond to known transposons, suggesting transposition as a possible mechanism of spread (Zhao et al., 1998). Following is a synthetic account of other evidences indicating that hybridization may trigger transposition and be a plausible mechanism of repatterning in hybrid genomes.

Hybrids as triggers of genomic instability and transposition

Sturtevant (1939) reported, as far as I know, the best early documented case of mutation increase in hybrids. Crossing two, so called, "races" of *Drosophila pseudoobscura*, later recognized as two different species *(D. pseudoobscura* and *D. persimilis)*, he observed, in backcrosses, mutation frequencies two figures higher than normal spontaneous mutation rates ever recorded. Later, increases in rates of chromosomal rearrangements in hybrids have been reported in *Nicotiana* species, and *Caledia* and *Chironomus* subspecies (see references in Labrador and Fontdevila, 1994). All these observations were qualified as episodes of genetic instability and their relationship to hybridization was not clear until some observations relating TE transposition and hybrids were reported in *Chironomus* hybrids (Schmidt, 1984) and *Drosophila* (see references in Fontdevila, 1992). However, evidence of enhanced transposition in these experiments was indirect, based, mainly, on observed reverse mutations due to TE excision.

The first direct observation of increased transposition in species hybrids, using chromosomal in situ hybridization techniques, was reported by Labrador and Fontdevila (1994) in hybrids between *Drosophila buzzatii* and *D. koepferae*, two sibling species that coexist in the arid zones of Bolivia and NW Argentina. Under experimental conditions they produce F_1 hybrid progeny consisting of sterile males and fertile females. These females can be backcrossed to parental *D. buzzatti* males and their female progeny backcrossed again during several generations. After a few backcrosses, this procedure allows us to obtain a collection of individuals with a *D. buzzatii* genome introgressed with genomic portions of *D. koepferae* (introgressed hybrids). Naveira and Fontdevila (1985) observed that progenies of some introgressed hybrids displayed an excess of new chromosomal rearrangements that could be qualified as an episode of genetic instability mediated by interspecific hybridization. This burst of new rearrangements was similar to that previously observed with *Nicotiana*, *Caledia* and *Chironomus*. Mainly, the relationship found between TE transposition and production of new rearrangements in *Chironomus* hybrids suggested that transposition could also be induced by the *buzzatii/koepferae* hybridization.

This prediction was tested by Labrador et al. (1999) using *Osvaldo*, a retrotransposon isolated from *D. buzzatii* (Pantazidis et al., 1999). The screening of new insertions by in situ hybridization was performed in the second backcross progeny and showed that transposition rates are one order of magnitude higher in introgressed hybrids ($1.5–3.9 \times 10^{-2}$ per element per generation) than in parental *D. buzzatii* (8.5×10^{-3}). These results (Table 2) confirmed those previously obtained in a similar experiment by Labrador and Fontdevila (1994). However, in this experiment the use of an inbred *D. buzzatii* stock and a lower sample size impeded the authors from making strong conclusions. The experiment of Labrador et al. (1999), on the other hand, allows performing a robust quantitative test. All these experiments show unambiguously that Osvaldo transposition occurs in bursts, as new insertions often appear in clusters of several insertions per larva, something that was suggested only by circumstantial evidence for other elements (Biemont et al., 1987; Nuzhdin and Mackay, 1994). This precludes standard chi-square comparisons between samples because distribution is non-Poisson. Labrador et al. (1999) showed that the best fit was obtained with the "Poisson with zeroes" distribution, which was used to perform paired tests of homogeneity. All tests between nonhybrid stocks and each of the hybrids showed a highly significant heterogeneity. This statistical treatment is the first quantitatively documented evidence of transposition increase in interspecific hybrids and makes the results very robust. The strength of these results benefit also by direct cytological methods of detection, namely in situ hybridization on chromosome slides using an *Osvaldo* probe. The *Osvaldo-buzzatii* system has the advantage of having a low copy number per genome, facilitating the direct detection of new insertions by comparisons between progeny of introgressed lines and parental individuals, in which original insertion positions were previously characterized. Both, quantitative treatment of transposition rates and direct observation of transposition add to the firm conclusion that hybrids are triggers of genetic instability and transposition.

What is the mechanism that triggers transposition in hybrids?

There is great interest to know what the host genome response is to the "parasitic" invasive behavior of TEs. Recently, the view that methylation evolved as a genomic defence against parasitic DNA (Barlow, 1993; Yoder et al., 1997) has been advanced as a challenge to the epigenetic regulatory function of methylation (but see Simmen et al., 1999 for an alternative view). In fact, both views are not incompatible, since mechanisms that have originated to control parasitic DNA may have evolved later as regulators of genome expression (Kidwell and Lisch, 2001). Regardless of the origin of the mechanism, there is recent evidence that methylation can play an important role in hybrid transposition release.

In an experiment with hybrids between *Macropus eugenii* and *Wallabia bicolor*, two kangaroo species, O'Neill et al. (1998) reported a coupled observation of transposon mobilization and chromosomal reorganizations, including extended centromeres, resulting from sequence amplification, and new rearrangements. When methylation status was compared between parental and hybrid genomic DNA an elevated loss of methylcytosine was found in hybrids. The significant homology found between hybrid unmethylated DNA sequences and several retroviral genes, prompted these authors to conclude that hybrid sequences derived from a novel retroviral element, named KERV (from Kangaroo Endogenous RetroVirus). Analysis of extended hybrid centromeres showed that they contain many highly repeated copies of KERV, confirming its implication in hybrid chromosomal and genome reorganization mediated by DNA undermethylation.

Plant hybrids show also that DNA methylation and retrotransposition are causally connected. Thus, Liu and Wendel (2000) working with rice lines introgressed with genomic fractions from wild rice *(Zizonia latifolia)*, reported that within the first few generations following hybridization an initial burst of retrotransposon activation is correlated with cytosine demethylation. In general, they witnessed the simultaneous presence of novel heritable morphological traits, undermethylation and regulatory changes of retrotransposition. These results not only suggest a causal link between demethylation and transposition activity but, and most important, that host response to introgression of foreign genomic material is a rapid activation of TEs, followed by an equally fast silencing of transposition.

These results are of utmost importance for understanding the mechanism of TE mobilization in hybrids, but methylation is not universal and many invertebrates, *Drosophila* among them, do not show methylation at all. Recently, the molecular link between DNA methyl groups and the nucleosome inactive chromatin structure has been deciphered (Razin, 1998). These studies indicate that the primary function in transcriptional repression may be deacetylation. In *Drosophila* and yeast, protein factors bind to specific silencer sequences (repressor) and serve to anchor to the DNA a repression complex responsible for histone deacetylation. Removal of acetyl moieties from specific lysine residues on histones, uncovers the positively charged lysine residues, which interact with DNA, restrict nucleosome mobility and make the transcription machinery inaccessible to promoters. Silencer sequences are methylcytosine residues in stable mammalian repression, but they can be other specific DNA sequences that respond to physiological changes. In summary, the general mechanism that explains transposition inactivation may be deacetylation. In many organisms deacetylation is coupled with methylation, but not necessarily so in others.

Transposon dynamics of genome evolution

Hybrid species are one example of genomes that show an intensive repatterning associated with transposition bursts, but other transposition episodes have been related to different genomic and environmental stress events, such as cell culturing and microbial infections (Grandbastien, 1998; Melayah et al., 2001). An educated guess indicates that genome evolution consists of a series of episodes of reorganization in which transposition may play a significant role. As an experimental example, Moran et al. (1999) have demonstrated that L1 retrotransposons transpose at high frequency in human cultured cells, mobilizing with them genomic sequences (exons and promoters) into existing genes. Since L1 elements make up a substantial part

(15%) of the human genome, their mobilization is of utmost importance to genome evolution.

This model contrasts with reports of synteny among closely related genomes. Yet, molecular markers are increasingly more refined and allow detecting gene reorganizations that were impossible in the past. This approach has been used with success several times and the evolutionary history of maize may serve as an example (SanMiguel et al., 1998). Sorghum and maize *Adh1* regions are highly conserved, but three sorghum homologous genes are located elsewhere in the maize genome. The major difference between both regions is the presence in maize of clusters of retrotransposons, interspersed with low copy-number loci that are absent in sorghum. That accounts for most of the size difference between both Adh regions. These retrotransposons inserted in a transposition burst that occurred about 3 million years ago. Studies like this show important episodes of genome repatterning at the fine level and are essential to understanding the role of transposition in genome evolution.

Transposition mobilization by stress, genomic or environmental, can be interpreted as an adaptive mechanism of TEs that ensures that a large number of elements are transmitted to those few hosts that manage to survive. From the perspective of the host, it will be beneficial to increase variability in periods of stress. It is common knowledge that TE insertions are responsible for gene mutations, ranging in percentage from 15–20% in mammals to more than 80% in *Drosophila*. Often these insertions generate novel patterns of gene expression, which are tissue specific and respond to signals associated with TEs, as has been documented in *Drosophila*, *Antirrhinum*, maize, sea urchin and humans (Kidwell and Lisch, 1997). Moreover, TEs have an important role in generating large genome rearrangements, accomplished by recombination between homologous TEs sequences in different chromosomal locations (Lim, 1988). Thus, nothing mystical exists about the benefit of the host by means of co-opting TEs for new host functions. In summary, the dynamics of rapid genome organization by transpositions bursts, followed in many cases by immediate silencing of transposition, as reported above, allows us to view host-TE relationships under a broad picture ranging from extreme parasitism, such as population invasions by TEs in hybrid dysgenesis, to perfect mutualism, related to TE exaptation by the host (Kidwell and Lisch, 2001).

Are there scenarios for hybrid evolution by transposition?

Hybrid zones between marginal populations are among the most favored scenarios for hybrid evolution. Marginal populations inhabit ecologically stressful environments, often associated with disturbed or transitional (ecotone) areas, which provide an array of new open habitats to be invaded successfully by hybrids. Yet, F_1 hybrids are rare due to pre- and postfertilization barriers to the formation of the initial hybrid generation, diminishing their probability of establishment. However, multiple opportunities of hybridization in these contact zones overcomes this difficulty by generating natural hybrid swarms that consists of a few parental and F_1 individuals coexisting with an abundance of second generation F_2 individuals and backcrossed introgressed individuals. The establishment of hybrids in contact zones is a two-way process that combines great opportunities of establishment in open newly created habitats with large facilities of repeated crosses between (and among) first generation hybrids and parental individuals, setting off a runaway process that leads to an array of backcrossed introgressed genotypes of high evolutionary potential.

The role of selection in the establishment of new hybrids is dependent not only on adaptation, through exogenous (ecological) selection, to habitats created in contact zones, but also on endogenous selection trying to maximize fitness. This endogenous purifying selection is only against certain sterile and/or inviable hybrids of the hybrid swarm and not against "all" hybrids, as the tension zone model, championed by Barton and Hewitt, proposes (see discussion in Arnold, 1997, pp. 122–140). The variety of introgressed genotypes in hybrid zones facilitates this selective regime, favoring those hybrids that show high levels of fitness. This has been proved in *Iris* hybrids between *I. fulva* and *I. brevicaulis* where a high correlation exists between embryo inviability and the number of *I. fulva* genetic markers present in the progeny from *I. brevicaulis*-like maternal plants, suggesting that endogenous selection is acting against intermediate hybrid individuals, that is, those that contain the highest number of alien genetic elements (Arnold, 1997). In a similar way, Rieseberg et al. (1996), working with *H. anomalus*, found that similar linkage groups of genes exist in several artificial hybrid lines with high fertility. As stated above, these lines were obtained after a few generations of crossing, buttressing the rapid genome repatterning of these introgressed lines.

Rapidity is crucial to the establishment of hybrid lineages. It has been argued that, at least, this seems plausible in speciation by fixation of underdominant small chromosomal rearrangements that might mediate reproductive isolation and, eventually, speciation. Fontdevila (1992) argued that the probability of fixation of these rearrangements is low, often insignificant, in large populations under the conventional mutation rates, but in small hybrid populations, where genetic drift acts strongly and transposition-mediated mutation, point and chromosomal alike, is significantly increased, this probability is greatly improved. The cases discussed above illustrate processes of rapid genome repatterning in hybrid species (homoploid and alloploid) and, also, of evidence of transposition and chromosomal rearrangement increase, so they are in agreement with the proposed model.

This proposed scenario (Fig. 1) is dependent upon the synchronous occurrence of, at least, four processes in contact zones. Namely, (a) transposon bursts fuel genome reorganization by increasing levels of genome transpositions and point insertions, (b) exogenous selection allows the establishment of some high fitness hybrid genotypes, (c) endogenous selection favors reorganized genomes that show high fertility and viability, and (d) small effective population size of the hybrid zone increases fixation by drift.

The present review summarizes strong scattered experimental and natural evidence for all these processes. It will take, however, more work to show that all these processes act synchronously. Nonetheless, the coupling between hybrid instability and natural hybridization has been reported in a few cases. One example that combines clinal and hybrid observations of chromosome reorganizations in nature with experimental rapid chromosomal changes refers to subspecies of the grasshopper *Caledia captiva* (Shaw et al., 1993). Two of these taxa (the Torresian and Moreton subspecies) differ by many pericentric rearrangements and the presence-absence of blocks of heterochromatin, exhibiting a latitudinal cline along the seaboards of Australia. Shaw (1994) proposed that *Caledia* centromeres are rapidly evolving and chromosome reorganization, per se, may play a significant role in speciation. Experimentally, Shaw et al. (1983) observed that, although F_2 progeny is inviable, experimental backcrossed hybrids showed 50% of viability and around 12% of these viables contained novel chromosome rearrangements. Interestingly, similar chromosomal rearrangements found in a hybrid zone between both *Caledia* subspecies suggested that this experimental chromosomal instability might occur in natural conditions as well.

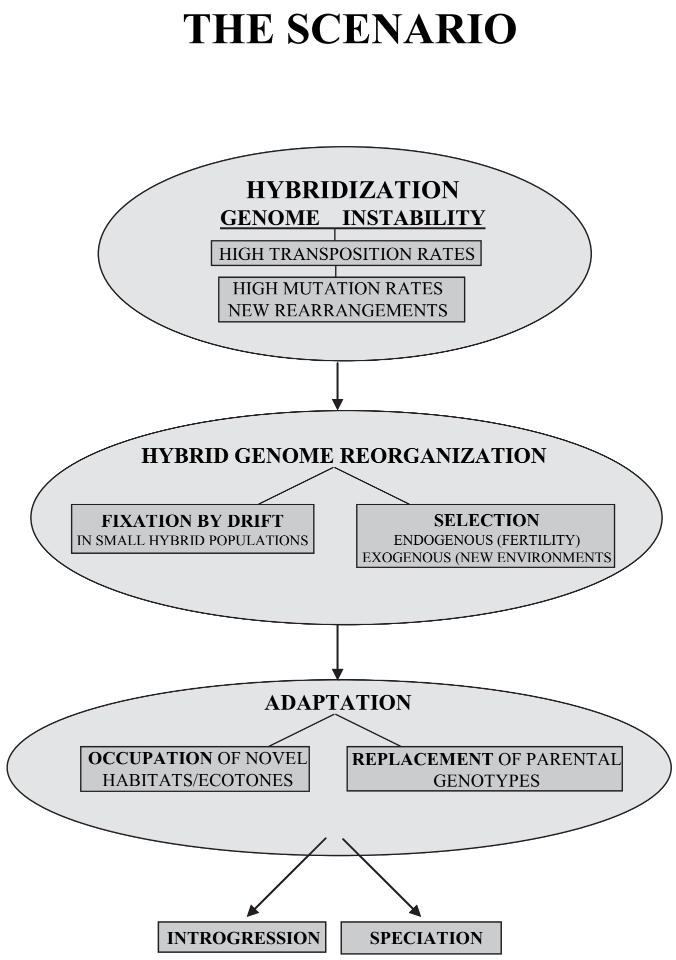

Fig. 1. Flow chart of the natural scenario of hybrid genome evolution by transposition. The initial (upper) part of the chart depicts how hybridization promotes genome instability through high transposition rates that induce new rearrangements and high mutation rates. The middle part shows how the ensuing hybrid genome reorganization is stabilized by drift fixation and selection (endogenous and exogenous). These processes lead to adaptation (the lower part) either by occupation of novel environments, new ecotones in many cases, or by replacement of parental species. The final step of this scenario is reticulate evolution by introgression or the evolution of a new species.

The idea that centromere repatterning is a consequence of activation of TEs is founded in the present evidence of the role of TEs as basic components of heterochromatin (Dimitri and Junakovic, 1999; O'Neill et al., 1998) and as promoters of rearrangements. Moreover, the putative selective value of transposon mediated heterochromatic rearrangements, deduced from clinal karyotypic variation, is being assessed in altitudinal clines of barley populations (Kalendar et al., 2000) as well.

Conclusions

The general idea of TEs as promoters of genome evolution was pioneered by McClintock (1980) in her early statement: *"Since the types of genome restructuring induced by such elements know few limits, their extensive release, followed by stabilization, would give rise to new species or even genera".* Here, we focus on the episodic occurrence of bursts of TE transposition in hybridization and their tremendous impact on the genome reorganization that may lead to introgression and even to hybrid speciation. Hybrid speciation is reviewed here to emphasize that hybridization is not always a dead end, as the BSC might suggest, but a potential source of new array of hybrids (hybrid swarms) that may establish themselves, eventually in new ecotone habitats, and evolve as new species. One common feature of the process that accompanies hybridization is the rapidity of genome repatterning which is hardly explained by the conventional mutation and recombination rates. Rather, transposition bursts ensuing hybridization suggest their involvement in these rapid genome reorganizations. The proposed evolutionary scenario is dependent upon the synchronous occurrence of this mobilization with selection (exogenous and endogenous) and fixation by drift in small demes found in hybrid zones. A few natural scenarios have been found in accordance with this model, but it will take, however, more work to show that all these processes act in concert.

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