

Evolutionary consequences of diploid–polyploid hybrid zones in wild species

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Hybridization and, in particular, the maintenance of hybrid zones have traditionally received considerable attention because of their important contribution to the understanding of evolutionary patterns and processes^{1–4}. Hybrid zones are often active sites of evolutionary change because hybridization and introgression can: (1) increase genetic diversity within species, (2) cause the transfer of genetic adaptations, (3) induce the breakdown or reinforce reproductive barriers between closely related groups, and (4) lead to the emergence of new ecotypes or species^{1,3,4}. Although hybrid zones between diploid genetic entities have been the subject of several recent reviews^{2,4}, those involving two cytotypes with different ploidy levels (Box 1) have not received such attention.

Hybrid zones that involve two different cytotypes with different ploidy levels are of special interest for several reasons. First, the production of highly sterile hybrids (e.g. triploids produced in most diploid–tetraploid contact zones) acts as a major constraint to reproductive interactions between ploidy levels. Second, they reproduce certain conditions that occur in the establishment of polyploids. Third, they influence the dynamics and further evolution of polyploid complexes. Each of these different aspects of diploid–polyploid hybrid zones are the subject of this review.

Origin and structure of hybrid zones involving different ploidy levels

Hybrid zones involving two ploidy levels can result from two different processes. First, they can form as a direct consequence of the emergence of a neopolyploid within a diploid population (what we refer to as a primary origin of the hybrid zone). Alternatively, they arise following secondary contact between diploid and polyploid populations that were geographically separated and might therefore have differentiated in allopatry (secondary origin of hybrid zone). A primary hybrid zone can result from two different processes. First, a polyploid can occur and establish in a population of a single diploid species, or when there is contact between two populations of the same diploid species that have differentiated in allopatry. This evolutionary process, which involves a single species, defines

Hybrid zones between cytotypes with different ploidy levels are particularly interesting for studying the ecology and the evolution of reproductive interactions between closely related taxa.

Diploid–polyploid hybrid zones differ fundamentally from those between diploids in that they reflect certain conditions that are characteristic of the early stage of polyploid establishment, and allow tests of hypotheses relating to the dynamics and evolution of polyploid complexes. Recent theoretical and empirical studies have provided important data on the evolution of isolating mechanisms in diploid–polyploid contact zones, but have also shown that introgression might counteract the evolution of isolating mechanisms.

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autopolyploidy^{5,6}. Second, two related diploid species can hybridize, producing an allopolyploid⁶.

When secondary contact occurs, the diploid and polyploid populations might thus have accumulated several fixed genetic differences that would not have arisen in circumstances of a primary origin. To date, most of the known hybrid zones (if not all) involving diploids and autopolyploids are thought to result from secondary contacts^{7–10}. In most of these hybrid zones, the distribution of cytotypes is parapatric and only a few hybrids are normally recorded^{9,11}. In several diploid–autopolyploid contact zones the absence of, or low genetic differentiation between, cytotypes could indicate either a recent origin of the polyploid or a primary origin of the hybrid zone¹¹. Secondary hybridization involving allopolyploids and their diploid parents have not often been observed in nature. In the *Senecio* (Asteraceae) complex, although hybrids artificially produced from the allohexaploid *Senecio*

cambresis and one of its parents (*Senecio vulgaris*) were fertile, they were not found in wild populations¹². Primary hybrid zones between natural allopolyploids and their diploid relatives have been reported in several allopolyploid complexes for which the time of emergence is known^{11,13}.

In a hybrid zone between sexual diploids and polyploids, two forms of hybrid can be distinguished (Fig. 1). Type I hybrids have a ploidy level intermediate between the parents, such as triploids in the case of diploid–tetraploid crosses, whereas type II hybrids have the same ploidy level as one of the parents. Only type II hybrids (diploid and triploid) are produced in the presence of sexual diploids and asexual triploids¹⁴. Type I hybrids are often sterile, whereas type II hybrids are as fit or even better than the parents⁵. Both type I and type II hybrids might have considerable influence on gene transfer between ploidy levels, increasing genetic diversity of the polyploid and influencing the dynamics of the hybrid zone^{5,6}.

Gene flow between diploids and polyploids can occur directly through type II hybrids or indirectly via type I hybrids (e.g. triploid bridge)^{5,6,15}. In some sexual taxa, the production of $2n$ gametes (Box 1) and the high fitness of type II compared with the absence of established type I

hybrids suggest that gene flow occurs mainly from diploids to tetraploids^{10,11,16}. However, in other situations, bilateral gene flow via established type I hybrids was found^{6,14,15}.

The existence of genetic patterns between diploid and polyploids is frequently interpreted as evidence for multiple origins in polyploids. However, the evidence put forward for multiple origins can often be interpreted in other ways¹¹. In particular, gene flow by $2n$ gametes, followed by the establishment of the introgressant, might produce similar patterns. Moreover, in whitlow grass (*Draba*, Brassicaceae), evidence of both recurrent polyploidization and gene flow between different ploidy levels has been obtained, leading to complex taxonomic relationships¹⁷.

The evolution of isolation mechanisms in diploid–polyploid hybrid zones

The possible scenarios concerning the origin of both auto- and allopolyploids has recently been reviewed⁶. However, as stressed by Ramsey and Schemske⁶, much work is needed to test among these scenarios. The factors that influence the maintenance of two ploidy levels in primary and secondary reproductive contacts also remain poorly studied^{18,19}. Because neopolyploids occur in a diploid population, their establishment will depend directly on a capacity to maintain a viable population during successive generations or to rapidly colonize new areas.

Conditions for autopolyploid establishment

The conditions allowing stable coexistence of polyploids and diploids under random mating have been examined in several theoretical approaches. Levin²⁰ first considered the evolution of a mixture of semelparous and allogamous diploids and tetraploids producing only lethal type I hybrids (triploids). This model, known as the 'minority cytotype exclusion principle' showed that the proportion of the rarer cytotype decreased rapidly as a result of positive frequency-dependent selection, ultimately leading to extinction of the rarer cytotype. In other words, the rare cytotype produces a higher

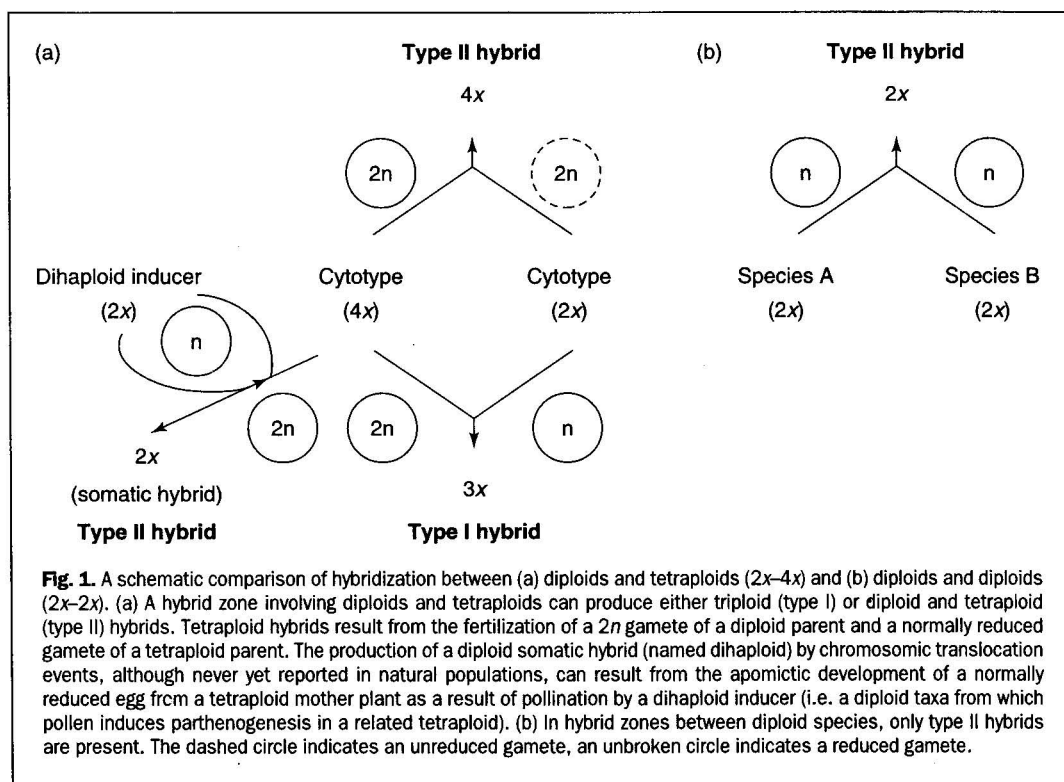


Fig. 1. A schematic comparison of hybridization between (a) diploids and tetraploids ($2x-4x$) and (b) diploids and diploids ($2x-2x$). (a) A hybrid zone involving diploids and tetraploids can produce either triploid (type I) or diploid and tetraploid (type II) hybrids. Tetraploid hybrids result from the fertilization of a $2n$ gamete of a diploid parent and a normally reduced gamete of a tetraploid parent. The production of a diploid somatic hybrid (named dihaploid) by chromosomal translocation events, although never yet reported in natural populations, can result from the apomictic development of a normally reduced egg from a tetraploid mother plant as a result of pollination by a dihaploid inducer (i.e. a diploid taxa from which pollen induces parthenogenesis in a related tetraploid). (b) In hybrid zones between diploid species, only type II hybrids are present. The dashed circle indicates an unreduced gamete, an unbroken circle indicates a reduced gamete.

proportion of inviable triploid offspring as a consequence of pollination by the common cytotype. Other models have since investigated the role of several parameters in the maintenance of a viable polyploid population under random mating, and focused on the following:

- The rate of $2n$ gamete production by the diploids and the fitness of the polyploids.
- The relative competitive ability of cytotypes.
- The life history of polyploids.
- Demographic stochasticity.

Models developed by Felber²¹ and Bever and Felber²² have shown that when diploids produce $2n$ gametes, higher fitness of the polyploid combined with partial fertility of

Box 1. Glossary

- Allogamous or outcrossing:** an allogamous or outcrossing individual is partially or obligatorily fecundated by pollen or spermatozooids from another individual.
- Allopatry:** two groups of individuals live in allopatry if they are spatially isolated.
- Allopolyploid:** polyploid formed by the fusion of $2n$ gametes from two distinct species, or by doubling of the somatic chromosome number of an interspecific hybrid at the diploid stage.
- Apomictic:** an apomictic organism reproduces directly from its somatic or sexual cells, without fecundation.
- Autogamous or selfing:** an autogamous or selfing individual is partially or obligatorily fecundated by its own pollen or spermatozooids.
- Autopolyploid:** polyploid formed by the fusion of two genomes of the same species.
- Cytotype:** refers to a group of individuals sharing the same cytological characteristics (e.g. the same ploidy level).
- $2n$ gametes:** gametes with the somatic chromosome number; $2n$ gametes are due to meiotic failure governed by genetic or environmental factors⁵.
- Minority cytotype exclusion:** a model¹⁹ of frequency-dependent selection against the rarer cytotype when two populations with different ploidy levels grow in sympatry.
- Neopolyploid:** a new polyploid organism arising in a population of organisms with lower ploidy levels.
- Parapatry:** two populations live in parapatry if their distributions touch each other but do not intermingle.
- Ploidy level:** characterizes the degree of polyploidy of an organism (e.g. diploid and tetraploid).
- Semelparous:** organisms that reproduce several times during their lifetime.
- Sympatry:** characterizes situations in which two groups grow in mixture.
- Triploid block:** this describes the failure of endosperm development, and is responsible for the abortion of a high proportion of triploid progenies produced in $4x-2x$ and $2x-4x$ crosses^{5,6}.

Table 1. Example of postzygotic and prezygotic reproductive isolation observed in natural diploid–polyploid contact zones^a

Family	Polyploid complex	Ploidy levels	Postzygotic isolation	Prezygotic isolation mechanism				Refs
				Habitat differentiation	Phenological differentiation	Behavioral barrier	Reproductive system	
Plants								
Juglandaceae	<i>Carya ovata</i> – <i>C. tomentosa</i>	2x and 4x	no	no	no	?	yes	52
Fabaceae	<i>Lotus corniculatus</i> s.l.	2x and 4x	triploid block	yes	yes	?	?	38,53
Saxifragaceae	<i>Heuchera grossularifolia</i>	2x and 4x	?	?	yes	?	?	51
Plantaginaceae	<i>Plantago media</i>	2x and 4x	triploid block	no	yes	?	no	40
Asteraceae	<i>Taraxacum</i> spp.	2x and 3x	?	no	no	?	yes	14
Poaceae	<i>Anthoxanthum alpinum</i>	2x and 4x	triploid block	yes	yes	?	yes	8
	<i>Arrhenatherum elatius</i>	2x and 4x	3x sterility	?	yes	?	yes	9
	<i>Dactylis glomerata</i>	2x and 4x	3x sterility	yes	yes	?	?	16,37
	<i>Tragopogon</i> spp.	2x and 4x	?	yes	?	?	?	31
Animals								
Artemiidae	<i>Artemia pathenogenetica</i>	2x, 4x and 5x	?	yes	?	?	?	35
Bufoidea	<i>Bufo viridis</i>	2x and 4x	3x sterility	?	?	yes	?	24,42
Hylidae	<i>Hyla versicolor</i> – <i>H. chrysoscelis</i>	2x and 4x	3x sterility	?	?	yes	?	41

^aKey: ?, unknown; characters in bold and italic indicate possible reinforcement; 2x, diploid; 3x, triploid; 4x, tetraploid; 5x, pentaploid.

type I hybrids can promote the establishment and stable coexistence of the polyploid. However, the production of $2n$ gametes by diploids in natural populations is unknown in many species, even though $2n$ gametes and viable triploids that have partial fertility are produced frequently in controlled experiments^{5,6}. Also, triploid individuals have been found in most hybrid zones between diploids and autotetraploids^{7,9,23,24}. In their models, Fowler and Levin²⁵ demonstrated that a greater competitive ability of the polyploids cannot permit their maintenance *per se*. However, when a higher competitive ability is combined with higher fecundity, selfing or habitat segregation between cytotypes, the likelihood of polyploid maintenance increases²⁶. Recently, Rodriguez²⁷ has shown that demographic stochasticity and iteroparity of a polyploid can enhance its chance of successful establishment in a diploid population. Only a few experimental works are available to improve the relevance of such models^{28,29}. Vogel *et al.* suggest that within the fern genus *Asplenium* apomictic autotetraploids colonize new areas more rapidly because they can self-fertilize (so a single spore can generate an adult plant that can reproduce alone by selfing) than sexual diploids, which cannot self-fertilize³⁰. This difference in colonizing ability between cytotypes might have helped autotetraploids to escape minority cytotype exclusion in diploid parental populations after the last glaciation: autotetraploid *Asplenium* spp. are now widespread in Northern Europe whereas diploids are restricted to Mediterranean refugia.

Conditions for the establishment of allopolyploids

No theoretical investigation has focused on the factors that specifically govern the establishment of allopolyploids following hybridization between two diploid species. However, most of the results obtained in autopolyploid models (i.e. habitat differentiation and reproductive system evolution) can be extended to allopolyploids. Thompson and Lumaret¹⁹ have examined the conditions for allopolyploid establishment. Establishment and spread of allopolyploids could result from local exclusion of diploid parents, such as in the *Tragopogon* polyploid complex in northern USA (Ref. 31), or by offspring of the diploid progenitors colonizing intermediate habitat,

leading to a greater partitioning of the habitat³². Empirical data indicate that an allopolyploid can be fitter than either parents under certain conditions^{13,33}. Allopolyploids can be considered as fixed hybrids and might illustrate the hybrid-superiority hypothesis of Moore³⁴, who postulated that hybrid zones can be maintained if hybrids are more fit than parental phenotypes in some environments. Higher average fitness of the hybrid compared with the pure species might be a distinctive feature of hybrid zones involving allopolyploids.

The evolution of isolating mechanisms between cytotypes of different ploidy levels

Recent studies of hybrid zones involving two ploidy levels have provided much important information concerning the evolution of different isolating mechanisms between cytotypes (Table 1). The evolution of assortative mating causing prezygotic isolation can result directly from polyploidization *per se* or via selection (such as the production of inviable hybrids). The relative role of polyploidization and reinforcement in the evolution of prezygotic isolation mechanisms appears to be species and context dependent. Numerous empirical and experimental studies of hybrid zones in plant or animal polyploid complexes suggest that the evolution of assortative mating can be attained by a variety of factors, such as ecological specialization, flowering time divergence, behavioural isolation and selfing or vegetative propagation (Table 1).

Selection for ecological specialization in diploid–tetraploid hybrid zones might limit gene exchange among cytotypes. In several polyploid complexes, spatial segregation has been related to the different ecological requirements of the cytotypes^{8,35}, suggesting that their relative fitness is a function of the environment. Experimental data suggest that polyploidization might increase ecological flexibility or colonization ability³⁶ and hence increase the probability that polyploids evade minority cytotype exclusion^{11,19} (i.e. colonize and establish in areas where diploids are absent, as in the fern genus *Asplenium*³⁰).

In many hybrid zones between plant cytotypes, the occurrence of flowering time divergence is a common isolating mechanism^{7,9,37,38}. In two grass species, cock's foot (*Dactylis glomerata*) and tall oat-grass (*Arrhenatherum elatius*),

the occurrence of concordant flowering divergence in both natural and controlled environments strongly suggests that this trait is genetically fixed^{9,37}. Several studies indicate that reinforcement (i.e. selection) rather than polyploidization is the cause of flowering time divergence. For example, Bretagnolle and Lumaret³⁹ found no divergence between diploid and neopolyploid *Dactylis glomerata* obtained by sexual polyploidization, although flowering time divergence exists in diploids and related tetraploids collected in a natural hybrid zone and grown in controlled conditions. Some evidence for selection that reinforces flowering time divergence between cytotypes has recently been observed (P. van Dijk, PhD thesis, University of Groningen, 1991; but see Ref. 9). The conditions allowing such reinforcement of flowering time divergence between cytotypes caused by inviable type I hybrids have been studied in an isolation-by-distance model⁴⁰; flowering divergence by reinforcement can evolve in a hybrid zone if cytotypes have a patchy or parapatric distribution.

Behavioural isolating mechanisms between taxa with different ploidy levels have been reported in many frog and toad species^{24,41,42}. In several species, the call structure is markedly different between diploids and polyploids, which has led to assortative mating^{24,41}. For example, the advertisement call of diploid green toads (*Bufo viridis*, Bufonidae) has a spectral and temporal structure that is markedly different from tetraploids in the hybrid zone⁴². The abrupt evolution of assortative mating as a direct response to polyploidization in relation to behavioural mechanisms could also be a major component of the successful establishment or coexistence of animal-pollinated species. Polyploidization in plants pollinated by animals could affect the attractiveness of flowers for pollinators because chromosome doubling can directly affect organ size and metabolite content. Higher attractiveness of polyploid flowers might enhance their relative fitness compared with diploid ones and consistently increase the likelihood of their maintenance.

Finally, the evolution of uniparental reproduction (i.e. asexual reproduction or selfing) can be an important component of both the establishment and the coexistence of diploids and polyploids^{19,20,26}. The evolution of asexual reproduction as a direct consequence of polyploidy is an abrupt process that can isolate polyploids from diploids. However, even if asexual reproduction is frequently or almost exclusively associated with polyploidy, particularly in animals, there is no evidence that this has been selected to avoid reproductive contact between polyploids and related diploids.

Theoretical models have demonstrated that selfing can increase the likelihood of polyploid maintenance in hybrid zones^{20,26}, although the evolution of selfing is constrained by the consequence of inbreeding on fitness²². Experimental studies do not show a clear relationship between inbreeding depression, selfing rate and ploidy level^{19,22,43,44}. Selfing rate was higher in both diploids and autotetraploids of the grass *Arrhenatherum elatius* in hybrid zones compared with allopatric populations, suggesting reinforcement by selfing in the contact zone⁹ (Fig. 2). In *Anthoxanthum alpinum* (Poaceae), there was an increase in self-compatibility in both contact zones and pure zones in tetraploids compared with diploids (C. Zerroual Humbert-Droz, PhD thesis, Université de Neuchâtel, 1995). However, such differences were not observed in diploid and tetraploid *Plantago media* (Plantaginaceae) within hybrid zones⁴⁰. Gametic selection can also lead to assortative mating in hybrid zones. For example, under controlled conditions,

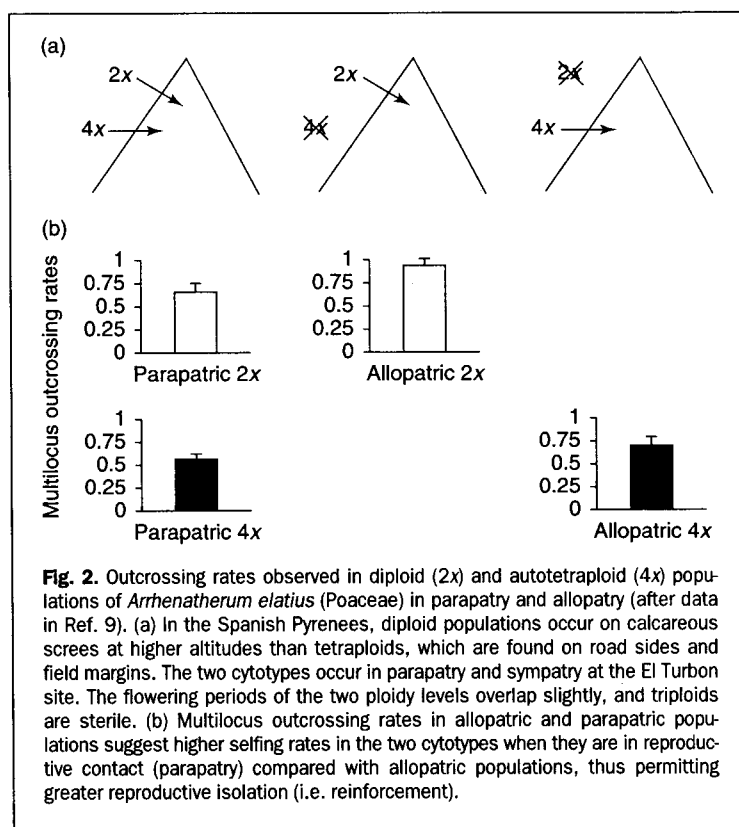


Fig. 2. Outcrossing rates observed in diploid (2x) and autotetraploid (4x) populations of *Arrhenatherum elatius* (Poaceae) in parapatry and allopatry (after data in Ref. 9). (a) In the Spanish Pyrenees, diploid populations occur on calcareous screes at higher altitudes than tetraploids, which are found on road sides and field margins. The two cytotypes occur in parapatry and sympatry at the El Turbon site. The flowering periods of the two ploidy levels overlap slightly, and triploids are sterile. (b) Multilocus outcrossing rates in allopatric and parapatric populations suggest higher selfing rates in the two cytotypes when they are in reproductive contact (parapatry) compared with allopatric populations, thus permitting greater reproductive isolation (i.e. reinforcement).

diploid pollen from triploid plants induced self-fertilization in diploid *Taraxacum* (Asteraceae)⁴⁵.

Although several studies suggest that various isolating mechanisms have evolved to reinforce postmating isolation between related cytotypes, most of these suffer from inadequate comparisons between contact zones and allopatric populations (Table 1). Thus, assortative mating causing prezygotic isolation in hybrid zones could result from either polyploidization itself or selection.

The role of hybrid zones in the evolution of polyploid complexes

We have argued that assortative mating causing prezygotic isolation can evolve in many hybrid zones involving different ploidy levels. In contrast, evidence of gene flow is repeatedly documented, suggesting that isolation between ploidy levels is not complete. Such reproductive interactions might have important antagonistic consequences for the evolution of polyploid complexes.

The production of sterile hybrids (e.g. triploids produced in diploid–tetraploid contact zones) can favour the evolution of reproductive isolation (as already discussed), and hence might play a critical role (i.e. promoting stability) in the local distribution of related cytotypes. However, some benefits of gene flow between related cytotypes are well known. First, although it has never been proved experimentally, it has often been argued that gene flow from diploids to polyploids inflates the genetic diversity of polyploids or both ploidy levels. For example, in *Taraxacum*, partial reproductive isolation and bidirectional gene flow between sympatric sexual diploids and facultative apomictic triploids suggest that hybridization helps to maintain high levels of genetic diversity (i.e. adaptive potential to long-term environmental changes), whereas apomixis (reproduction without fertilization) will favour a high degree of local adaptation¹⁴. In the case of apomixis, gene flow between ploidy levels could be maintained by selection.

Second, gene flow might favour the transfer of adaptation from one cytotype to the other. In a recent paper, Rieseberg *et al.*⁴⁶ demonstrated that, although interactions between coadapted genes strongly constrain the genomic composition of hybrids in diploid *Helianthus* (Asteraceae), a non-negligible proportion of these gene combinations might be favourable to the adaptive evolution of hybrids. In theory, it is thus possible that such unidirectional 'transfer of adaptation' from diploids to tetraploids by the production of type II hybrids inflates tetraploid adaptability to diploid environments⁴⁷ and hence, as often suggested, their competitive superiority²⁸ compared with diploids.

The third possible consequence of introgression is the origin of new adaptations or new types. This is illustrated, for example, by *Senecio*, for which two types of tetraploid-stabilized introgressant originated following hybridization between the indigenous tetraploid *S. vulgaris* and the introduced diploid *S. squalidus*⁴⁸. Finally, gene transfer might create genetic novelties, causing the production of new enzymes⁴⁹, which, combined with disruptive selection, might lead to niche differentiation and allow polyploids to colonize new areas.

Factors other than gene flow and the evolution of reproductive isolation could play a crucial role in the maintenance of related cytotypes in contact zones. For example, one factor that has recently been addressed is the variation in pathogen resistance among related cytotypes. Guégan and Morand⁵⁰ suggested that a positive correlation between parasite richness and ploidy level in cyprinid fish species results from more efficient specific resistances as a consequence of higher genetic diversity in polyploids, which might provide a chance for polyploids to combat pathogens more efficiently. Recent work by Thompson *et al.*⁵¹ has shown lower levels of infestation by a specific pathogen (*Greya politella*) in tetraploid *Heuchera grossulariifolia* (Saxifragaceae) than in diploid populations. In mixed cytotype zones, tetraploids flowered earlier than diploids, perhaps as a result of the evolution of reproductive isolation. In such contact zones, higher rates of pathogen attack were reported in tetraploids compared with sympatric diploids. The authors suggested that this overlap in flowering dates of tetraploids *H. grossulariifolia* and another host, *Lithragma parviflorum*, could provide a chance for the pathogen to increase female reproductive success by widening the range of available hosts. Higher levels of infestation in tetraploids might then theoretically favour their own local exclusion. This illustrates two antagonistic selective forces concerning polyploidization and pathogen resistance. Future studies should focus on the sensitivity of allopatric and sympatric or parapatric diploid and tetraploid populations to pathogens.

Conclusions

Recent research has provided useful information about processes acting in hybrid zones involving taxa and/or cytotypes of different ploidy level. Such information is of fundamental importance for our general understanding of the different factors that allow polyploid establishment and evolution. Several aspects of diploid–polyploid hybrid zones merit more attention. First, the importance in prezygotic isolation of the direct consequences of polyploidization and of reinforcement need to be clearly identified. Second, the role played by $2n$ gametes in gene flow and introgression, although suspected to be important, also needs further exploration. Third, the evolution of prezygotic isolation is antagonistic to some beneficial genetic interactions whose importance remains to be defined. Fourth,

more theoretical models and empirical data are needed concerning allopolyploids.

Finally, two new avenues of research merit consideration. First, the influence of polyploidization on floral traits and hence pollinator behaviour could be a major component of the evolutionary stability of diploid–polyploid hybrid zones. Second, interactions with other taxa, such as competition or host–parasite interactions, could play a role in determining polyploid establishment and in the maintenance of hybrid zones.

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