**The emerging importance of cross-ploidy hybridisation and introgression**

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**Abstract**

**Introduction**

Climate change, habitat disturbance, and large-scale translocations resulting from human activities are increasing contacts between species previously isolated by geographical and ecological barriers, thus raising their potential to hybridise (Crispo et al., 2011, Brennan et al., 2014, Larson et al., 2019). Closely related species isolated only by prezygotic barriers are more likely to hybridise (Vallejo-Marin and Hiscock, 2016), but even species isolated by very strong postzygotic barriers do hybridise in some instances. Polyploidy (see Glossary), which is particularly common in plants, creates a very strong postzygotic barrier between species that differ in ploidy. Cross-ploidy hybridisation is therefore usually considered rare because hybrids will have unbalanced chromosome content and therefore irregular pairing of chromosomes, rendering the hybrid infertile. Should a triploid hybrid form, it is normally either completely or partially sterile, due to the formation of malfunctioning gametes containing unbalanced chromosome numbers. On occasion, however, some species differing in ploidy do produce hybrid offspring. The importance of such events is not to be underestimated; for example, cross-ploidy hybridisation has led to the origin of some very recently originated plant species, which are now models for the study of polyploid speciation (Vallejo-Marin and Hiscock, 2016), and also to the origin of some of our most important crop plants, including wheat, sweet potato and sugar cane. Nonetheless, the frequency of cross-ploidy (or interploidy) hybridisation in the wild is a neglected topic, with information related to it scattered through the literature. Here, we bring this information together and emphasise its biological significance.

The first known artificial hybrid from crossing two parents of differing ploidy level was created by Kölreuter in 1761 between diploid *Nicotiana paniculata* and allotetraploid *N.* *rustica.* This hybrid was known as the first “botanical mule” due to its shrivelled anthers and malformed ovaries, indicative of sterility (Roberts, 1929). Further artificial crosses demonstrated the formation of other cross-ploidy hybrids that were partially or completely sterile, but nothing was discovered of the frequency or importance of the phenomenon in the wild until much later (Lawrence, 1936). Beginning around the mid C20th, cytogenetic studies became more frequent and revealed extensive ploidy variation both within and between species, and which could be used to explain evolutionary relationships (Love and Love, 1943, Stebbins, 1956). However, it was with the availability of multiple nuclear markers in the 1990s that researchers reliably detected hybridisation and introgression between species of differing ploidy (Nason et al., 1992, Abbott et al., 1992a). Now, by examining many thousands of genetic markers or the complete genomes of target species, there is potential to detect cases of adaptive introgression (Suarez-Gonzalez et al., 2018). Moreover, through focusing on specific genes, examples are now known of cross-ploidy introgression resulting in the transfer of particular traits that markedly affect the biology and fitness of recipient species (Kim et al., 2008, Chapman and Abbott, 2010, Baduel et al., 2018, Monnahan et al., 2019)

While there have been many recent reviews on the mechanisms that underlie polyploidy and the prevalence of polyploids in nature (e.g. (Alix et al., 2017, Marques et al., 2018, Soltis et al., 2004, Chen, 2010, Kohler et al., 2010), and on the importance of natural hybridisation (Abbott et al., 2013, Suarez-Gonzalez et al., 2018, Soltis and Soltis, 2009, Todesco et al., 2016), our aim is to reconcile early work on cytological variation with recent work on genomics, to consider whether cross-ploidy hybridisation may be more prevalent and important than previously known. We first summarise the ways in which cross-ploidy hybrids may form. Next, we reviewthe prevalence of cross-ploidy hybridisation, both in the case of the British and Irish flora, which includes comprehensive data on hybridisation and ploidy, and in the wider published literature, allowing us to generalise about the occurrence in nature. Lastly, we explore the biology of cross-ploidy hybrids and the potential long-term evolutionary outcomes, and discuss how advances in sequencing technology and analytical tools may aid detection to assess more accurately the state of cross-ploidy hybridisation in nature. We emphasise case studies in flowering plants, where hybridisation and polyploidy are particularly prevalent and well-documented, but also consider other organismal groups where cross-ploidy hybridisation may occur.

**Mechanisms of cross-ploidy hybrid formation and persistence**

the ploidy ratio of the pollen:style in plants is of particular importance(Stace, 1975, Watkins, 1932), and following fertilisation is a period where endosperm development and (epi)genetic compatibilities are critical (Bomblies and Weigel, 2007, Lafon-Placette and Kohler, 2016).

There are two main pathways to creation of cross-ploidy hybrids; either through reduced or unreduced gametes. Reduced (“normal”) gametes of the both parental species results in the generation of a hybrid with intermediate ploidy. These hybrids, usually triploids derived from diploid-tetraploid crosses, are common and found in a variety of taxa where congeners co-occur, for example *Aconitum*, *Ficaria*, *Dactylorhiza* and *Senecio* (Sutkowska et al., 2017, Popelka et al., 2019, De Hert et al., 2012, Irwin and Abbott, 1992). A barrier to the creation of these hybrids through reduced gametes is known under the umbrella term ‘triploid block’ (Ramsey and Schemske, 1998, Kolar et al., 2017). Early work on experimental diploid-autopolyploid crosses established the presence of a triploid block and that direction of crosses was important (Valentine and Woodell, 1960, Stebbins, 1971, Thompson, 1930). The major cause of triploid block is attributed to genomic conflict in the maternal endosperm, which is usually triploid and composed of a ratio of two maternal and one paternal genomes (Lafon-Placette and Kohler, 2016). Deviations from this ratio cause the endosperm to malfunction in development and function (Kohler et al., 2010). Reciprocal crosses differ in their likelihood of success, and it is a general phenomenon that crosses where the higher ploidy parent is female are more likely to produce viable offspring, due to endosperm ratios which are better tolerated (Burton and Husband, 2000); Figure XX panels **a** and **b**). Triploid block may also be caused by the action of allelic incompatibilities at an early stage in development, although this topic is little explored (Scott and Bolbol, 2013). A second possibility in the creation of cross-ploidy hybrids is where the lower ploidy parent produces unreduced (“polyploid”) gametes. Unreduced gamete production is on average 0.1-2% per individual, with rare individuals and hybrids that produce considerably higher frequencies (>85%) (Kreiner et al., 2017a, Mason and Pires, 2015, Kreiner et al., 2017b). In addition, many different taxa produce unreduced gametes, and their production also varies with environmental variables (Baduel et al., 2018, Rice et al., 2019). Successful crosses occur more readily when unreduced gametes are produced by the diploid parent, thus restoring the gamete ploidy to that of the higher ploidy parent (Figure XX panel **c**) (Ramsey and Schemske, 1998).

After a cross-ploidy hybrid has formed, three outcomes may occur. The hybrid individual or population may either die before reaching maturity or go extinct, act as a conduit to gene flow between ploidy levels, or persist and establish to form a new hybrid entity or species. Firstly, extinction of the hybrid is highly likely if it is formed at low frequencies and parental species are rare (i.e. low propagule pressure; (Fowler and Levin, 2016)). The growth and development of the hybrid can be affected by bringing together incompatible parental allelic combinations, causing the hybrid to be unfit (e.g. hybrid necrosis; (Bomblies and Weigel, 2007)). Ultimately, fertility of an F1 hybrid will determine its persistence in a population, as even low levels of outcrossing can promote gene flow between ploidy levels through backcrossing with parental species. For a triploid F1 hybrid, there are two pathways to generate a backcross of equivalent ploidy to one of the parental species. Firstly, the triploid F1 may produce reduced pollen which combines with reduced pollen from the diploid male parent (Figure XX panel **a**) which has been hypothesised to occur in *Euphrasia* and *Aconitum* (Yeo, 1956, Sutkowska et al., 2017). Secondly, the triploid F1 hybrid can produce unreduced gametes that can either combine with reduced gametes from the tetraploid parent or unreduced gametes from the diploid parent (Figure XX, panel **b**; e.g. *Senecio eboracensis*; (Lowe and Abbott, 2004)). Tetraploids therefore are much more readily produced, as in addition to the two pathways mentioned, tetraploids can be produced in a single generation following cross-ploidy hybridisation (Figure XX panel **c**). The bias towards tetraploid production has been known since Stebbins in the 1950s (Stebbins, 1956) and is the reason why introgression in the direction of the tetraploid is more common (Baduel et al., 2018).

**Frequency and occurrence of natural cross-ploidy hybrids**

Of major interest is how common cross-ploidy hybrids are in nature given the varied constraints of both pre and postzygotic isolation in their generation . In cross-ploidy hybridisation the usual reproductive barriers to cross species mating apply, such as differences in geography, phenology, morphology and mating system etc. (Laport et al., 2016, Kay, 2006, Martin and Willis, 2007), along with specific factors associated with ploidy level difference between parental species, such as the the sterility barriers outlined above. The evidence required to prove cross-ploidy hybridisation is confirmation of parental ploidy differences, which may come from chromosome counts (Rice et al., 2015), genome size estimates (Leitch, 2019) or genomic information (Ranallo-Benavidez et al., 2020), and evidence of hybridisation, which may be from genetic data or from other sources such as morphology (Rieseberg and Ellstrand, 1993); though see issues with using morphological data to detect hybrids below).

Although worldwide, the majority of plant species are diploid (~67%, (Rice et al., 2019), extensive variability in ploidy levels exist at all taxonomic levels and scales (Kolar et al., 2017, Soltis et al., 2010). Both the spatial and phylogenetic distribution of ploidy variation are unlikely to be uniform however, due to climatic and clade specific effects on unreduced gamete formation (Kreiner et al., 2017a, Bretagnolle and Thompson, 1995, Rice et al., 2019). The current wealth of cytological data suggests, however, that at least 10% of plant species are autopolyploids, with allopolyploids estimated to be at least as frequent (Kolar et al., 2017, Soltis et al., 2010, Barker et al., 2016). In contrast to flowering plants, polyploidy in animals and fungi is thought to be rare, famously so in mammals and birds, though many examples are known in certain lineages of amphibians, teleost fish and reptiles (Spoelhof et al., 2020).

While there are extensive estimates of ploidy variation across the tree of life, the frequency of cross-ploidy hybridisation remains unknown. Our best general estimate of this in plants may come for the

the British and Irish flora, which contains a manageable number of native species (~1500, excluding large taxonomically complex groups (Stace, 2019)), and is exceptional in having near complete information on species chromosome counts (BSBI, 2019), and the extent of natural hybridity (Stace et al., 2015). A recent study of the British flora showed species with the same ploidy are 35% more likely to produce hybrids than parents of differing ploidy, when accounting for parental geographic distributions and phylogenetic effects (ref). To further characterise the prevelance of cross-ploidy hybridisation, we looked at variation across families. Most of the 1295 species for which there is detailed ploidy information are diploids (56%), with higher ploidy levels becoming exponentially less common (Figure XX panel a). Between families, however, the distribution of ploidy levels changes significantly, which alters the raw material for cross-ploidy hybridisation to act on (Supplementary Figure XX). In terms of hybridisation, there are 909 known hybrids present in the flora (Stace et al., 2015). Of the 588 hybrids that contain ploidy information (321 hybrids lack appropriate data), 203 cross-ploidy hybrids have formed in Britain and Ireland (35%; Supplementary Table XX), in comparison to 385 intraploidy hybrids (65%). Cross-ploidy hybrids occur in 67 genera, with over a quarter present in the genera Rumex (Polygonaceae, 24), Salix (Salicaceae, 19) and Euphrasia (Orobanchaceae, 13; Figure XX). The majority (55%) of cross-ploidy hybrids involve diploid-tetraploid crosses, with higher order ploidy crosses closely following (43%), and diploid-triploid crosses in the minority (2%). In addition to flowering plants, cross-ploidy hybridisation is likely to be prevalent in other plant groups within the British and Irish flora, such as ferns and fern allies, due to highly variable ploidies and abundant hybridisation. Although the literature on this is currently limited, one dramatic example, inferred based on morphology and habitat, occurs in the lycopod genus *Isoetes*, where the diploid *I. echinospora* (2n = 22) hybridises with the decaploid *I. lacustric* (2n = 110) to produce a hexaploid hybrid (2n = 66).

Inferring hybridisation from morphology, geography, cytology and limited genetic data, as is the case with many hybrids in the British and Irish flora, overlooks cryptic hybridisation and introgression that can be detected with multiple nuclear genetic markers. Moreover, the extent of cross-ploidy hybridisation in this flora is likely to be affected by extensive habitat disturbance and recent postglacial divergence. A wider survey of published studies of hybridisation based on multiple genetic markers or strong cytogenetic evidence reveals 43 different parental species combinations from 48 studies resulting in cross-ploidy hybridisation, with such hybrids present in 33 genera from 16 angiosperm families, three fern families, and three animal families (Table 1). Diploid-tetraploid crosses are found in 32 of the 43 parental crosses, with the rest being higher ploidy crosses. This confirms that cross-ploidy hybridisation is likely to be much more widespread than is currently appreciated.

The taxonomic spread of cross-ploidy hybridisation is especially broad in angiosperms, as evidenced by data both from the British and Irish flora and the wider literature. For example, monocots are well represented (Liliaceae, Orchidaceae, Poaceae), as are basal eudicots (Ranunculaceae, Papaveraceae) and throughout the rest of the phylogenetic tree scattered in the Fabids, Malvids and Superastrids. This distribution indicates cross-ploidy hybridisation is very widespread and potentially abundant throughout the flowering plant phylogeny (Figure X). On the other hand, the conspicuous absence of records from large, diverse families with variable ploidy, such as Rubiaceae potentially indicate a phylogenetic skew in cross-ploidy hybridisation. Cases of such hybridisation are not just phylogenetically but also geographically widespread, with examples reported from across four continents, though tropical regions are poorly represented and most studies report hybridisation in large temperate or cosmopolitan plant families (e.g. Asteraceae and Orchidaceae). In terms of life form, most well-documented cross-ploidy hybrids (with the notable exception of *Euphrasia*) are perennial, a factor which correlates strongly with hybridisation regardless of parental ploidy level (Mitchell et al., 2019).

In animal groups where diploids and polyploids are both present there may be cross-ploidy hybridisation and subsequent introgression, though based on the published literature this is very uncommon, with only three well-studied examples (Table 1). In many other cases where taxa with contrasting ploidies mate introgression is limited, as the hybrid derivatives are hybridogenetic taxa which lack recombination. For example, the edible frog *Pelophylax esculentus* is an extremely ecologically successful and widespread hybrid species formed between the diploid taxa *P. ridibundus* and *P. lessonae.* It includes two cytotypes, a diploid and a triploid, with the triploid formed and maintained by haploid sperm fertilising unreduced eggs from a diploid hybrid female (Hoffmann et al., 2015). However, it appears to be in a state of flux, with no documented all-triploid populations, and tetraploids extremely rare. Opportunities for novel allelic combinations and introgression are limited as the parental genomes rarely recombine.

**Table 1 –** Studies reporting cross-ploidy hybrids based on cytological and/or molecular genetic analyses. Details are provided of the family, hybridising species, broad geographic locality, and the direction of introgression (if known). Superscripts indicate whether the polyploids are allopolyploid (allo) or autopolyploid (auto). Note that the ploidy refers to evidence of cross-ploidy hybridisation based on material presented in the specific study; other ploidy levels may also be found for these species.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Family** | **Hybridising species** | **Location** | **Direction to** | **Reference** |
| ***Animals*** | | | | |
| Bufonidae | *Bufo turanensis* (2n = 2x =22) X *Bufo pewzowi* (2n = 4x = 44)allo | Kyrgyzstan | Diploid | (Stöck et al., 2010) |
| Cyprinidae | *Squalius alburnoides* (2n = 2x = 50; 3n = 75; 4n = 100) X *S. pyrenaicus* (2n = 2x = 50)allo | Iberia | - | (Alves et al., 2001, Crespo-López et al., 2007) |
| Myobatrachidae | *Neobatrachus sutor* (2n = 2x = 24) x *N. kunapalari* (2n = 4x = 48)auto | Australia | Tetraploid | (Novikova et al., 2020) |
| ***Plants*** | | | | |
| Aspleniaceae | *Asplenium scolopendrium* (2n = 2x = 72) x *A. adiantum-nigrum* (2n = 4x = 144) | Britain | - | (Stace et al., 2015) |
| Cyatheaceae | *Gymnosphaera denticulata* (2n = 2x = 138) x *G. metteniana* (2n = 4x = 274)allo | China | Tetraploid | (Wang et al., 2020) |
| Dryopteridaceae | *Polystichum setiferum* (2n = 2x = 82) x *P. aculeatum* (2n = 4x = 164) | Britain | - | (Manton, 1950) |
| Asteraceae | *Achillea clype*olata (2n = 2x = 18) x *A. collina* (2n = 4x = 36)allo | Bulgaria | Tetraploid | (Guo et al., 2005) |
| Asteraceae | *Achillea setacea* (2n = 2x = 18) x *Achillea collina* (2n = 4x = 36) |  |  | (Ma et al., 2010) |
| Asteraceae | *Achillea asplenifolia* (2n = 2x = 18) x *Achillea collina* (2n = 4x = 36) |  |  | (Ma et al., 2010) |
| Asteraceae | *Centaurea pseudophrygia* (2n = 2x = 22) x *C. jacea* (2n = 4x = 44) | Czech Republic | - | (Koutecky et al., 2011) |
| Asteraceae | *C. indicum* (2n = 4x = 36) and *C. vestitum* (2n = 6x = 54) | China | Both |  |
| Asteraceae | *Cirsium carniolicum* ssp. *rufescens* (2n = 2x = 16) x *C. palustre* (2n = 4x = 34) | France | Tetraploid | (Segarra-Moragues et al., 2007) |
| Asteraceae | *Ixeris repens* (2n = 2x = 16) x *I. debilis* (2n = 6x = 48)auto | Japan | Hexaploid(?) | (Denda and Yokota, 2003) |
| Asteraceae | *Packera paupercula* (2n = 4x = 44) x *P. indecora* (2n = 8x = 88) | USA; Michigan | - | (Kowal et al., 2011) |
| Asteraceae | *Senecio madagascariensis* (2n = 2x) x *S. pinnatifolius* (2n = 4x) | Australia | - | (Prentis et al., 2007) |
| Asteraceae | *Senecio squalidus* (2n = 2x = 20) x *S. vulgaris* (2n = 4x = 40)allo | Britain | Tetraploid; chromosome doubling | (Abbott et al., 2007); (Irwin and Abbott, 1992); (Abbott et al., 1992b); (Chapman and Abbott, 2010); (Abbott and Lowe, 2004) |
| Betulaceae | *Betula albosinensis (tet) x B. Platyphylla (dip)* |  |  |  |
| Betulaceae | *Betula nana* (2n = 2x = 28) x *B. pubescens* (2n = 4x = 56)allo | Britain | Tetraploid; both(?) | (Wang et al., 2014); (Thorsson et al., 2007); (Palme et al., 2004) |
| Betulaceae | *Betula pendula* (2n = 2x = 28) x *B. pubescens* (2n = 4x = 56)allo | Britain | Tetraploid | (Zohren et al., 2016) |
| Betulaceae | *Betula* × *purpusii* (2n = 5x = 70) x *B. alleghaniensis* (2n = 6x = 84)allo | Michigan; USA | Hexaploid | (Barnes and Dancik, 1985) |
| Brassicaceae | *Cardamine apennina* (2n =2x = 16) x *C.* *amporitana* (2n = 4x = 32) | Italy | Tetraploid | (Lihova et al., 2004) |
| Brassicaceae | *Cardamine* × *insueta* (2n = 3x = 24) x *C. pratensis* (2n = 4x = 32) | Switzerland | - | (Mandakova et al., 2013) |
| Brassicaceae | *Cochlearia officinalis* (2n = 4x = 24) x *C. danica* (2n = 6x = 42) | Britain | Tetraploid | (Fearn, 1977) |
| Brassicaceae | *Draba incana* (2n = 4x = 32) x *D. norvegica* (2n = 6x = 48)allo | Scandinavia | - | (Brochmann et al., 1992) |
| Brassicaceae | *Draba nivalis* (2n = 2x = 16) x *D. daurica* (2n = 8x = 64) | Scandinavia | - | (Brochmann et al., 1992) |
| Brassicaceae | *Draba arctica* (2n = 10x = 80) x *D. corymbosa* (2n = 16x = 128)allo | Scandinavia | - | (Brochmann et al., 1992) |
| Brassicaceae | *Rorippa austraica* (2n = 2x = 16) x *R. sylvestris* (2n = 4x/6x = 32/48) | Germany | Both | (Bleeker, 2003); see also (Bleeker, 2007) |
| Fabaceae | *Lotus stepposus* (2n = 2x = 12) x *L. × ucrainicus* (2n = 4x =24)allo | Ukraine, Turkmenistan, Kazakhstan, Mongolia | - | (Kramina et al., 2018) |
| Liliaceae | *Erythronium mesochoreum* (2n = 2x = 22) x *E. albidum* (2n = 4x = 44) | Nebraska; USA | - | (Roccaforte et al., 2015) |
| Orchidaceae | *Dactylorhiza fuchsii* (2n = 2x = 40) x *D. praetermissa* (2n = 4x = 80)allo | Belgium | - | (De Hert et al., 2012) |
| Orchidaceae | Dactylorhiza incarnata (2n = 2x = 40) x *D. praetermissa* (2n = 4x = 80)allo | Belgium | - | (De Hert et al., 2012); (De Hert et al., 2011) |
| Orchidaceae | *Dactylorhiza incarnata* subsp. *cruenta* (2n = 2x = 40) x *D. lapponica* (2n = 4x = 80)allo | Norway | Tetraploid | (Aagaard et al., 2005) |
| Orchidaceae | *Dactylorhiza incarnata* (2n = 2x = 40) x *D.* *traunsteineri (*2n = 4x = 80)allo | Sweden | Tetraploid | (Hedren, 2003); see also (Balao et al., 2017) |
| Orchidaceae | *Dactylorhiza fuchsii* (2n = 2x = 40) x *D. maculata* (2n = 4x = 80)auto | Europe to Caucasus | - | (Shipunov et al., 2004) |
| Orchidaceae | *Epidendrum fulgens* (2n = 2x = 24) x *E. puniceoluteum* (2n = 4x = 52) | Brazil | Tetraploid | (Pinheiro et al., 2010) |
| Orobanchaceae | *Euphrasia anglica* (2n = 2x = 22) x *E. micrantha* (2n = 4x = 44)allo | Britain | Diploid(?) | (Yeo, 1956); (French et al., 2008) |
| Phrymaceae | *Mimulus guttatus* (2n = 2x = 28) x *M. luteus* (2n = 4x = 60-2)allo | Britain | Chromosome doubling | (Vallejo-Marin, 2012) |
| Plantaginaceae | *Callitriche cophocarpa* (2n = 2x = 10) x *C.* *platycarpa* (2n = 4x = 20)allo | Europe | - | (Prancl et al., 2014) |
| Poaceae | *Miscanthus sacchariflorus (2n = 4x = 76)* auto *x M. sinensis (2n = 2x = 38)* | Korea and Japan | Tetraploid |  |
| Poaceae | *Vulpia fasciculata* (2n = 4x = 28) x *Festuca rubra* (2n = 6x = 42) | Britain | Hexaploid(?) | (Bailey et al., 1993) |
| Polygalaceae | *Polygala calcarea* (2n = 2x = 34) x *P. vulgaris* (2n = 4x = 68) | Britain | Tetraploid | (Lack, 1995) |
| Polygonaceae | *Fallopica sachaliensis* (2n = 4x = 44) x *F.* *japonica* var *japonica* (2n = 8x = 88) | Britain | - | (Bailey, 2013); see also (Bailey and Wisskirchen, 2004) and (Hollingsworth et al., 1999) |
| Polygonaceae | *Rumex obtusifolius* (2n = 4x = 40) x *R. aquaticus* (2n = 20x = 200) | Britain | 20-ploid | (Ruhsam et al., 2015) |
| Primulaceae | *Dodecatheon frenchii* (2n = 2x = 44) x *D. meadia* (2n = 4x = 88) | Illinois; USA | Tetraploid | (Oberle et al., 2012) |
| Rannunculaceae | *Aconitum variegatum* (2n = 2x = 16) x *A. firmum* (2n = 4x = 32)allo | Europe | Diploid? | (Sutkowska et al., 2017) |
| Rannunculaceae | *Ficaria calthifolia* (2n = 2x = 16) x *F. verna* subsp. *verna* (2n = 4x = 32) | Europe | - | (Popelka et al., 2019) |
| Rosaceae | *Rosa rugosa* (2n = 2x = 14) x *R. mollis* (2n = 4x = 28) | Europe | Tetraploid | (Kellner et al., 2012) |
| Violaceae | *Viola reichenbachiana* (2n = 2x = 20) x *V.* *riviniana* (2n = 4x = 40)allo | Germany | - | (Neuffer et al., 1999); see also (Migdalek et al., 2017) |
| Violaceae | *Viola epipsila (2n = 4x = 24) x V. palustris (2n = 8x = 48)*allo | Poland | Putative F1s dominate | Żabicka et al. 2020 |



**Figure XX – Distribution of ploidy levels across the British and Irish flora between and within species.** Shown are the number of species at each ploidy level which are not known to have multiple cytotypes. Odd ploidies are less frequent than even ploidies, resulting in a ‘saw tooth’ pattern. The most highly polyploid species is *Leucanthemum maximum* at 22-ploid.



**Figure XX – Distribution of cross-ploidy hybrids across the British and Irish flora.** The number of cross-ploidy (dark bar) and intra-ploidy (light bar) hybrids are shown per family, in the context of family-level phylogenetic relationships from *matK* and *rbcL*. Faded family names indicate missing ploidy data, and red family names highlight those families which contain five or more different ploidy levels. Numbers in parentheses are the number of cross-ploidy hybrids formed per family.

**General features of cross-ploidy hybridisation**

Cross-ploidy hybrids can arise in a variety of situations. Many, but not all, examples occur in contact zones between parental species with contrasting ploidy, where hybrid zones and hybrid swarms may form. Some of these hybrid zones have shifted over time (e.g. *Betula*, (Wang et al., 2014), or are mosaic in structure (Popelka et al., 2019). In addition, there are notable differences in genetic structure between contact zones, with some comprising a swarm of F1, F2 and backcrossed hybrids (Fearn, 1977), indicating low genetic divergence between parental species (Edmands, 2002), while others contain only a few early generation hybrids, suggesting that parental species are more distantly related, and show higher levels of pre and post-zygotic isolation (Koutecky et al., 2011). Moreover, the direction of introgression is overwhelmingly towards the higher ploidy parent (21 out of 26 studies in Table 1 that reported directionality). This is unsurprising as the union of an unreduced 2*n* = 2*x* gamete of a diploid and a reduced n = 2*x* gamete of a tetraploid provides a direct pathway for introgression in this direction, whereas the alternative direction is a two-step process via the triploid bridge (Stebbins, 1971, Baduel et al., 2018). As such, only two plant studies and one animal study report the opposite scenario (*Aconitum* and *Euphrasia*, *Neobatrachus* (Sutkowska et al., 2017, Yeo, 1956), and a further two studies report bidirectional introgression (in *Betula* and *Rorippa*, (Thorsson et al., 2007, Bleeker, 2003). However, other factors may still pose limits for introgression in the direction of the higher ploidy parent. Polyploids evolve meiotic stability to ensure reliable segregation of additional chromosomes at meiosis, with loci underlying tetraploid meiotic stability shown to be under selection in natural populations of autotetraploid *Arabidopsis arenosa* (Hollister et al., 2012). Cytogenetic evidence in *Arabidopsis* suggests introgression from diploids to tetraploids may introduce genetic variants that disrupt regular meiosis in tetraploids (Morgan et al., 2020).

Hybrids may also occur in the absence of one or both parents, normally where greater lifespans allow persistence long after hybrid formation (Bailey, 2013, Preston and Pearman, 2015). Where cross-ploidy hybrids are present without their parents, they may represent stable lineages that survive through asexual reproduction (e.g. vegetative reproduction or apomixis), and are therefore different to some ephemeral forms present in hybrid zones. On occasion, recent cross-ploidy hybridisation has led to speciation (<200 years). This has occurred in the plant genera *Senecio* (Lowe and Abbott, 2004, Abbott and Lowe, 2004) and *Mimulus* (Vallejo-Marin, 2012). These hybrids are also notable in the context of the British Isles, as they involve alien species as either one, or both parental species. Similarly, in *Rosa* one of the parents, while in *Fallopia* both parents, involved in cross-ploidy hybridisation are alien species (Table 1). Human mediated translocations of species clearly have a profound effect on cross-ploidy hybridisation. Older hybrid species (10,000+ years) have also originated in a similar way to *Senecio* and *Mimulus* hybrid species, with this inferred either through morphology and cytogenetic analysis, or through sequence analysis showing ‘ghost’ subgenomes of allopolyploid species (e.g. *Euphrasia, Packera,* (Yeo, 1956, Kowal et al., 2011).

For persistence of a hybrid lineage to occur, reproductive isolation between the newly formed hybrid and the parental progenitors is paramount. Unlike cases of polyploid hybrid speciation where the hybrid is of differing ploidy level to both parents, backcrossed F1 hybrids derived from cross-ploidy hybridisation will match one parental ploidy and therefore lack the strong reproductive barrier that polyploidy confers. In this case, other factors contribute to reproductive isolation, including ecological selection, niche differentiation, selfing, and chromosomomal or genetic sterility barriers (Gross and Rieseberg, 2005, Rieseberg, 1997, Grant, 1981). Lastly, reproductive isolation of a cross-ploidy hybrid can occur by the doubling of the triploid F1 chromosome complement to produce a fertile hexaploid that is isolated by ploidy level from the parental species, as with *Senecio cambrensis* (Abbott and Lowe, 2004) and *Mimulus peregrinus* (Vallejo-Marin, 2012).

A key determinant of genetic variation in cross-ploidy hybrids will be whether the polyploid parent(s) are auto or allopolyploids. In allotetraploid parents characterised by disomic inheritance, preferential chromosome pairing between the most similar, homeologous subgenomes, may lead to a subset of polyploid variation introgressing. In contrast, in autotetraploids with tetrasomic inheritance, free recombination between chromosomes may allow any region of the tetraploid to introgress. According to our literature survey, in 20 of 23 studies for which relevant information is available the higher ploidy parent was an allopolyploid. While allopolyploids garner more research interest than autopolyploids in studies of hybridisation (Spoelhof et al., 2017), the higher number of studies reporting allopolyploids may be biologically significant. For example, chromosome pairing of an allotetraploid subgenome more related to the diploid parent could lead to higher probabilities of successful hybridisation than in diploid-autotetraploid hybridisation, where chromosome pairing is disrupted.

In addition to cross-ploidy hybridisation between species, much early work, both theoretical and empirical, has explored crosses within mixed-ploidy species complexes (Fowler and Levin, 1984, Levin, 1975, Lumaret and Barrientos, 1990). The outcomes of crosses within (diploid x autopolyploid) or between species (diploid x autopolyploid/allopolyploid) are similar in many cases; with triploid hybrids still formed (Vandijk et al., 1992, De Hert et al., 2012), unreduced gametes remaining an important driver of hybridisation (Lihova et al., 2004, Baduel et al., 2018), and the direction of introgression is usually towards the higher ploidy parent (Table XX; (Stebbins, 1956, Pinheiro et al., 2010). On the other hand, between species hybridisation can lead to higher levels of genetic variation through fixed heterozygosity in hybrids, and backcrossing to parental species, resulting in higher fitness (Ramsey and Schemske, 2002). In addition, the higher the divergence between species, the higher the likelihood of whole genome duplication post hybridisation, and therefore the generation of novel polyploid species (Paun et al., 2009). A further feature to emerge from studies of mixed-ploidy species is that successful cross-ploidy hybridisation may occur more frequently between cytotypes of higher ploidy (e.g. tetraploids and hexaploids) than of lower ploidy (e.g. diploids and tetraploids) (Greiner and Oberpreiler, 2012, Hulber et al., 2015, Sutherland et al., 2020). However, despite the apparent weakening of postzygotic barriers at higher ploidy levels, prezygotic barriers may be strong enough for such cross-ploidy hybridization to remain rare (Greiner and Oberpreiler, 2012, Hulber et al., 2015).

More than 60 years ago, Stebbins (1956) proposed that within polyploid complexes a widespread tetraploid could acquire genes via unilateral introgression from ecogeographicaly isolated diploid taxa occurring sympatrically with it in different parts of its range. In this way, several different forms of a tetraploid might originate, with each one bearing a close resemblance to the local diploid it hybridised with. Based on cytotaxonomic evidence, Stebbins (1956, 1971) suggested this has occurred in numerous polyploid complexes of a number of plant genera, including *Dactylis*, *Knautia*, *Grindelia*, *Phacelia* and *Campanula*. Recently, genomic evidence has been obtained to provide support for Stebbins’ proposal from work conducted on a polyploid complex comprising diploid and tetraploid forms of *Arabidopsis arenosa* in Europe (Arnold et al., 2015). Genomic analysis indicates that autotetraploid *A. arenosa* arose once before splitting into five major lineages as it spread into different parts of Central Europe (Arnold et al., 2015). For two of the lineages, there is evidence that particular haplotypes, not found in any other tetraploid lineage, are shared with proximal diploid forms of *A. arenosa*, indicating these haplotypes were acquired from the local diploid type and are adaptive (Arnold et al., 2015). In addition, one of the five tetraploid lineages is a ruderal form, widely distributed along the railways of Central and Northern Europe. Subsequent analysis indicates that the widespread lowland form of this early flowering and rapid cycling “railroad ecotype” likely originated as a result of introgression of genes from diploid *A. arenosa* occurring on the Baltic Coast of Germany and Poland into local populations of the tetraploid (Baduel et al. 2018a; Monnahan et al. 2019).

**Future perspectives**

While cross-ploidy hybridisation is likely more common than once thought, particularly in plants, there is still much uncertainty in our understanding of the phenomenon. To better determine the frequency of cross-ploidy hybridisation, we need to broaden the taxonomic scope under study. There is currently a dearth of information on animal examples, even though polyploid incidence can be high in some groups (e.g. insects, decapods, fish, and amphibians; (Otto and Whitton, 2000)). Further, while we found many angiosperm examples, half were derived from the large families Asteraceae and Orchidaceae. A broader scope will also determine more readily whether there is a phylogenetic signal to the phenomenon, and which attributes, from ecological to genetic factors, facilitate cross-ploidy hybridisation and introgression. More detailed mechanistic research across a wide variety of taxa will also reveal the underlying genomic variants that allow chromosomes to pair in newly formed polyploid hybrids (Morgan et al., 2020), which is important in establishment and persistence of hybrids. Most research on cross-ploidy hybridisation so far has focused on either contact zones or cryptic introgression; studying stabilised hybrids outside of these situations will provide a more detailed picture of how these lineages persist, and under which conditions (e.g. see Abbott et al. 1998 and references within). Genomic sequencing promises to reveal cross-ploidy hybridisation more easily (Wang et al., 2020), quantify the directionality of introgression accurately (Zohren et al., 2016), and determine parental genomic contributions to cross-ploidy hybrids (Bertioli et al., 2016). The latter point is particularly important, as hybrids may be introgressed at only a few loci in the genome. Detecting these few loci requires a high contiguity polyploid genome assembly, preferably with phase information, and new sequencing methods and software are beginning to address these problems (Zhang et al., 2019). Specifically, long-read Oxford Nanopore Technologies and Pacific BioSciences sequencing, as well as Hi-C and BioNano for scaffolding are producing highly improved, contiguous genome assemblies, and population long-read sequencing will be able to detect fine level introgression more easily. In addition, sequencing of diploid relatives, and haploid tissue in ferns will allow us to distinguish between subgenomes and work out phase. Given the extensive ploidy variation throughout plants and animals, and the high degree of hybridisation detected in these groups, cross-ploidy hybridisation may be more important in plant and animal evolution than is currently recognised.

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**Supplementary:**

Tables of chromosome and ploidy counts for species with single ploidy level, and both

Websites, Observable notebooks for graphs.

Table XX: Search strings for Google Scholar searches.

|  |  |
| --- | --- |
| Journal | Search string |
| Molecular Ecology | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:”Molecular Ecology” |
| Evolution | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid site:onlinelibrary.wiley.com source:”Evolution” -source:”and Evolution” -source:”Organic Evolution” |
| Heredity | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:”Heredity” |
| Annals of Botany | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:”Annals of Botany” |
| American Journal of Botany | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:” American Journal of Botany” |
| New Phytologist | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:” New Phytologist” |
| PNAS | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:” PNAS” |
| Biological Journal of the Linnean Society | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:” Biological Journal of the Linnean Society” |
| Botanical Journal of the Linnean Society | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:” Botanical Journal of the Linnean Society” |
| Journal of Evolutionary Biology | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:” Journal of Evolutionary Biology” |
| PLoS One | Ploidy hybrid genetic introgression diploid OR tetraploid OR hexaploidy OR octoploid source:” PLoS One” |

**Note:** other examples were added if they were deemed to be important and/or well known.

**Figure XX – The distribution of ploidy levels across the British and Irish flora between species in the four families with the highest number of species.** Shown are Rosaceae, Poaceae, Asteraceae and Fabaceae. Each family has distinct distributions of ploidy levels.



**Glossary**

**Autopolyploid**. Polyploid derived from whole genome duplication of a single individual (i.e. not involving hybridisation).

**Allopolyploid**. Polyploid derived from two distinct parental species (i.e. involving hybridisation).

**Disomic inheritance**. Where homeologous chromosomes preferentially (or exclusively) pair with each other, leading to a subset of possible allelic combinations. This is most common in allotetraploids.

**Contact zone**. An area where two divergent populations or species meet and interact. This may give rise to a cline of hybrids in a **hybrid zone** or a less structured mixture of hybrids in a **hybrid swarm**.

**Natural hybridisation.** Cross mating of different species that have incomplete reproductive isolation in nature.

**Polyploid**. An organism containing more than two pairs of chromosomes, as a result of whole genome duplication.

**Unreduced gamete.** A sperm or egg cell formed through meiotic failure that has the somatic (2n) rather than haploid (n) chromosome number.

**Introgression**. Gene flow between species mediated by hybridisation and backcrossing.

**Subgenome.** The genome contributed by one parental progenitor in an allotetraploid with disomic inheritance.

**Tetrasomic inheritance**. Where each homologous chromosome pairs randomly, leading to all possible allelic combinations in equal frequencies. This is most common in autotetraploids, where all copies of the chromosomes are highly related.

**Box 1. Polyploid evolution**

Polyploidy is the condition where a cell contains more than two sets of chromosomes as a result of whole genome duplication (WGD). The two major routes to polyploidy are either through WGD of a single species chromosome complement, known as autopolyploidy or through hybridisation between two species followed by WGD, known as allopolyploidy (Ramsey and Schemske, 1998). It is driven especially by the production of unreduced gametes in diploid species (Moghe and Shiu, 2014) and this is affected by a range of factors including specific genes (Ravi et al., 2008) and environmental stresses (Rice et al., 2019). Although worldwide, the majority of plant species are diploid (~67%, (Rice et al., 2019), extensive variability in ploidy levels exist at all taxonomic levels and scales (Kolar et al., 2017, Soltis et al., 2010). Both the spatial and phylogenetic distribution of ploidy variation are unlikely to be uniform however, due to climatic and clade specific effects on unreduced gamete formation (Kreiner et al., 2017a, Bretagnolle and Thompson, 1995, Rice et al., 2019). Historically, autopolyploidy has been regarded as both less frequent and less important in an evolutionary context, than allopolyploidy (Soltis et al., 2010). The current wealth of cytological data suggests, however, that at least 10% of species are autopolyploids, with allopolyploids estimated to be at least as frequent (Kolar et al., 2017, Soltis et al., 2010, Barker et al., 2016). Allopolyploids have received more attention as they are mainly distinctive morphological taxa described as species, while autopolyploids are often morphologically cryptic and lumped into species complexes (Ramsey and Ramsey, 2014, Barker et al., 2016). Polyploidy has been important over evolutionary time in the genesis of new plant and animal lineages (Otto and Whitton, 2000), and its signature is imprinted several times over in the genome of every flowering plant (Wendel et al., 2016). Both polyploid speciation conferring immediate reproductive isolation (Whitton, 2004) and polytopic origins of polyploids can lead to new lineage formation (Thompson and Merg, 2008). There is also increasing evidence that polyploidy facilitates lineage diversification, though this remains a controversial topic (Wood et al., 2009, Han et al., 2020, Ren et al., 2018). Polyploidy is also associated with major shifts in ecology and morphology across a wide variety of plant species (Paule et al., 2017, Husband et al., 2016, Parisod et al., 2010).

**Box 2. Ploidy differences as a reproductive barrier**

Ploidy differences have often been cited as strong reproductive barriers to hybridisation in plants (Husband and Sabara, 2004, Sutherland and Galloway, 2017). Cross-ploidy hybridisation is therefore usually considered rare because hybrids will have unbalanced chromosome content and therefore irregular pairing of chromosomes, rendering the hybrid infertile. This infertility prevents or limits the formation of backcross hybrids and the potential for introgression. In cross-ploidy hybridisation the usual reproductive barriers to cross species mating apply, along with specific factors associated with ploidy level difference between parental species. In addition to reproductive barriers caused by differences in geography, phenology, morphology and mating system etc. (Laport et al., 2016, Kay, 2006, Martin and Willis, 2007), the ploidy ratio of the pollen:style is important (Stace, 1975, Watkins, 1932), and following fertilisation is a period where endosperm development and (epi)genetic compatibilities are critical (Bomblies and Weigel, 2007, Lafon-Placette and Kohler, 2016).

There are two main pathways to creation of cross-ploidy hybrids; either through reduced or unreduced gametes. Reduced (“normal”) gametes of the both parental species results in the generation of a hybrid with intermediate ploidy. These hybrids, usually triploids derived from diploid-tetraploid crosses, are common and found in a variety of taxa where congeners co-occur, for example *Aconitum*, *Ficaria*, *Dactylorhiza* and *Senecio* (Sutkowska et al., 2017, Popelka et al., 2019, De Hert et al., 2012, Irwin and Abbott, 1992). A barrier to the creation of these hybrids through reduced gametes is known under the umbrella term ‘triploid block’ (Ramsey and Schemske, 1998, Kolar et al., 2017). Early work on experimental diploid-autopolyploid crosses established the presence of a triploid block and that direction of crosses was important (Valentine and Woodell, 1960, Stebbins, 1971, Thompson, 1930). The major cause of triploid block is attributed to genomic conflict in the maternal endosperm, which is usually triploid and composed of a ratio of two maternal and one paternal genomes (Lafon-Placette and Kohler, 2016). Deviations from this ratio cause the endosperm to malfunction in development and function (Kohler et al., 2010). Reciprocal crosses differ in their likelihood of success, and it is a general phenomenon that crosses where the higher ploidy parent is female are more likely to produce viable offspring, due to endosperm ratios which are better tolerated (Burton and Husband, 2000); Figure XX panels **a** and **b**). Triploid block may also be caused by the action of allelic incompatibilities at an early stage in development, although this topic is little explored (Scott and Bolbol, 2013). A second possibility in the creation of cross-ploidy hybrids is where the lower ploidy parent produces unreduced (“polyploid”) gametes. Unreduced gamete production is on average 0.1-2% per individual, with rare individuals and hybrids that produce considerably higher frequencies (>85%) (Kreiner et al., 2017a, Mason and Pires, 2015, Kreiner et al., 2017b). In addition, many different taxa produce unreduced gametes, and their production also varies with environmental variables (Baduel et al., 2018, Rice et al., 2019). Successful crosses occur more readily when unreduced gametes are produced by the diploid parent, thus restoring the gamete ploidy to that of the higher ploidy parent (Figure XX panel **c**) (Ramsey and Schemske, 1998).



**Figure XX – Potential outcomes of hybridisation between diploid and tetraploid species.** In each panel, the top two circles refer to the parental species, the middle two ellipses to the gametes produced from each parent, the bottom left box to the F1 hybrid and the bottom right bold box to the endosperm. Panels **a** and **b** consider hybridisation with reduced gametes and therefore generate triploid hybrids, while panels **c** and **d** consider hybridisation where one parent produces unreduced gametes. In particular, panel **c** illustrates that a fertile polyploid can be generated in a single generation. Figure generated with graphviz (Ellson et al., 2002).

**Box 3. Outcomes of cross-ploidy hybridisation**



**Figure XX – Potential outcomes of a triploid F1 backcrossing to the parental species.** In both panels, the schematic follows that of Figure XX panel **a**. Interrupted lines indicate backcrosses to parental species. In panel **a** the triploid F1 hybrid produces reduced gametes that combine with reduced gametes from the diploid male parent. In panel **b** there are two pathways to produce a tetraploid F1 backcross: firstly the unreduced gametes from the triploid F1 can combine with reduced gametes from the female tetraploid parent, secondly the unreduced gametes from the triploid F1 can combine with unreduced gametes from the diploid male parent. Figure generated with graphviz (Ellson et al., 2002).