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# The emerging importance of cross-ploidy hybridisation and introgression

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## Abstract

Natural hybridisation is now recognised as pervasive in its occurrence across the Tree of Life. Resurgent interest in natural hybridisation fuelled by developments in genomics has led to an improved understanding of the genetic factors that promote or prevent species cross-mating. Despite this body of work overturning many widely held assumptions about the genetic barriers to hybridisation, it is still widely thought that ploidy differences between species will be an absolute barrier to hybridisation and introgression. Here, we revisit this assumption, reviewing findings from surveys of polyploidy and hybridisation in the wild. In a case study in the British flora, 203 hybrids representing 35% of hybrids with suitable data have formed via cross-ploidy matings, while a wider literature search revealed 59 studies (56 in plants and 3 in animals) in which cross-ploidy hybridisation has been confirmed with genetic data. These results show cross-ploidy hybridisation is readily overlooked, and potentially common in some groups. General findings from these studies include strong directionality of hybridisation, with introgression usually towards the higher ploidy parent, and cross-ploidy hybridisation being more likely to involve allopolyploids than autopolyploids. Evidence for adaptive introgression across a ploidy barrier and cases of cross-ploidy hybrid speciation shows the potential for important evolutionary outcomes.

## KEYWORDS

hybrid species, hybrid zone, hybridization, interploidy, introgression, polyploidy

## 1 | 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 (Brennan et al., 2014; Crispo et al., 2011; Larson et al., 2019). Closely related species isolated only by prezygotic barriers are more likely to hybridise (Vallejo-Marin & Hiscock, 2016), but even species isolated by

very strong postzygotic barriers do hybridise in some instances. Polyploidy (whole genome duplication), which is particularly common in plants, creates a very strong postzygotic barrier between species. 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 (Ramsey & Schemske, 1998). Should a hybrid form, it is normally either completely or partially sterile, due to the formation of malfunctioning gametes containing unbalanced chromosome

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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 some very recently originated plant species, which are now models for the study of polyploid speciation (Vallejo-Marín & Hiscock, 2016), and also to the origin of some of our most important crop plants, including wheat, sweet potato, sugar cane, and oilseed rape (Matsuoka, 2011; Wang et al., 2023; Yang et al., 2017; Zhang et al., 2018). Nonetheless, the frequency of cross-ploidy (or inter-ploidy) hybridisation in the wild is a neglected topic with information scattered through the literature. Here, we bring this information together and consider 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-20th century, cytogenetic studies became more frequent and revealed extensive ploidy variation both within and among species, with this ploidy information used to infer evolutionary relationships (Love & 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 (Abbott, Ashton, & Forbes, 1992; Nason et al., 1992). Now, by examining many thousands of genetic markers or the complete genomes of target species, there is the 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 (Baduel et al., 2018; Chapman & Abbott, 2010; Kim et al., 2008; Monnahan et al., 2019).

While there have been many recent reviews on the prevalence of polyploids in nature (e.g. Alix et al., 2017; Chen, 2010; Kohler et al., 2010; Marques et al., 2018; Soltis et al., 2004), and on the importance of natural hybridisation (Abbott et al., 2013; Moran et al., 2021; Soltis & Soltis, 2009; Suarez-Gonzalez et al., 2018; Taylor & Larson, 2019; Todesco et al., 2016), cross-ploidy hybridisation remains a largely neglected topic. Our aim is to reconcile work on polyploidy and hybridisation, to consider whether cross-ploidy hybridisation may be more prevalent and important than previously recognised. We first summarise the ways in which cross-ploidy hybrids may form. Next, we review the 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 where cases of cross-ploidy hybridisation have been confirmed using genetic approaches, with this wider survey allowing us to generalise about the occurrence in nature. Lastly, we explore the biology of cross-ploidy hybrids and the potential

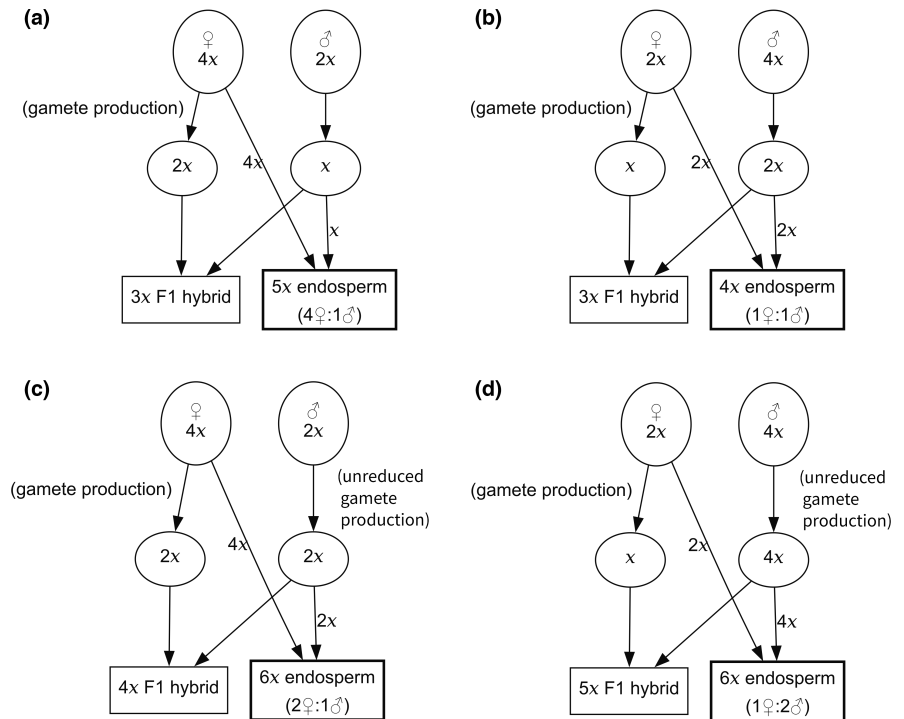
long-term evolutionary outcomes, and discuss how advances in genomic sequencing and analytical tools may aid detection to assess more accurately the state of cross-ploidy hybridisation in nature. We emphasise case studies in flowering plants, where hybridisation and polyploidy are particularly prevalent and well-documented, but also consider other organismal groups where cross-ploidy hybridisation may occur.

## 2 | MECHANISMS OF CROSS-PLOIDY HYBRID FORMATION AND PERSISTENCE

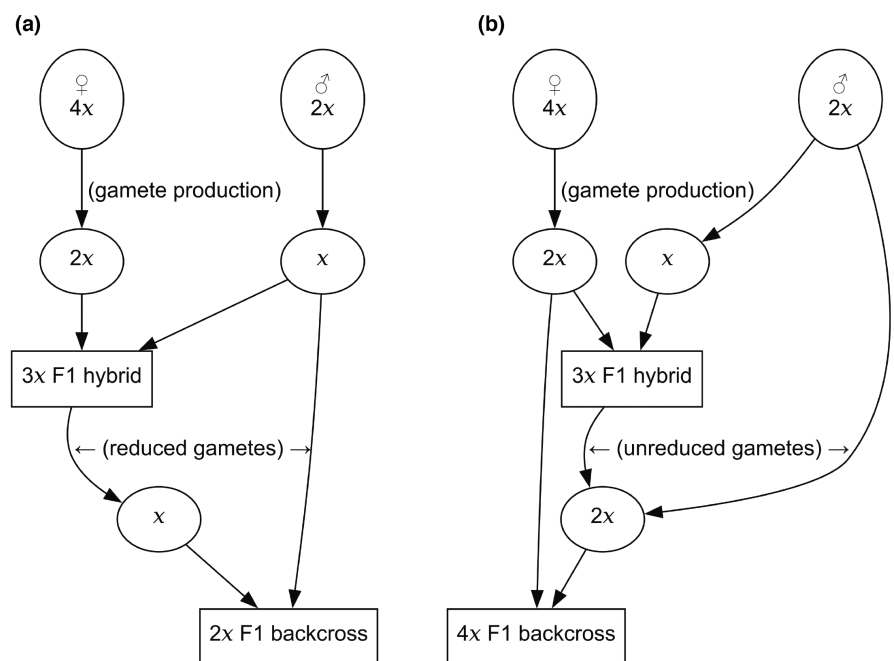
There are two main pathways to the creation of cross-ploidy hybrids: through either reduced or unreduced gametes from parents of differing ploidy. Reduced ('normal') gametes of both parental species result in a hybrid with intermediate ploidy. These hybrids, usually triploids derived from diploid-tetraploid crosses, are common and found in a variety of taxa where congeners co-occur (De Hert et al., 2012; Irwin & Abbott, 1992; Popelka et al., 2019; Sutkowska et al., 2017). A barrier to the creation of these hybrids through reduced gametes is known under the umbrella term 'triploid block' (Ramsey & Schemske, 1998; Kolář et al., 2017). Early work on experimental diploid-autopolyploid crosses established the presence of a triploid block and that the direction of crosses was important (Stebbins, 1971; Thompson, 1930; Valentine & Woodell, 1960). 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 & Köhler, 2016). Deviations from this ratio cause the endosperm to malfunction in development and function (Köhler et al., 2010). Reciprocal crosses differ in their likelihood of success, and it is a general phenomenon that crosses in which the higher ploidy parent is female are more likely to produce viable offspring, due to endosperm ratios which are better tolerated (Burton & Husband, 2000; Figure 1a, 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 et al., 2013). A second possibility in the creation of cross-ploidy hybrids involves the lower ploidy parent producing 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, 2017b; Mason & Pires, 2015). 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 in diploid-tetraploid crosses when unreduced gametes are produced by the diploid parent, thus restoring the gamete ploidy to that of the higher ploidy parent (Figure 1c; Ramsey & Schemske, 1998).

After a cross-ploidy hybrid has formed, there are a number of possible outcomes. Firstly, the hybrid may be ephemeral and go extinct, especially if it is formed at low frequencies (i.e. low propagule pressure, Fowler & Levin, 2016) and if it wastes reproductive output by mating with its parents (i.e. minority cytotype

**FIGURE 1** 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 c and d consider hybridisation where one parent produces unreduced gametes. In particular, c illustrates that a fertile polyploid can be generated in a single generation. Figure generated with graphviz (Ellson et al., 2002), with source code available at [https://github.com/Euphrasiologist/cross\\_ploidy](https://github.com/Euphrasiologist/cross_ploidy).



**FIGURE 2** Potential outcomes of a triploid F1 backcrossing to the parental species. In both panels, the schematic follows that of Figure 1a. In a, the triploid F1 hybrid produces reduced gametes that combine with reduced gametes from the diploid male parent. In 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) and source code is available at [https://github.com/Euphrasiologist/cross\\_ploidy](https://github.com/Euphrasiologist/cross_ploidy).



disadvantage, Fowler & Levin, 1984; Levin, 1975). The growth and development of the hybrid can be affected by incompatible parental allelic combinations, causing the hybrid to be unfit (e.g. hybrid necrosis, Bomblies & Weigel, 2007), further reducing its likelihood of survival. Alternatively, if the hybrid persists, it may have the opportunity to act as a conduit to gene flow between ploidy levels. Ultimately, fertility of an F1 hybrid will be a major determinant of the longer term outcomes, with even low levels of F1 hybrid fertility facilitating potentially important gene flow through backcrossing with parental species (Arnold et al., 1999). For a triploid F1 hybrid created from a diploid-tetraploid cross,

there are two pathways to generate a backcross of equivalent ploidy to one of the parental species. Firstly, the triploid F1 may produce reduced gametes which combines with reduced gametes from the diploid male parent (Figure 2a) which has been hypothesised to occur in *Euphrasia* and *Aconitum* (Sutkowska et al., 2017; Yeo, 1956). Secondly, the triploid F1 hybrid can produce unreduced or balanced gametes that can either combine with reduced gametes from the tetraploid parent or unreduced gametes from the diploid parent (Figure 2b; e.g. *Senecio eboracensis*, Lowe & Abbott, 2004). Tetraploids, therefore, are much more readily produced, as in addition to the two pathways mentioned, tetraploids

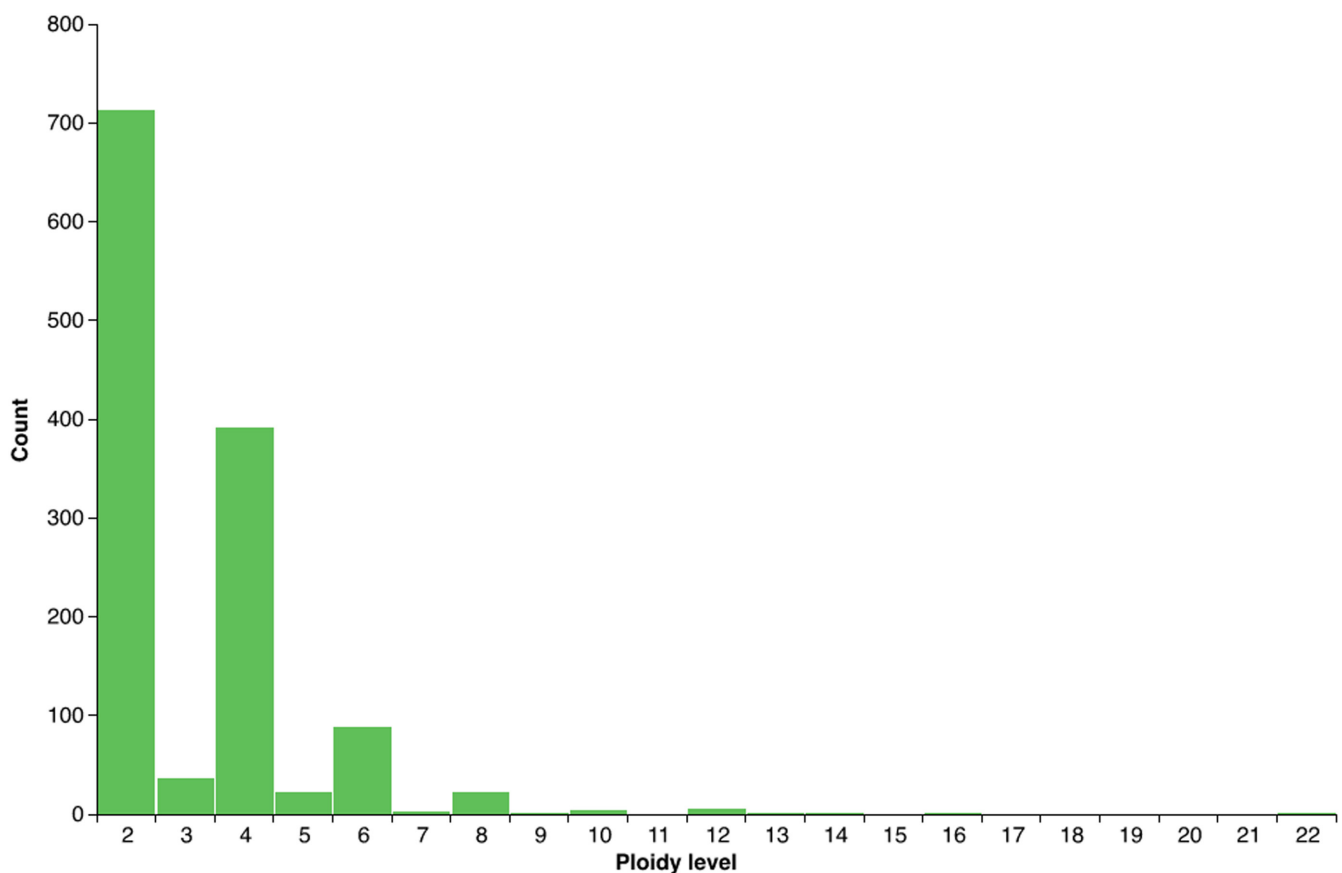
can be produced in a single generation following cross-ploidy hybridisation (Figure 1c). The bias towards tetraploid production has been known since the 1950s (Stebbins, 1956) and is the reason why introgression in the direction of the tetraploid is more common (Baduel et al., 2018).

### 3 | FREQUENCY AND OCCURRENCE OF NATURAL CROSS-POIDY 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 (Kay, 2006; Laport et al., 2016; Martin & Willis, 2007), along with specific factors associated with ploidy level difference between parental species, such as 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 et al., 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 & Ellstrand, 1993; though see issues with using morphological data to detect hybrids, below).

There are increasingly comprehensive surveys of ploidy variation that provide key contextual information as to where cross-ploidy hybrids could occur, and set an upper boundary in terms of their number. Worldwide, the majority of plant species are diploid (Rice et al., 2019); however, extensive variability in ploidy levels exists at all taxonomic levels and scales (Kolář et al., 2017; Soltis et al., 2010). For example, the genus *Sedum* in the Crassulaceae ranges from diploid to 80-ploid, which is currently the highest known among flowering plants (Bennett & Leitch, 1997). Many commonly studied species also exhibit ploidy variation such as *Senecio carolinensis* (diploid to 9-ploid; Kolář et al., 2017), and this variation correlates with latitudinal gradients (Zhang, Wang, et al., 2019; Zhang, Zhang, et al., 2019). Climatic effects, which include latitude, along with clade specific effects, are known to have a role in unreduced gamete formation, a key factor in polyploid genesis (Bretagnolle & Thomson, 1995; Kreiner et al., 2017a; Rice et al., 2019). In contrast to flowering plants,



**FIGURE 3** Distribution of ploidy levels across the British and Irish flora. This includes all flowering plant species 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. Ploidy is based on Brown et al. (2023), with additional data inferred based on comparisons of genome sizes (Leitch et al., 2019) and chromosome counts (Henniges et al., 2022) for British native flowering plant species ( $n = 1295$  species with data, see Table S2). Script to generate the plot can be found at [https://github.com/Euphrasiologist/cross\\_ploidy](https://github.com/Euphrasiologist/cross_ploidy).

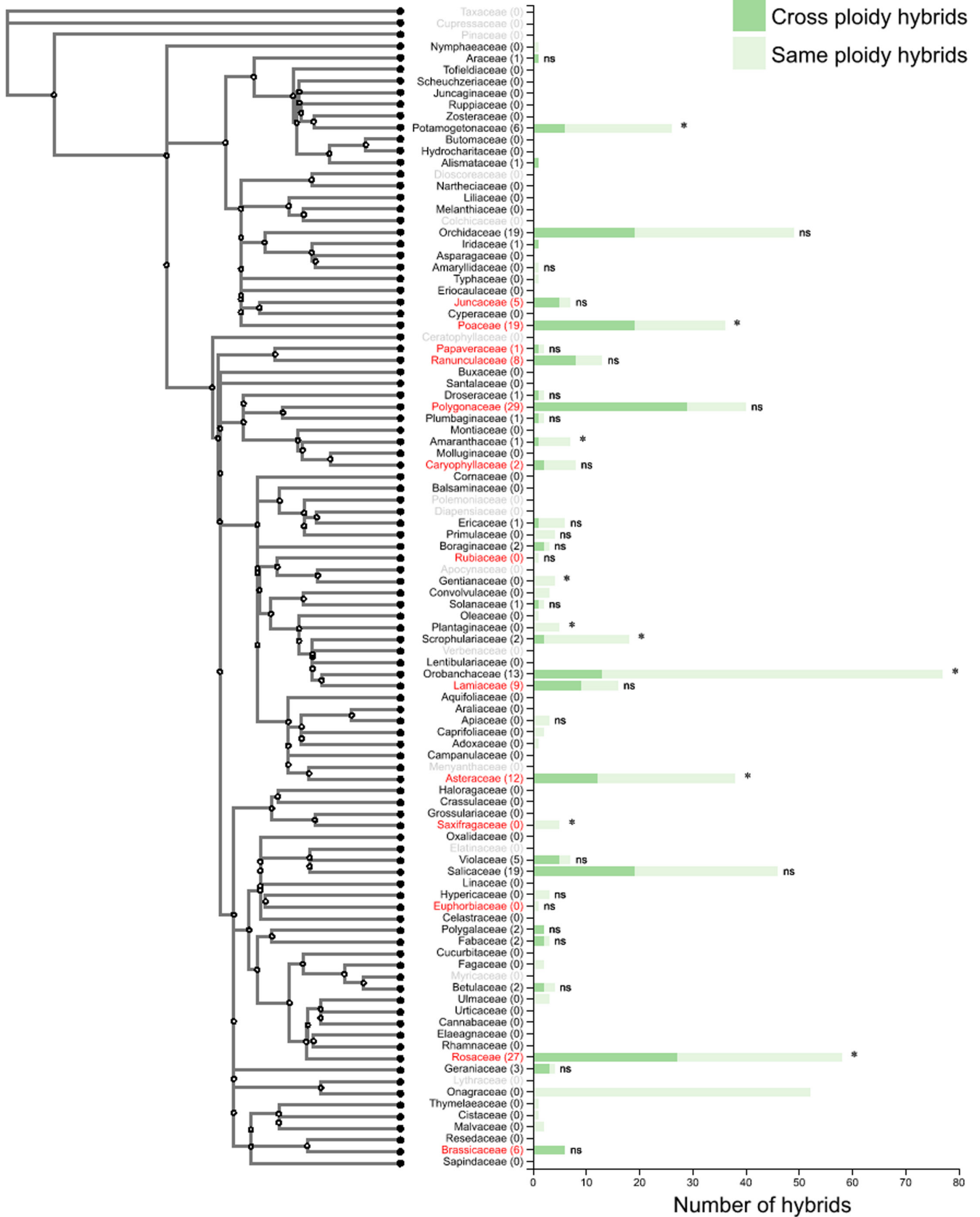


FIGURE 4 (Legend on next page)



**FIGURE 4** Distribution of cross-ploidy hybrids in the British and Irish flora. The number of cross-ploidy (dark bars) and intra-ploidy (light bars) hybrids is shown per family, in the context of known phylogenetic relationships. The number of hybrids per family is compiled based on Stace et al. (2015), while phylogenetic relationships are based on the three-locus species level phylogeny presented in Brown et al. (2023), subsampling the tree to one tip per family. 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. For each family, the results of a chi-squared test to assess whether there are statistically significantly more intra-ploidy hybrids than expected given the number of possible species combinations (\*), or if this test is non-significant (ns), is shown (details in Table S3). In no case were there significantly more cross-ploidy hybrids than expected given the number of species combinations. Data generation, tree subsampling analysis and plot generation can be found at [https://github.com/Euphrasiologist/cross\\_ploidy](https://github.com/Euphrasiologist/cross_ploidy).

polyploidy in animals 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 from the British and Irish flora, which contains a manageable number of native species (~1500, excluding large taxonomically complex groups, Stace, 2019). The British flora is exceptional in having near complete information on species chromosome counts (Henniges et al., 2022) and the extent of natural hybridity (Stace et al., 2015). The extensive data on hybridisation in the British flora have previously been used to estimate that 25% of plant species in the flora hybridise (Mallet, 2005), providing a general estimate for the frequency of hybridisation across diverse plant genera. More recently, a study employing phylogenetic mixed models showed that species that differ in ploidy are 35% less likely to form a hybrid (Brown et al., 2023), though there are still numerous cross-ploidy hybrids, which highlights that ploidy level is far from an absolute barrier to hybridisation.

To further quantify the potential for cross-ploidy hybridisation, we re-evaluated the available data for the British flora. Ploidy levels for hybridising species presented in Brown et al. (2023), supplemented with additional ploidy estimates for non-hybridising species based on available genome size data (Leitch et al., 2019) and chromosome counts (Henniges et al., 2022) for British native flowering plant species ( $n=1295$  species with data, Table S1), show most species are diploids (56%), with higher ploidy levels becoming exponentially less common (Figure 3). However, there is notable variation when ploidy level is evaluated across the phylogeny for the British flora, with some families showing much more ploidy variation than others, altering the raw material on which cross-ploidy hybridisation can act (Figure S1). In terms of the frequency of cross-ploidy hybrids, we re-analysed the data compiled in Brown et al. (2023), to quantify their occurrence. Of the 588 hybrids that have ploidy information for both parents (321 hybrids have parents that lack appropriate data), 203 cross-ploidy hybrids have formed (35%; Table S2), in comparison to 385 intraploidy hybrids (65%). Cross-ploidy hybrids occur in 67 genera, with over a quarter present in *Rumex* (Polygonaceae, 24), *Salix* (Salicaceae, 19) and *Euphrasia* (Orobanchaceae, 13; Figure 4). The majority (55%) of cross-ploidy hybrids involve diploid–tetraploid crosses, with higher order even-ploidy crosses closely following (43%), and diploid–triploid crosses in the minority (2%). Notably, 12 of 36 families that include cross-ploidy hybrids have more cross-ploidy hybrids

than intra-ploidy hybrids. While this is never significantly more than expected based on chi-squared tests comparing the observed against expected hybrids given the number of potential species pairs (see Table S3), these results show that cross-ploidy hybrids are relatively common in the British flora, with ploidy a less strong barrier to at least early generation hybrid formation than is widely thought.

Inferring hybridisation from morphology, geography, cytology and limited genetic data, as is the case with many examples in the British and Irish flora (as well as in other many floras, e.g. detailed studies of hybridisation between diploid and triploid dandelions in mainland Europe, Mártonfióvá, 2015), provides valuable insights into the likely occurrence of hybrids, but may overlook cryptic hybridisation and introgression that can be detected with genetic markers. Moreover, the extent of cross-ploidy hybridisation in the British 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 (criteria for inclusion listed in Table S4) reveals 49 different parental species combinations from 59 studies resulting in cross-ploidy hybridisation, with such hybrids present in 36 genera from 17 angiosperm families, three fern families and three animal families (Table 1). Diploid–tetraploid crosses are found in 35 of the 49 parental crosses, with the rest being higher ploidy crosses. This confirms that cross-ploidy hybridisation is likely to be much more common 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 4). The conspicuous absence of records from large, diverse families with variable ploidy, such as Rubiaceae, potentially indicates 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; see Schley et al., 2022, for discussion of overlooked polyploidy and hybridisation in the tropics). In terms of life form, most well-documented cross-ploidy hybrids (with the

TABLE 1 Studies reporting cross-ploidy hybrids based on genetic analyses.

Family	Hybridising species	Location	Direction of hybridisation/introgression	References
<b>Animals</b>				
Bufo	<i>Bufo turanensis</i> (2n = 2x = 22) × <i>Bufo pewzowi</i> (2n = 4x = 44) <sup>allo</sup>	Kyrgyzstan	Diploid	Stöck et al. (2010)
Cyprinidae	<i>Squalius alburnoides</i> (2n = 2x = 50; 3n = 75; 4n = 100) × <i>S. pyrenaicus</i> (2n = 2x = 50) <sup>allo</sup>	Iberia	-	Alves et al. (2001); Crespo-López et al. (2007)
Myobatrachidae	<i>Neobatrachus sutor</i> (2n = 2x = 24) × <i>N. kunapalari</i> (2n = 4x = 48) <sup>auto</sup>	Australia	Tetraploid	Novikova et al. (2020)
<b>Plants</b>				
Aspleniaceae	<i>Asplenium scolopendrium</i> (2n = 2x = 72) × <i>A. adiantum-nigrum</i> (2n = 4x = 144)	Britain	-	Stace et al. (2015)
Cyatheaceae	<i>Gymnosphaera denticulata</i> (2n = 2x = 138) × <i>G. metteniana</i> (2n = 4x = 274) <sup>allo</sup>	China	Tetraploid	Wang et al. (2020)
Dryopteridaceae	<i>Polystichum setiferum</i> (2n = 2x = 82) × <i>P. aculeatum</i> (2n = 4x = 164)	Britain	-	Manton (1950)
Asteraceae	<i>Achillea clypeolata</i> (2n = 2x = 18) × <i>A. collina</i> (2n = 4x = 36) <sup>allo</sup>	Bulgaria	Tetraploid	Guo et al. (2005)
Asteraceae	<i>Achillea setacea</i> (2n = 2x = 18) × <i>Achillea collina</i> (2n = 4x = 36)			Ma et al. (2010)
Asteraceae	<i>Achillea asplenifolia</i> (2n = 2x = 18) × <i>Achillea collina</i> (2n = 4x = 36)			Ma et al. (2010)
Asteraceae	<i>Centaurea pseudophrygia</i> (2n = 2x = 22) × <i>C. jacea</i> (2n = 4x = 44)	Czech Republic	-	Koutecky et al. (2011)
Asteraceae	<i>Chrysanthemum indicum</i> (2n = 4x = 36) and <i>C. vestitum</i> (2n = 6x = 54)	China	Both	Qi et al. (2022)
Asteraceae	<i>Cirsium carniolicum</i> ssp. <i>rufescens</i> (2n = 2x = 16) × <i>C. palustre</i> (2n = 4x = 34)	France	Tetraploid	Segarra-Moragues et al. (2007)
Asteraceae	<i>Ixeris repens</i> (2n = 2x = 16) × <i>I. debilis</i> (2n = 6x = 48) <sup>auto</sup>	Japan	Hexaploid(?)	Denda and Yokota (2003)
Asteraceae	<i>Packera paupercula</i> (2n = 4x = 44) × <i>P. indecora</i> (2n = 8x = 88)	USA; Michigan	-	Kowal et al. (2011)
Asteraceae	<i>Senecio madagascariensis</i> (2n = 2x = ?) × <i>S. pinnatifolius</i> (2n = 4x = ?)	Australia	-	Prentis et al. (2007)
Asteraceae	<i>Senecio squallidus</i> (2n = 2x = 20) × <i>S. vulgaris</i> (2n = 4x = 40) <sup>allo</sup>	Britain	Tetraploid; chromosome doubling	Abbott et al. (2007); Irwin and Abbott (1992); Abbott, Irwin, and Ashton (1992); Chapman and Abbott (2010); Abbott and Lowe (2004)
Betulaceae	<i>Betula nana</i> (2n = 2x = 28) × <i>B. pubescens</i> (2n = 4x = 56) <sup>allo</sup>	Britain	Tetraploid; both(?)	Wang et al. (2014); Thorsson et al. (2007); Palme et al. (2004)
Betulaceae	<i>Betula pendula</i> (2n = 2x = 28) × <i>B. pubescens</i> (2n = 4x = 56) <sup>allo</sup>	Britain	Tetraploid	Zohren et al. (2016)
Betulaceae	<i>Betula × purpusii</i> (2n = 5x = 70) × <i>B. alleghaniensis</i> (2n = 6x = 84) <sup>allo</sup>	Michigan; USA	Hexaploid	Barnes and Dandik (1985)
Brassicaceae	<i>Cardamine apennina</i> (2n = 2x = 16) × <i>C. amporitana</i> (2n = 4x = 32)	Italy	Tetraploid	Lihova et al. (2004)
Brassicaceae	<i>Cardamine × insueta</i> (2n = 3x = 24) × <i>C. pratensis</i> (2n = 4x = 32)	Switzerland	-	Mandakova et al. (2013)
Brassicaceae	<i>Cochlearia officinalis</i> (2n = 4x = 24) × <i>C. danica</i> (2n = 6x = 42)	Britain	Tetraploid	Fearn (1977)
Brassicaceae	<i>Draba incana</i> (2n = 4x = 32) × <i>D. norvegica</i> (2n = 6x = 48) <sup>allo</sup>	Scandinavia	-	Brochmann et al. (1992)
Brassicaceae	<i>Draba nivalis</i> (2n = 2x = 16) × <i>D. daurica</i> (2n = 8x = 64)	Scandinavia	-	Brochmann et al. (1992)
Brassicaceae	<i>Draba arctica</i> (2n = 10x = 80) × <i>D. corymbosa</i> (2n = 16x = 128) <sup>allo</sup>	Scandinavia	-	Brochmann et al. (1992)

(Continues)



TABLE 1 (Continued)

Family	Hybridising species	Location	Direction of hybridisation/introgression	References
Brassicaceae	<i>Rorippa austriaca</i> ( $2n = 2x = 16$ ) $\times$ <i>R. sylvestris</i> ( $2n = 4x/6x = 32/48$ )	Germany	Both	Bleeker (2003), see also Bleeker (2007)
Fabaceae	<i>Lotus stepposus</i> ( $2n = 2x = 12$ ) $\times$ <i>L. ucrainicus</i> ( $2n = 4x = 24$ ) <sup>allo</sup>	Ukraine, Turkmenistan, Kazakhstan, Mongolia	-	Kramina et al. (2018)
Gesneriaceae	<i>Ranonda nathaliae</i> ( $2n = 2x = 48$ ) $\times$ <i>R. serbica</i> ( $2n = 6x = 144$ )	Balkan Peninsula	Both	Lazarević et al. (2022)
Liliaceae	<i>Erythronium mesochoreum</i> ( $2n = 2x = 22$ ) $\times$ <i>E. albidum</i> ( $2n = 4x = 44$ )	Nebraska, USA	-	Roccaforte et al. (2015)
Orchidaceae	<i>Dactylorhiza fuchsii</i> ( $2n = 2x = 40$ ) $\times$ <i>D. praetermissa</i> ( $2n = 4x = 80$ ) <sup>allo</sup>	Belgium	-	De Hert et al. (2012)
Orchidaceae	<i>Dactylorhiza incarnata</i> ( $2n = 2x = 40$ ) $\times$ <i>D. praetermissa</i> ( $2n = 4x = 80$ ) <sup>allo</sup>	Belgium	-	De Hert et al. (2012); De Hert et al. (2011)
Orchidaceae	<i>Dactylorhiza incarnata</i> subsp. <i>cruenta</i> ( $2n = 2x = 40$ ) $\times$ <i>D. lapponica</i> ( $2n = 4x = 80$ ) <sup>allo</sup>	Norway	Tetraploid	Aagaard et al. (2005)
Orchidaceae	<i>Dactylorhiza incarnata</i> ( $2n = 2x = 40$ ) $\times$ <i>D. traunsteineri</i> ( $2n = 4x = 80$ ) <sup>allo</sup>	Sweden	Tetraploid	Hedren (2003); see also Balao et al. (2017)
Orchidaceae	<i>Dactylorhiza fuchsii</i> ( $2n = 2x = 40$ ) $\times$ <i>D. maculata</i> ( $2n = 4x = 80$ ) <sup>auto</sup>	Europe to Caucasus	-	Shipunov et al. (2004)
Orchidaceae	<i>Epidendrum fulgens</i> ( $2n = 2x = 24$ ) $\times$ <i>E. puniceoluteum</i> ( $2n = 4x = 52$ )	Brazil	Tetraploid	Pinheiro et al. (2010)
Orobanchaceae	<i>Euphrasia anglica</i> ( $2n = 2x = 22$ ) $\times$ <i>E. micrantha</i> ( $2n = 4x = 44$ ) <sup>allo</sup>	Britain	Diploid(?)	Yeo (1956); French et al. (2008)
Phrymaceae	<i>Mimulus guttatus</i> ( $2n = 2x = 28$ ) $\times$ <i>M. luteus</i> ( $2n = 4x = 60-2$ ) <sup>allo</sup>	Britain	Chromosome doubling	Vallejo-Marín (2012)
Plantaginaceae	<i>Callitriche cophocarpa</i> ( $2n = 2x = 10$ ) $\times$ <i>C. platycarpa</i> ( $2n = 4x = 20$ ) <sup>allo</sup>	Europe	-	Pranci et al. (2014)
Poaceae	<i>Miscanthus sacchariflorus</i> ( $2n = 4x = 76$ ) <sup>auto</sup> $\times$ <i>M. sinensis</i> ( $2n = 2x = 38$ )	Korea and Japan	Tetraploid	Clark et al. (2019)
Poaceae	<i>Vulpia fasciculata</i> ( $2n = 4x = 28$ ) $\times$ <i>Festuca rubra</i> ( $2n = 6x = 42$ )	Britain	Hexaploid(?)	Bailey et al. (1993)
Polygalaceae	<i>Polygala calcarea</i> ( $2n = 2x = 34$ ) $\times$ <i>P. vulgaris</i> ( $2n = 4x = 68$ )	Britain	Tetraploid	Lack (1995)
Polygonaceae	<i>Fallopia sachalinensis</i> ( $2n = 4x = 44$ ) $\times$ <i>F. japonica</i> var. <i>japonica</i> ( $2n = 8x = 88$ )	Britain	-	Bailey (2013); see also Bailey and Wisskirchen (2004) and Hollingsworth et al. (1999)
Polygonaceae	<i>Rumex obtusifolius</i> ( $2n = 4x = 40$ ) $\times$ <i>R. aquaticus</i> ( $2n = 20x = 200$ )	Britain	20-ploid	Ruhsam et al. (2015)
Primulaceae	<i>Dodecatheon frenchii</i> ( $2n = 2x = 44$ ) $\times$ <i>D. meadia</i> ( $2n = 4x = 88$ )	Illinois, USA	Tetraploid	Oberle et al. (2012)
Ranunculaceae	<i>Aconitum variegatum</i> ( $2n = 2x = 16$ ) $\times$ <i>A. firmum</i> ( $2n = 4x = 32$ ) <sup>allo</sup>	Europe	Diploid?	Sutkowska et al. (2017)
Ranunculaceae	<i>Ficaria valthofolia</i> ( $2n = 2x = 16$ ) $\times$ <i>F. verna</i> subsp. <i>verna</i> ( $2n = 4x = 32$ )	Europe	-	Popelka et al. (2019)
Rosaceae	<i>Rosa rugosa</i> ( $2n = 2x = 14$ ) $\times$ <i>R. mollis</i> ( $2n = 4x = 28$ )	Europe	Tetraploid	Kellner et al. (2012)
Violaceae	<i>Viola reichenbachiana</i> ( $2n = 2x = 20$ ) $\times$ <i>V. riviniana</i> ( $2n = 4x = 40$ ) <sup>allo</sup>	Germany	-	Neuffer et al. (1999); see also Migdalek et al. (2017)
Violaceae	<i>Viola epipsila</i> ( $2n = 4x = 24$ ) $\times$ <i>V. palustris</i> ( $2n = 8x = 48$ ) <sup>allo</sup>	Poland	Putative F1s dominate	Żabicka et al. (2020)

Note: Details are provided of the family, hybridising species, broad geographic locality and the direction that hybridisation and introgression are occurring towards (if known). Chromosome counts and ploidy are extracted from the original publication, with superscripts indicating whether the polyploids are allopolyploid (<sup>allo</sup>) or autopolyploid (<sup>auto</sup>) if this is known. Note that the ploidy is based on the specific study and other ploidy levels may also be found in these species. Studies are listed if they use multiple genetic markers, with full search criteria given in Table S4.

notable exception of *Euphrasia*) are perennial, a factor which is associated 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 are extremely rare. Opportunities for novel allelic combinations and introgression are limited as the parental genomes rarely recombine.

#### 4 | FACTORS AFFECTING CROSS-PLOIDY HYBRIDISATION AND INTROGRESSION

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), indicative of 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 reproductive isolation (Koutecky et al., 2011). Hybrids may also occur in the absence of one or both parents, normally when greater lifespans allow persistence long after hybrid formation (Bailey, 2013; Preston & 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.

The direction of introgression in cross-ploidy hybrids is overwhelmingly towards the higher ploidy parent (Table 1). This is unsurprising as the union of an unreduced  $2n=2x$  gamete of a diploid and a reduced  $n=2x$  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 (Baduel et al., 2018; Stebbins, 1971). 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 three studies report bidirectional introgression (in *Betula*, *Rorippa*, and *Chrysanthemum*,

Bleeker, 2003; Qi et al., 2022; Thorsson et al., 2007). However, other factors may still limit 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 alter regular meiosis in tetraploids (Morgan et al., 2020).

A key determinant of the outcomes of cross-ploidy hybridisation is the ploidy of the parents, and the mode of ploidy (whether the parents are auto or allopolyploids). In terms of ploidy, it is clear 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, Hülber 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 hybridisation to remain relatively rare (Hülber et al., 2015). In terms of mode of ploidy, cross-ploidy hybridisation involving allopolyploids may result in preferential chromosome pairing between the most similar, homeologous chromosomes, leading to introgression involving only one polyploid subgenome. 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 21 of 25 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.

#### 5 | EVOLUTIONARY OUTCOMES OF CROSS-PLOIDY HYBRIDISATION

Recent cross-ploidy hybridisation has led to notable examples of rapid speciation (<200 years). This has occurred in the plant genera *Senecio* (Abbott & Lowe, 2004; Lowe & Abbott, 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, alien species are involved in cross-ploidy hybridisation within *Rosa* and *Fallopia* (Table 1). Human-mediated translocations of species clearly have a profound effect on cross-ploidy hybridisation. Older hybrid species 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* and *Packera*, Becher et al., 2020; Kowal et al., 2011; Yeo, 1956).

For a hybrid lineage to persist, reproductive isolation between the newly formed hybrid and the parental progenitors is paramount. Unlike cases of polyploid hybrid speciation in which 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 must contribute to reproductive isolation, including ecological selection, niche differentiation, selfing and chromosomal or genetic sterility barriers (Grant, 1981; Gross & Rieseberg, 2005; Lowe & Abbott, 2004; Rieseberg, 1997). 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 & Lowe, 2004) and *Mimulus peregrinus* (Vallejo-Marin, 2012).

In addition to cross-ploidy hybridisation between species, much early work, both theoretical and empirical, has explored crosses within mixed-ploidy species complexes (Fowler & Levin, 1984; Levin, 1975; Lumaret & Barrientos, 1990). The outcomes of crosses within (diploid × autopolyploid) or between (diploid × autopolyploid/allopolyploid) species are similar in many cases, with triploid hybrids still formed (De Hert et al., 2012; Vandijk et al., 1992), unreduced gametes remaining an important driver of hybridisation (Baduel et al., 2018; Lihova et al., 2004) and the direction of introgression usually being towards the higher ploidy parent (Table 1; Pinheiro et al., 2010; Stebbins, 1956). 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 & 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).

More than 60 years ago, Stebbins (1956) proposed that, within polyploid complexes, a widespread tetraploid could repeatedly acquire genes via unilateral introgression from ecogeographically isolated diploid taxa that are each sympatric with the tetraploid 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 with which it hybridised. Based on cytotoxic 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 from a polyploid complex comprising diploid and tetraploid forms of *Arabidopsis arenosa* in Europe has supported for Stebbins' proposal (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., 2018; Monnahan et al., 2019).

## 6 | FUTURE PERSPECTIVES

A large body of recent research has revisited the role of major chromosomal features, such as chromosomal inversions, in promoting or preventing adaptation and speciation in hybridising taxa (e.g. Lee et al., 2017; Twyford & Friedman, 2015). This has overturned our understanding of the frequency and importance of structural chromosomal variation in the evolutionary process (reviewed in Hoffmann & Rieseberg, 2008; Wellenreuther & Bernatchez, 2018). Much could be learnt by applying similar approaches to the largely overlooked phenomenon of cross-ploidy hybridisation. While cross-ploidy hybridisation is likely more common than once thought, particularly in plants, there is still much uncertainty in our understanding of how this may shape evolution. Key priorities should be to broaden the taxonomic scope of study to understand the frequency of cross-ploidy hybridisation across the Tree of Life: to reveal potential factors that may promote or prevent cross-ploidy hybridisation, and to employ new genomic sequencing and analytical approaches to investigate the genomic basis of this phenomenon.

In terms of establishing the frequency of cross-ploidy hybridisation, 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 & Whitton, 2000). Furthermore, while we found many angiosperm examples, nearly half (17 out of 42) were derived from the large families Asteraceae and Orchidaceae. A broader scope will determine whether there is a phylogenetic signal to the phenomenon, and which attributes, including ecological and genetic factors, facilitate cross-ploidy hybridisation and introgression.

Studying the genomics of cross-ploidy hybridisation will allow us to more accurately understand the population dynamics of cross-ploidy hybrid zones (Zohren et al., 2016), as well as precisely determine parental genomic contributions to cross-ploidy hybrids and hybrid species (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 and emerging sequencing methods are beginning to address these problems (Zhang, Wang, et al., 2019; Zhang, Zhang, et al., 2019). In addition, sequencing of diploid relatives, and the application of more advanced approaches for separating the two subgenomes, such as those based on characteristic profile of different repeat content and transposable elements from each parental progenitor (e.g. Cerca et al., 2022), will be instrumental for understanding which subgenomes introgress.

Further genomic sequencing, aided by experimental work, will also provide more detailed insights into the genetic mechanisms that allow chromosomes to pair in newly formed polyploid hybrids (Morgan et al., 2020), which is important in establishment and persistence of hybrids. For example, in wheat (*Triticum aestivum*)—an allohexaploid composed of three related genomes—a single locus, *Ph1*, enforces strict homologous bivalent pairing. Suppression of *Ph1* allows meiotic pairing of homoeologous chromosomes, facilitating recombination and introgression (Li et al., 2017). Whether similar mechanisms occur in other polyploid systems remains largely uncharacterised.

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.

## AUTHOR CONTRIBUTIONS

All authors contributed to the writing of the manuscript.

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## CONFLICT OF INTEREST STATEMENT

No conflict to declare.

## DATA AVAILABILITY STATEMENT

No new data are included. The compilation of ploidy for the British flora, and the scripts used to generate figures, can be found at [https://github.com/Euphrasiologist/cross\\_ploidy](https://github.com/Euphrasiologist/cross_ploidy). A static version of the ploidy data is included in the [Support Information](#).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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