



Plant hybrids in the wild: evidence from biological recording

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Received 20 March 2015; revised 20 April 2015; accepted for publication 21 April 2015

Although plant hybrids are under-recorded by botanists, the hybrids of Britain and Ireland are as well known as those of any comparable area. Of the 909 accepted hybrids, 301 have at least one alien parent and these include 152 taxa that have been introduced to the wild (usually from horticultural sources) as hybrids. The parental distributions of the spontaneous hybrids are described as either nested or overlapping; some of the most remarkable hybrids have parents with contrasting European distributions that overlap very narrowly. There are few annual or biennial hybrids and they tend to be sterile and closely associated with the parents, except for numerous annual *Euphrasia* hybrids. Perennial hybrids with moderate fertility or the capacity for vegetative reproduction are recorded on average from more hectads than sterile, non-clonal perennials and some show considerable independence of their parental distributions. This independence may result from the decline of one parent or the spread of the hybrid; in many cases the explanation is unknown. Molecular methods have made invaluable contributions to our knowledge of some hybrids in recent years, but universal identification tools cannot currently be applied to plant hybrids so progress with such studies is likely to be piecemeal and slow. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**: 555–572.

ADDITIONAL KEYWORDS: annual – biennial – biogeography – clonal growth – distribution – fertility – perennial – sterility – vegetative reproduction.

INTRODUCTION

As mammals ourselves, we can easily assume that mammalian ways of doing things are the norm. However, as Evans (1972, p. 10) pointed out, ‘higher plants as organisms are not easily understood by the human mind...organisms so alien to us are full of surprises’. This is as true of hybridization as it is of many other aspects of their biology. Botanists took a long time to appreciate how many plant hybrids could be found in the wild, handicapped by what Mallet (2005) describes as ‘our almost instinctive, common-sense view that hybridization is always unnatural or extremely rare’. Even now that the frequent occurrence of hybrids is recognized it is, in Mallet’s words, ‘often attributed to environmental degradation: if hybridization is assumed to be unnatural, its presence must indicate some failure of the “balance of nature”’. However, the fact that

hybridization is known to have been involved in the origin of a significant proportion of plant species suggests that it was a feature of floras long before the large-scale modification of the environment by human activities.

The slow recognition of hybrids by botanists still influences the extent to which they are recorded today. Many identification manuals include only the commonest hybrids, and many botanists, similarly, only attempt to identify a few easily recognized examples. If we are to assess the significance of plant hybrids in the wild, we must therefore concentrate on the relatively few areas where they are at least moderately well known. Of these, ‘the British Isles is by far the most extensively studied’ (Ellstrand, Whitkus & Rieseberg, 1996). Our knowledge of the taxonomy, distribution and ecology of vascular plant hybrids in Britain and Ireland has recently been synthesized in the *Hybrid Flora of the British Isles* (Stace, Preston & Pearman, 2015). The current paper draws on this book to review the extent to which

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plant hybrids occur in the wild in this area. We define a hybrid as the product of a cross between plants that are classified as different taxa, rather than adopting the broader definitions of some authors that include crosses between conspecific but genetically distinct populations. Most reviews of plant hybridization have concentrated on its evolutionary significance (e.g. Arnold, 1992; Rieseberg, 1995, 1997; Ellstrand & Schierenbeck, 2000; Abbott *et al.*, 2003; Soltis & Soltis, 2009). We focus instead on hybrids themselves, rather than on hybrids as the potential progenitors of new species, and review those aspects of their biology about which biological recording is most informative: their frequency and persistence in the wild and the extent to which they occur independently of their parent species.

Nomenclature follows Stace (2010) and Stace *et al.* (2015). The area covered by this review includes Britain, the Isle of Man, Ireland and the Channel Islands, which is referred to for convenience as 'Britain and Ireland'. Some analyses exclude Ireland, as hybrids tend to be less well recorded there than in Britain.

RECORDING HYBRIDS IN BRITAIN AND IRELAND HISTORY

Although hybridization between plants was recognized in the 18th century, early knowledge was based primarily on artificial hybridization of plants in cultivation, or sometimes on the spontaneous hybridization of plants in gardens (Roberts, 1929). It was not until the 19th century that the widespread occurrence of hybrids in the wild came to be appreciated. In some cases plants that had previously been regarded as species, or as infraspecific variants, were later recognized as hybrids; in other cases hybrids were discovered as taxonomic specialists subjected genera to more detailed and critical study than they had hitherto received. The genus *Verbascum* was one in which the 'peculiar propensity to mix and form hybrids' (Withering, 1818) was recognized at an early date, a recognition no doubt facilitated by their showy flowers, which caused them to be grown as garden plants, their great propensity to hybridize and the sterility of the resulting hybrids. Acceptance of the widespread occurrence of hybrids in the genera *Salix* and *Epilobium* was achieved only after acrimonious controversies in the mid and late 19th century respectively (Stace, 1975). It was not until the end of the 19th century that hybrids were recognized in the aquatic genus *Potamogeton*, in which the intensive field studies of a devoted specialist, Alfred Fryer, was primarily responsible for establishing their frequent occurrence

in Britain (Preston, 1988, 1995). Although Fryer was one of several European specialists who realized the importance of *Potamogeton* hybrids at more or less the same time, in general knowledge of hybridization in Britain and Ireland tended to lag behind that in continental Europe. It was a German author, Focke (1881), who produced a thorough survey of all known hybrids towards the end of the 19th century (Stace, 1975, p. 20).

The pioneer *Atlas of the British Flora* (Perring & Walters, 1962) mapped only three known hybrids, *Crococsmia* × *crococsmiiflora*, *Spartina* × *townsendii* (including the fertile derivative later distinguished as *S. anglica*) and *Tilia* × *europaea*, although several more plants then mapped as species are now interpreted as hybrids. Its *Critical supplement* (Perring & Sell, 1968) made a much greater contribution, mapping 52 hybrid taxa in 32 genera, with particularly thorough treatments of *Mentha* and *Potamogeton*. However, it was the publication of an account of all known hybrids in *Hybridization and the flora of the British Isles* (Stace, 1975) that set the study of hybrids on a sound footing in Britain and Ireland, distinguishing those hybrids that were known with certainty from many that had been recorded erroneously. This stimulated many further studies, and it is probably from this time that the hybrids of Britain and Ireland came to be regarded as especially well studied. A particular feature of the 1975 book was Melville's account of *Rosa*. This was the first time that the extent of hybridization in this genus became apparent to British and Irish botanists, although there is still no consensus amongst European experts about the treatment of many taxa in this genus. The inclusion of all known hybrids in successive editions of Stace's *New Flora* (Stace, 1991, 1997, 2010), backed up by more detailed accounts of several hybrid-rich genera (e.g. Meikle, 1984; Graham & Primavesi, 1993; Preston, 1995), allowed hybrids to be covered by the Botanical Society of the British Isles 'Atlas 2000' project that led to the *New Atlas of the British & Irish flora* (Preston, Pearman & Dines, 2002). The existing taxonomic and distributional information was brought together for the new treatment (Stace *et al.*, 2015), which is supported by a database of the records on which the accounts are based.

The temporal biases in biological records described by Isaac & Pocock (2015) are certainly present in the hybrid database. In Figure 1 the variation in records over time is summarized by histograms that plot the dates of the first records for each hybrid in each hectad in which it is recorded. The records of all spontaneous hybrids (Fig. 1A) demonstrate a peak between 1881 and 1910, a period of very active floristic research, followed by a decline in the inter-war

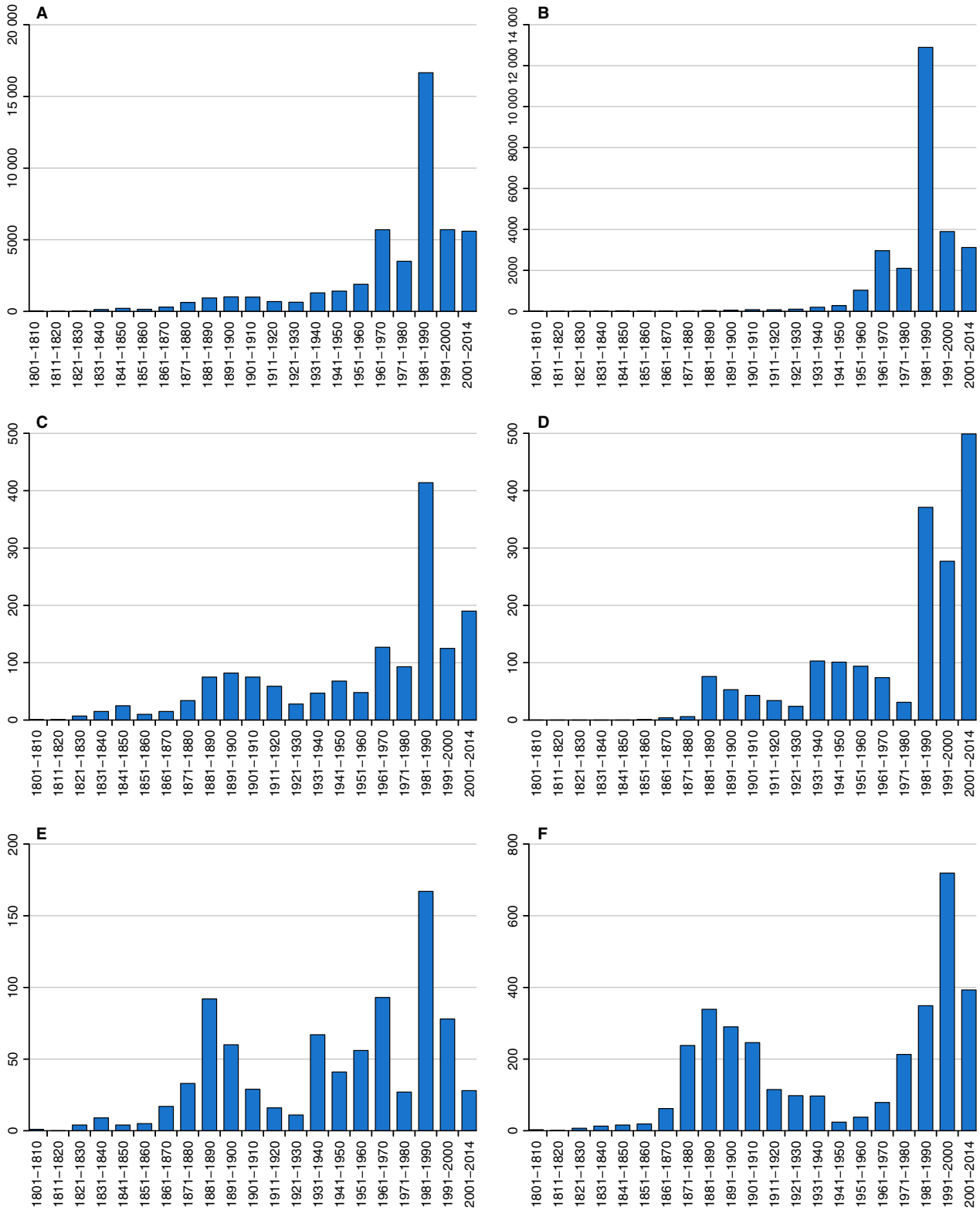


Figure 1. The dates of the first records from each hectad of (A) all spontaneous hybrids; (B) all introduced hybrids; (C) *Carex* hybrids; (D) *Epilobium* hybrids; (E) *Potamogeton* hybrids; (F) *Rosa* hybrids. Records for datespan 1987–1999 are included as 1981–1990. The numerous records dated 1987–1999 are plotted as 1980–1989; records that cover a date span of over 20 years are excluded.

years. The same pattern has been demonstrated for the number of plant specimens in herbaria (Rich, 2006), not surprisingly as many of the hybrid records are derived from herbarium material. The great increase in the number of records of hybrids in recent decades shows the combined effect of the increase in hectad recording since 1954 coupled with the increase in the interest in hybrids since 1975. The pattern for all introduced hybrids (Fig. 1B) shows fewer pre-1950 records; alien taxa were not well recorded until recently and many of the taxa covered by this figure are garden hybrids that were only synthesized, or arose accidentally, in the 19th or 20th centuries. Records of *Carex* hybrids (Fig. 1C) are similar to those for spontaneous hybrids as a whole, but this is not the case for *Epilobium* (Fig. 1D) in which the two peaks before 1981 reflect the interest stimulated by E.S. Marshall between 1889 and his death in 1919, and by G.M. Ash between 1931 and his death in 1959. In both *Potamogeton* (Fig. 1E) and *Rosa* (Fig. 1F) the late Victorian and Edwardian peak is evident. However, there are few *Rosa* records between 1941 and 1970, when there were no active national specialists, but this is not the case for *Potamogeton* as in these decades J.E. Dandy and G. Taylor were both studying the genus themselves and soliciting specimens from others.

UNDER-RECORDING OF HYBRIDS

Although hybrids are regarded as well recorded in Britain and Ireland, this is only relative to the situation elsewhere. They are under-recorded by comparison to vascular plant species, as shown by the frequent discovery of hitherto overlooked hybrids. A calculation of the rate of discovery is complicated by taxonomic changes and by differences between publications in the criteria for inclusion. If changes resulting from these factors, and plants introduced as hybrids, are disregarded, an average of 4.7 hybrids has been discovered annually over the last 40 years (Stace *et al.*, 2015).

Hybrids differ greatly in the ease to which they can be recorded by field botanists, and hence in the extent to which the available records provide an adequate reflection of their actual frequency and distributional range. A few hybrids, such as *Geum rivale* × *G. urbanum* and *Silene alba* × *S. dioica*, are well known and distinctive taxa, and are almost as well recorded as their parent species. Most are to some degree critical, and are therefore under-recorded except sometimes in areas where they have received the attention of expert botanists, or of specialists in particular taxa. Some, such as *Brassica napus* × *B. rapa*, are virtually undetectable by field recorders. Even the parents of this hybrid are

difficult to identify morphologically as the tetraploid *B. napus* is itself derived from hybridization of the diploids *B. oleracea* and *B. rapa*, and the hybrid has never been detected by field botanists. However, Wilkinson *et al.* (2000) used flow cytometry to investigate six riverside sites where wild populations of *B. rapa* subsp. *campestris* grew near crops of *B. napus* subsp. *oleifera*. Potential hybrids were discovered in three of the populations and confirmed by molecular markers. Wilkinson *et al.* (2003) estimated that there are probably c. 49 000 natural hybridization events annually in the United Kingdom, 32 000 of them in waterside habitats.

As this *Brassica* example shows, molecular methods clearly have the potential to identify hitherto unsuspected hybrids. In some genera such studies in Britain or elsewhere in Europe have already contributed a great deal to our understanding of hybridization in the wild. *Potamogeton* provides one such example, where the identity of many of the hybrids recognized previously has been confirmed but other, and sometimes surprising, populations of hybrids have been identified. The hybrid *Potamogeton pectinatus* × *P. vaginatus* is, for example, a robust plant that is now known to form persistent populations in rivers in Ireland, Britain, Denmark and Russia (Preston, Hollingsworth & Gornall, 1998; Bobrov & Chemeris, 2009; McMullan, Gornall & Preston, 2011). All these sites lie south of the range of *P. vaginatus*, a northern species that is absent from Ireland, Britain and Denmark, and has a European range centred on the Gulf of Bothnia in Sweden and Finland. Other genera in which molecular methods have been used to study hybrids to good effect include *Fallopia* (Hollingsworth *et al.*, 1998, 1999), *Mimulus* (Vallejo-Marin & Lye, 2013), *Senecio* (Abbott *et al.*, 2000, 2002; Kirk *et al.*, 2004), *Sorbus* (work summarized by Rich *et al.*, 2010), *Spartina* (Ferris, King & Gray, 1997), *Typha* (Kuehn, Minor & White, 1999; Snow *et al.*, 2010; Kirk, Connolly & Freeland, 2011) and the intergeneric hybrid × *Agropogon* (Zapiola & Mallory-Smith, 2012). Many of these molecular studies, including the cited studies of *Fallopia*, *Mimulus*, *Senecio* (by Abbott *et al.*), *Spartina*, *Typha* and × *Agropogon*, concern hybrids with at least one parent that is alien in the study area.

HOW MANY HYBRIDS ARE THERE IN BRITAIN AND IRELAND?

The 909 hybrids accepted from Britain and Ireland by Stace *et al.* (2015) are enumerated in Table 1. Most of them (744) are spontaneous hybrids, which are believed to have arisen here by hybridization in the

Table 1. Accepted hybrids, classified by criteria of taxonomic rank and native status

Hybrid	Nat × Nat	Nat × Arc	Nat × Neo	Arc × Arc	Arc × Neo	Neo × Neo	N/A	Total
Spontaneous hybrids	605	24	86	5	7	17		744
Native, one parent absent*							3	3
Hybrids of complex origin							10	10
Introduced as hybrids							152	152
Total taxa	605	24	86	5	7	17	165	909

Nat, native; Arc, archaeophyte; Neo, neophyte; N/A, not applicable.

*Apparently native hybrids but with only one parent present, or present as a native.

wild; these totals include taxa with some spontaneous and some introduced populations. Three hybrids appear to be native but one parent is absent as a native, so they are treated separately from the spontaneous hybrids. Ten hybrids of complex origin cannot easily be fitted into simple categories such as 'native × native' or 'native × neophyte'. They include the triple hybrids *Symphytum asperum* × *S. officinale* × *S. tuberosum*, which arises as a cross between the introduced hybrid *Symphytum asperum* × *S. officinale* and the neophyte *S. tuberosum*, and *Populus balsamifera* × *P. deltoides* × *P. nigra*, which has arisen spontaneously in one site (in Hackney) as the hybrid between two introduced hybrids *P. deltoides* × *P. nigra* and *P. balsamifera* × *P. deltoides* and in another (in Leeds) as the hybrid between *P. balsamifera* × *P. deltoides* and *P. nigra*, a species that is regarded as native in Britain but was planted in the Leeds locality. In addition to these 757 hybrids, there are an additional 152 hybrids that have been

introduced *as hybrids* and are now recorded as established introductions or frequent casuals in the wild.

The 605 native × native hybrids (which include hybrids between subspecies; there are 588 hybrids at specific rank) compare with a native flora of approximately 1450 species and subspecies (Hill, Preston & Roy, 2004; the apomictic microspecies of *Hieracium*, *Rubus* and *Taraxacum* are excluded from this total). There are seven genera that together contribute over half the native × native interspecific hybrids (Table 2). In five of these, *Euphrasia*, *Salix*, *Rosa*, *Epilobium* and *Rumex*, a substantial proportion of the possible hybrids has been recorded. The proportion is less in *Potamogeton* and especially in *Carex*, but *Carex* is much the largest genus in the flora. Hybridization in *Euphrasia* is discussed in more detail below. *Trifolium* is unique as a large genus in which no hybrids have been reliably recorded, and there is experimental evidence for the existence of very strong physiological barriers to hybridization

Table 2. The seven native genera with most interspecific hybrids, and five large genera (excluding primarily apomictic genera) with relatively few hybrids

Genus	No. native species	Relative size of genus (rank order)	No. native × native hybrids	% of possible hybrid combinations
<i>Genera with most hybrids</i>				
<i>Euphrasia</i>	19	6	69	40
<i>Salix</i>	14	7=	50	55
<i>Rosa</i>	12	11=	49	74
<i>Carex</i>	71	1	47	2
<i>Epilobium</i>	10	18=	31	69
<i>Rumex</i>	13	9=	28	36
<i>Potamogeton</i>	21	4	28	13
<i>Large genera with relatively few hybrids</i>				
<i>Juncus</i>	24	2	6	1
<i>Ranunculus</i>	22	3	14	6
<i>Trifolium</i>	20	5	0	0
<i>Saxifraga</i>	14	7=	3	3
<i>Veronica</i>	13	9=	1	1

Hybrids between subspecies are excluded.

between some members of this genus (Evans, 1962; Chen & Gibson, 1972). *Juncus*, *Ranunculus*, *Saxifraga* and *Veronica* are also large genera with a very small proportion of the potential hybrids. In some cases this is because the genus is heterogeneous, being composed of two or more taxonomically isolated subgenera or sections. *Ranunculus*, for example, is composed of two subgenera of similar size; hybrids are much more frequent in Subgenus *Batrachium* (10 native species, 13 hybrids) than in Subgenus *Ranunculus* (12 native species, 1 hybrid) and are not known between members of the two subgenera. The genera with most hybrids with at least one introduced parent are *Epilobium* (15), *Rumex* (15), *Verbascum* (14) and *Salix* (8). Three of these are amongst the genera listed in Table 2 with most native hybrids but *Verbascum* is additional; this is a genus with just four native species but numerous cultivated species, including nine that are sufficiently frequently recorded in the wild to be treated by Stace (2010).

There are 81 hybrids that have not been recorded since 1970, comprising 77 spontaneous and four introduced hybrids. Many of these hybrids are apparently extremely rare: 47 have only ever been confirmed from one locality and a further 17 from only two sites. A few of these hybrids are very cryptic, none more than *Eleocharis palustris* subsp. *palustris* × subsp. *vulgaris*, which was only discovered near Oxford when material was collected by chance for a student practical class. In some cases the failure to record hybrids is probably attributable to a lack of recent targeted fieldwork, such as five hybrids involving the montane species *Epilobium alsinifolium* and *E. anagallidifolium* that were studied *in situ* by E.S. Marshall before 1914 but have not received equivalent attention since. One of the five plant hybrids recorded from more than 4 hectads but not seen since 1970, *Cerastium fontanum* × *C. nigrescens*, also has a montane parent; the other four are the three binary hybrids involving *Centaurea jacea*, *C. nemoralis* and *C. nigra*, which have been neglected since they were studied by Marsden-Jones & Turrill (1954), and *Hypopitys monotropa* subsp. *hypophegea* × subsp. *monotropa*, similarly neglected since the accounts in Perring & Sell (1968) and Stace (1975). The sites of a few very rare hybrids have been destroyed by agricultural reclamation or by development, including a damp field in Wiltshire where *Cirsium acaule* × *C. dissectum* survived for over a century and a locality for *Mentha arvensis* × *M. suaveolens* at Salcombe, Devon. The absence of recent records of *Orchis militaris* × *O. simia*, which was found in the Chilterns in the 19th century, reflects the decline of both parents and the consequent reduction in the chance of hybridization.

BIOGEOGRAPHICAL CONSTRAINTS ON HYBRIDIZATION

Mapping the hectad distribution of hybrids against that of their parents (Figs 2–5) provides an effective way of understanding the biogeographical constraints on hybridization. It is helpful to envisage the ranges of any two species, including the parents of hybrids, as *nested*, *overlapping* or *vicarious*. In a nested distribution, (Table 3, Figs 2 and 3), the range of one species falls within that of the other. If the distribution of hybrid parent A is completely nested within that of parent B, there are squares containing both parents and squares with only parent B but no squares with only parent A. In an overlapping distribution (Table 4, Figs 4 and 5), some squares have both parents, some have only parent A and others only parent B. In vicarious distributions, there are no squares with both parents A and B.

There is no clear relationship between the nested or overlapping British ranges of species pairs and their wider ranges (Tables 3 and 4). Many of the pairs with nested distributions have similar wider ranges, and the range of *Drosera anglica* is nested within that of *D. rotundifolia* in both Britain and in

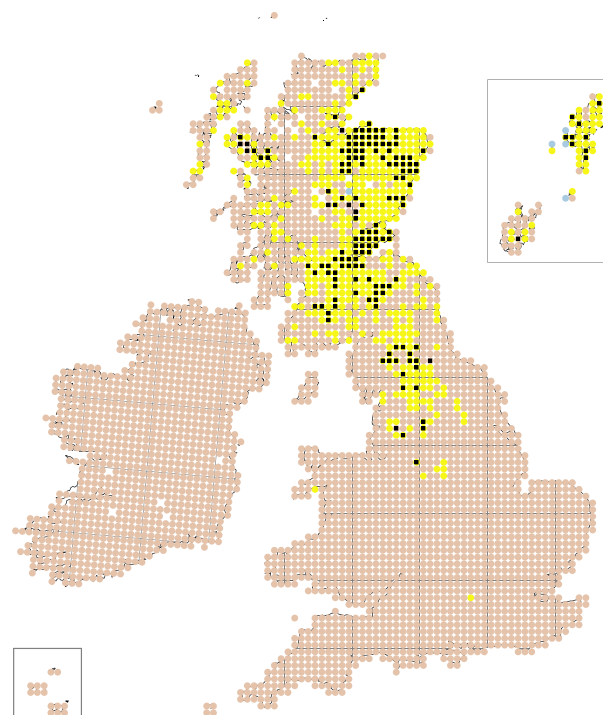


Figure 2. The distribution of *Rumex longifolius* is virtually nested within that of *R. obtusifolius*. Hectads with both species are yellow, those with one parent are pink (*R. obtusifolius*) or blue (*R. longifolius*), and records of the hybrid are shown as black squares.

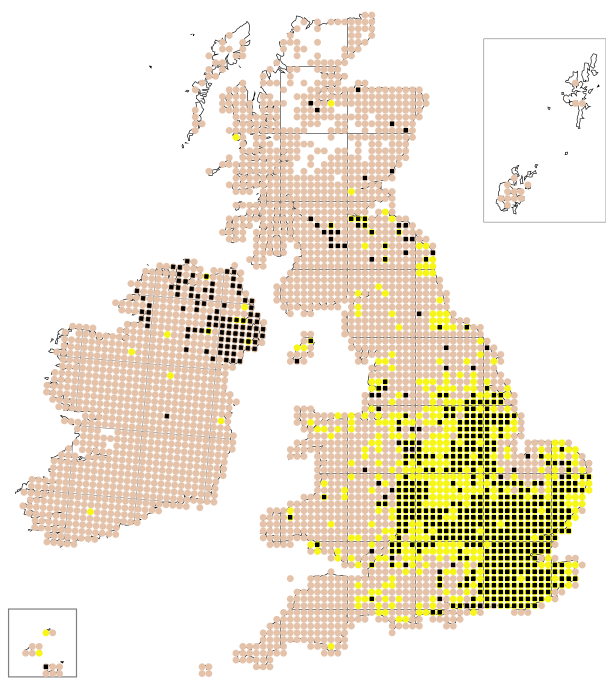


Figure 3. The distribution of *Crataegus laevigata* is completely nested within that of *C. monogyna*. Hectads with both species are yellow, those with *C. monogyna* are pink. The distribution of the hybrid (shown as black squares) has been extended by planting outside the range of the rarer parent.

the northern hemisphere (Circumpolar Boreal vs. Circumpolar Boreo-temperate). However, species with similar wider ranges may also have overlapping ranges in Britain. Some of the most notable hybrids have parents with very contrasting distributions with a very narrow overlap in Britain, such as *Juncus balticus* (Circumpolar Boreo-arctic-Montane) and *J. inflexus* (Eurosiberian Southern-temperate). The altitudinal separation of species is not clearly apparent on distribution maps. *Polystichum lonchitis* (Circumpolar Boreal) and *P. setiferum* (Submediterranean-Subatlantic) have a very narrow overlap in Britain but are also separated by altitude; however, they are found together in the highly oceanic climate of western Ireland, where they hybridize. The *Juncus* hybrid is not known outside Britain and the *Polystichum* hybrid is recorded only very rarely at high altitudes in southern Europe.

Species pairs with vicarious or almost vicarious distributions in Britain but that are recorded as hybridizing in mainland Europe include *Carex ericetorum* × *C. montana* (although the single record of this hybrid, made in Austria by Ritzberger (1891), must be regarded as dubious unless it can be confirmed from a surviving specimen), *Cirsium*

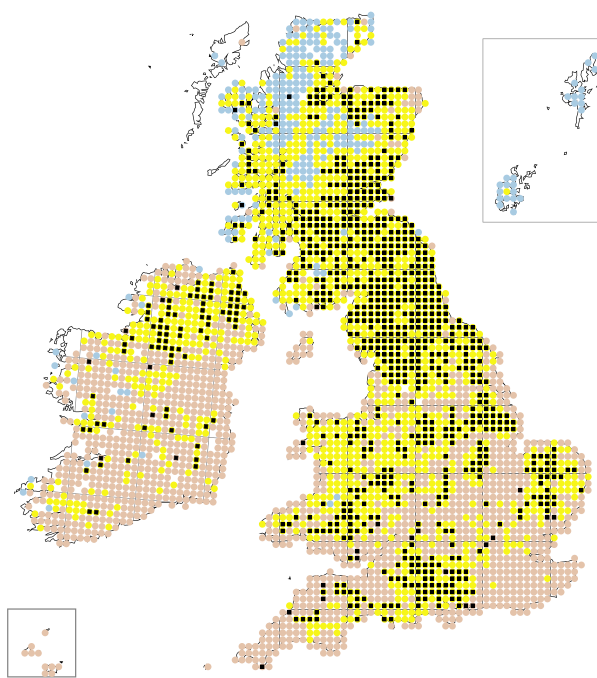


Figure 4. The distribution of the Temperate *Geum urbanum* overlaps broadly with that of the Boreo-Temperate *G. rivale*. Hectads with both species are yellow, those with one parent are pink (*G. urbanum*) or blue (*G. rivale*), and records of the hybrid are shown as black squares.

acaule × *C. heterophyllum* and *Pilosella caespitosa* × *P. peleteriana*.

The influence of human activities in breaking down geographical barriers to hybridization is apparent from the fact that 19% of the spontaneous hybrids (139 of 744) have at least one introduced parent; when the 10 complex hybrids and 152 introduced hybrids are taken into account, 33% (301 of 909) of the recorded hybrids involve introduced taxa. Some of these (e.g. *Epilobium montanum* × *E. pedunculare*, *Polystichum munitum* × *P. setiferum*, *Rumex cristatus* × *R. palustris*) are unknown elsewhere.

PERSISTENCE AND INDEPENDENCE OF SPONTANEOUS HYBRIDS

We have scored the 757 hybrids that do not owe their origin to direct introduction (Table 1) for four aspects of their biology and distribution: perennation, capacity for vegetative reproduction, fertility and the extent to which their distribution is independent of that of their parents (Table 5). These attributes have been assessed largely on the basis of

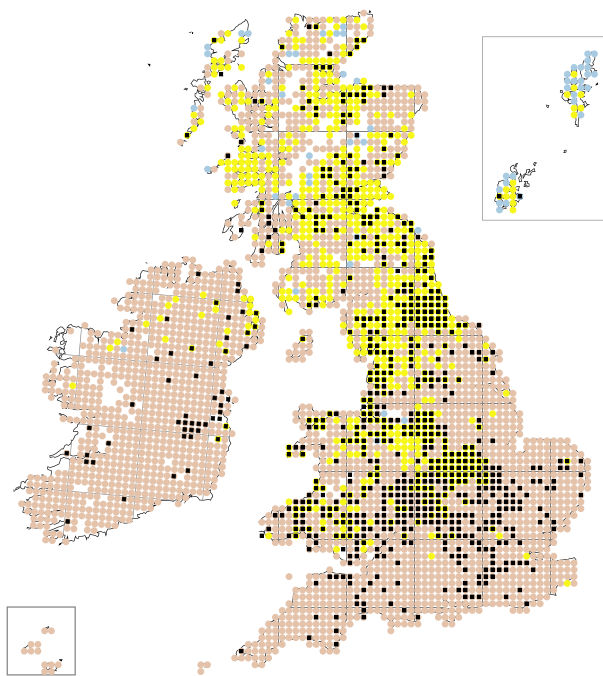


Figure 5. The distribution of the Temperate *Rosa canina* overlaps broadly with that of the Temperate but more northerly *R. caesia*. Hectads with both species are yellow, those species with one parent are pink (*R. canina*) or blue (*R. caesia*). The distribution of the hybrid (shown as black squares) extends well south of the range of *R. caesia*.

information provided by Stace *et al.* (2015), only rarely supplemented by other sources. In scoring characters of perennation, vegetative reproduction and fertility we have given preference to evidence from wild hybrids in Britain and Ireland if such plants appear to differ from artificial hybrids or those studied elsewhere, but we have drawn on evidence from further afield if this is all that is available. If there is variation within a hybrid in the capacity to reproduce vegetatively (e.g. in the presence of rhizomes), we have scored the hybrid as clonal even if only some individuals show this capacity. Fertility includes the capacity of hybrids to reproduce by seed, sexually or apomictically, when self-fertilized, crossed with other hybrid individuals or backcrossed to the parents. The independence of a hybrid from its parents is assessed primarily at the hectad scale, but other available information is taken into account. A population of a hybrid is not regarded as occurring independently of a parent if it is solely separated by small-scale topographic or ecological factors but is sufficiently close to be potentially part of the same inter-breeding population.

Of the 757 hybrids, 612 could be scored for all four characters listed in Table 5 whereas for 145 hybrids

the requisite information was not available for one or more characters. The most frequently missing characteristic is fertility (information not available for 107 hybrids, including 35 *Salix* hybrids, 31 orchid hybrids and 15 *Euphrasia* hybrids). Capacity for vegetative reproduction could not be scored for 27 hybrids, independence of parents for 22 and perennation for 5. The relationship between perennation, modes of reproduction and distributional independence of the parents is set out in Table 6.

ANNUAL HYBRIDS

Not surprisingly, all the sterile or only slightly fertile annual hybrids have distributions that are closely tied to those of their parents (Table 6). Examples of such hybrids include *Fumaria officinalis* × *F. parviflora*, of which only a single plant has ever been found, *Senecio squalidus* × *S. vulgaris*, which occurs rather rarely as a triploid hybrid in populations of its parents, and *Erodium cicutarium* × *E. lebelii*, which appears to be more frequent in mixed populations of the parent species.

Annual hybrids have a much higher proportion of fully fertile hybrids than the biennials or perennials. In part this may be because sterile annuals are so fleeting in their appearance that the chances of detection are less than those of sterile perennials. However, almost all the fully fertile annuals (58 of the total 62) are hybrids of *Euphrasia*. In this genus there are both diploid and tetraploid species and (with the exception of the isolated species *E. salisburgensis*) there are few sterility barriers between species at one or other ploidy level. Many of the fully fertile *Euphrasia* hybrids are, despite their fertility, usually found with their parents. However some, such as the tetraploid *E. confusa* × *E. nemorosa*, may replace the parents over large areas. Even the less widespread fertile hybrids may not be closely associated with the parents. Detailed studies in Cardiganshire (Chater, 2010), for example, have shown that the tetraploid *E. confusa* × *E. tetraquetra* is usually more abundant than *E. tetraquetra* and usually occurs in the absence of *E. confusa*. Some *Euphrasia* hybrids are regarded by Yeo (1978) as displaying ‘incipient speciation’; these are characterized by ‘extensive populations of comparatively uniform plants (compared with hybrid swarms), apparently of hybrid origin, occupying an area from which the putative parents are absent and often occupying a particular habitat consistently’. Sell & Murrell (2009) have argued that many of the recognized *Euphrasia* species are biologically subspecies, but they continued to recognize them as species for convenience. The other moderately or fully fertile annual hybrids that are frequently found in the absence of their parents (F = 2, 3; I = 2, 3) comprise

Table 3. Examples of parents of British and Irish hybrids with nested distributions

Parent A	Biogeographical element	British hectads with only parent A	Parent B	Biogeographical element	British hectads with only parent B	British hectads with both parents	British hectads with hybrid
<i>Cirsium tuberosum</i>	Suboc STemp	0	<i>C. acaule</i>	Euro Temp	737	23	17
<i>Crataegus laevigata</i>	Euro Temp	0	<i>C. monogyna</i>	Euro Temp	1746	789	499
<i>Drosera anglica</i>	Circ Bor	18	<i>D. rotundifolia</i>	Circ BorTemp	1149	597	164
<i>Ranunculus reptans</i>	Circ Bor	0	<i>R. flammula</i>	Euro Temp	2632	13	26
<i>Rosa stylosa</i>	Euro Temp	3	<i>R. arvensis</i>	Euro Temp	1187	354	64
<i>Rumex longifolius</i>	Euras Bor	5	<i>R. obtusifolius</i>	Euro Temp	2160	603	162
<i>Sagina saginoides</i>	Circ Arc	0	<i>S. procumbens</i>	Eurosib BorTemp	2747	59	42
<i>Viola rupestris</i>	Euras Temp	0	<i>V. riviniana</i>	Euro Temp	2748	8	5
<i>Ulex gallii</i>	Oc Temp	0	<i>U. europaeus</i>	Oc Temp	1646	986	67
<i>Ulmus minor</i>	Euro Temp	12	<i>U. glabra</i>	Euro Temp	1690	740	535

Arc, Arctic-montane; Bor, Boreal-montane; BorTemp, Boreo-temperate; Circ, Circumpolar; Euras, Eurasian; Euro, Euro-pean; Eurosib, Eurosiberian; STemp, Southern-temperate; Suboc, Suboceanic; Temp, Temperate. The biogeographical elements follow Preston & Hill (1997).

three *Atriplex* hybrids (*A. glabriuscula* × *A. longipes*, *A. glabriuscula* × *A. praecox*, *A. longipes* × *A. prostrata*) and *Viola arvensis* × *V. tricolor*.

Just as the annual hybrids are dominated by *Euphrasia*, the biennial hybrids are dominated by a single genus with species that are unduly prone to hybridization, *Verbascum*. This genus contributes 18 hybrids to the total of 25 biennials. Unlike *Euphrasia* hybrids, *Verbascum* hybrids are highly sterile. These, and other sterile or only slightly fertile biennial hybrids, are usually associated with their parents and the exceptions, *Verbascum bombyciferum* × *V. phlomoides* (I = 2) and *Verbascum nigrum* × *V. phoeniceum* (I = 3), are too rare to be significant departures from the rule. The former has been recorded once, growing in the absence of its parents (which are garden escapes), and the latter has been found twice, in both cases in the absence of the alien parent, *V. phlomoides*. The one fully fertile biennial hybrid frequently found in the absence of its parents (I = 2) is *Oenothera biennis* × *O. glazioviana*. *Oenothera glazioviana* (female) × *O. biennis* differs morphologically from the reciprocal hybrid and is the commoner plant; it is sometimes been treated as a species, *O. fallax*, rather than a hybrid, e.g. by Rostański (1982) and Rostański & Karlsson (2010).

PERENNIAL HYBRIDS

The great majority of spontaneous hybrids recorded in Britain and Ireland are perennials (80% of the 757 non-introduced hybrids and 80% of the 612 hybrids for which full data are available). In Table 6 they are divided between non-clonal and clonal perennials. The proportion of hybrids that frequently or usually occur in the absence of one or both parents (I = 2, 3) is greater for the clonal hybrids (33%) than for the non-clonal (10%). If only hybrids that are sterile or have low fertility (F = 0, 1) are considered the difference is even greater, 31% as opposed to 3%.

Non-clonal perennials

Characteristic examples of sterile, non-clonal hybrids (F = 0) that occur with their parents (I = 0) include *Asplenium obovatum* × *A. scolopendrium*, *Carex paniculata* × *C. remota*, *Erica tetralix* × *E. vagans* and *Spergularia marina* × *S. rupicola*, as well as intergeneric hybrids such as *Coeloglossum viride* × *Gymnadenia conopsea* and *Festuca rubra* × *Vulpia fasciculata*. Such hybrids are usually found as singletons or in small numbers; many are rare. These hybrids may fail to persist in individual sites for more than the life-time of the individual plant, or a site may

Table 4. Examples of parents of British and Irish hybrids with overlapping distributions

Parent A	Biogeographical element	British hectads with only parent A	Parent B	Biogeographical element	British hectads with only parent B	British hectads with both parents	British hectads with hybrid
<i>Carex canescens</i>	Circ Bor	507	<i>C. paniculata</i>	Euro Temp	837	705	4
<i>Dactylorhiza fuchsii</i>	EurosibTemp	639	<i>D. maculata</i>	Eurosib BorTemp	443	1600	155
<i>Dactylorhiza praetermissa</i>	Oc Temp	908	<i>D. purpurella</i>	Oc Bor	1085	131	15
<i>Geum rivale</i>	Eurosib BorTemp	218	<i>G. urbanum</i>	EurosibTemp	800	1555	777
<i>Juncus balticus</i>	Circ BorArc	87	<i>J. inflexus</i>	Eurosib STemp	1780	9	3
<i>Polystichum aculeatum</i>	Euras Temp	677	<i>P. setiferum</i>	Submed-Subatl	322	994	106
<i>Rosa arvensis</i>	Euro Temp	1198	<i>R. caesia</i>	Euro Temp	503	343	13
<i>Rosa caesia</i>	Euro Temp	60	<i>R. canina</i>	Euro Temp	1710	786	337
<i>Salix aurita</i>	Euro BorTemp	243	<i>S. caprea</i>	Euras BorTemp	555	1885	108
<i>Viola canina</i>	Eurosib BorTemp	983	<i>V. lactea</i>	Oc Temp	66	118	34

BorArc, Boreo-Arctic; Submed-Subatl, Submediterranean-Subatlantic; for other abbreviations, see Table 3. The biogeographical elements follow Preston & Hill (1997).

continue to support the hybrid if conditions are suitable for its re-establishment. A few sterile hybrids have a greater degree of independence ($I = 2, 3$). In the case of *Dryopteris cristata* \times *D. carthusiana* and *Salix aurita* \times *S. cinerea* the presence of the hybrid in the absence of *D. cristata* or *S. aurita* may reflect the gradual decline of these parents, but the explanation for the presence of *D. carthusiana* \times *D. expansa* in the absence of *D. expansa* is less clear. *Lolium perenne* \times *Schedonorus pratensis* often grows with its parents in grassland but it also occurs without *S. pratensis* as a casual in farmyards, on dung heaps or on rubbish tips, where it presumably arises from introduced seed. Finally *Sorbus aucuparia* \times *S. scalaris* occurs as a single tree in the absence of its putative parent *S. scalaris*, which is presumed to grow in a nearby garden; it may be that in this case the isolation of the hybrid simply reflects the failure to record the rarer parent. An analogous hybrid is *Senecio cinerea* \times *S. jacobaea* ($I = 1, F = 2$) that sometimes arises as a cross between garden plants of *S. cinerea* and nearby wild populations of *S. jacobaea*.

Hybrids at the most fertile end of the spectrum ($F = 3$) that occur with their parents ($I = 0$) often give rise to hybrid swarms and introgressed populations; these include *Dactylorhiza maculata* \times *D. praetermissa*, *D. maculata* \times *D. purpurea*, *Geum rivale* \times *G. urbanum* (Fig. 4) and *Primula elatior* \times *P. vulgaris*. However, this is not always the case, especially for the woody hybrids in the genus *Rosa* and *Salix*. The fertile hybrids ($F = 2, 3$), which

may occur independently of the parents ($I = 2, 3$), cover a number of different situations. *Centaurea jacea* \times *C. nigra* sometimes persists in populations after the introduced *C. jacea* has died out, whereas *Tilia cordata* \times *T. platyphylla* is rare as a native hybrid but planting has extended its range well beyond that of its parents. *Quercus petraea* \times *Q. robur* appears to occur in the absence of at least one parent in native woodland, but its distribution has also been greatly modified by planting. Similarly some records of *Crataegus laevigata* \times *C. monogyna* in hedges may reflect its earlier occurrence as a native hybrid but many are clearly planted, most obviously in Ireland where *C. laevigata* is no longer known as a native (Fig. 3). It is often impossible to say whether some fertile hybrid populations are persisting in areas in which both parents grew but from which one has subsequently died out, or whether they have spread beyond the range of the rarer parent. Such conundrums are presented by the distribution of hybrids such as *Hypericum humifusum* \times *H. linariifolium*, *Potentilla crantzii* \times *P. tabernaemontana*, *Ranunculus omiophyllus* \times *R. tripartitus* and *Rosa caesia* \times *R. canina* (Fig. 5). The distinction between hybrids and species is not always clear, and *Rosa caesia* \times *R. canina* is treated as one or more species by continental rhodologists. Similarly, Sell & Murrell (2014) have recently given specific recognition to plants hitherto treated by British botanists as *Potentilla crantzii* \times *P. tabernaemontana* and that are, like both parents, apomictic.

Table 5. Coding of the characters of spontaneous hybrids

Character	Category	Abbreviation	Notes
Perennation (P)	Annual	A	
	Biennial	B	
	Perennial	P	Includes plants that may be annual or perennial
Capacity for vegetative reproduction (V)	Non-clonal perennial	0	No specialized means of vegetative reproduction
	Clonal perennial	1	With specialized means of vegetative reproduction, coded according to categories of Hill <i>et al.</i> (2004, pp. 7–8), sometimes simplified
Fertility (F)	Sterile or virtually so	0	
	With slight fertility	1	
	Moderately fertile, but fertility less than that of parents	2	
	As fertile or almost as fertile as parents	3	
Extent to which British and Irish distribution is independent of parents (I)	Always or almost always with parents	0	
	Occasionally without one or both parents	1	
	Frequently without one or both parents	2	
	Usually or always without one or both parents	3	

Table 6. Fertility (F) and Independence (I) of the 612 of the 757 spontaneous hybrids for which information is available

Independence	Annuals				Biennials				Non-clonal perennials				Clonal perennials				Total
	F0	F1	F2	F3	F0	F1	F2	F3	F0	F1	F2	F3	F0	F1	F2	F3	
I0	21	8	6	40	16	1	2	1	71	56	42	30	59	23	29	11	416
I1	0	0	0	5	1	0	1	0	8	10	12	10	14	9	9	4	83
I2	0	0	1	14	1	0	0	1	3	1	4	15	10	13	6	5	74
I3	0	0	2	3	1	0	0	0	1	0	1	1	21	3	1	5	39
Total	21	8	9	62	19	1	3	2	83	67	59	56	104	48	45	25	612

For the explanation of the Fertility and Independence scores, see Table 5.

Clonal perennials

Most clonal perennial hybrids are rhizomatous or stoloniferous, sucker from the roots or root at the nodes; other modes of reproduction are more rare (Table 7). Despite their capacity for vegetative spread, over half such hybrids (55%) usually occur with the parents (I = 0). Examples spanning to range of fertility include *Holcus lanatus* × *H. mollis* and *Potamogeton lucens* × *P. perfoliatus* (F = 0), *Elymus repens* × *Hordeum secalinum* and *Epilobium montanum* × *E. pedunculare* (F = 1), *Alnus glutinosa* × *A. incana* and *Myosotis laxa* × *M. scorpioides*

(F = 2) and *Cerastium arvense* × *C. tomentosum* and *Salix herbacea* × *S. repens* (F = 3).

The proportion of clonal perennials that shows some independence of their parents increases with their degree of fertility (Table 6). In some cases the reasons for the marked degree of independence (I = 2) of more or less sterile hybrids (F = 0, 1) are clear. *Schoenoplectus tabernaemontani* × *S. triqueter* has persisted in river estuaries from which the rare and declining *S. triqueter* has been lost in the last century, whereas *Stachys palustris* × *S. sylvatica* has been spread as a cultivated plant and also

Table 7. Modes of vegetative reproduction in hybrids

Method of reproduction	Abbreviation(s) (Hill <i>et al.</i> , 2004)	Number of hybrids	Examples
Rhizomes or stolons	Rhiz, Stol	151	<i>Calystegia sepium</i> × <i>C. sylvatica</i> , <i>Epilobium palustre</i> × <i>E. parviflorum</i> , <i>Equisetum hyemale</i> × <i>E. ramosissimum</i>
Suckering from roots	Root	34	<i>Rosa canina</i> × <i>R. spinosissima</i> , <i>Ulmus glabra</i> × <i>minor</i> , <i>Viola canina</i> × <i>V. persicifolia</i>
Creeping and rooting at nodes	Node	20	<i>Epilobium brunnescens</i> × <i>E. ciliatum</i> , <i>Ranunculus flammula</i> × <i>R. reptans</i> , <i>Sagina procumbens</i> × <i>S. saginoides</i>
Detaching ramets			
Above ground	DRa	6	<i>Potamogeton acutifolius</i> × <i>P. berchtoldii</i>
On inflorescence	DRi	2	<i>Poa alpina</i> × <i>P. flexuosa</i> , <i>Trichophorum cespitosum</i> × <i>T. germanicum</i>
Detaching ramets above ground and Rhizomes	DRa and Rhiz	5	<i>Potamogeton berchtoldii</i> × <i>P. coloratus</i>
Fragmenting	Irreg, Frag	6	<i>Carex divulsa</i> × <i>C. remota</i> , <i>Ranunculus fluitans</i> × <i>R. peltatus</i>
Stems tip-rooting	Tip	4	<i>Rubus caesius</i> × <i>R. ulmifolius</i>
Offsets from tubers or bulbs	Otb	4	<i>Ficaria verna</i> subsp. <i>verna</i> × subsp. <i>fertilis</i> , <i>Galanthus nivalis</i> × <i>G. plicatus</i>
Plantlets formed on leaves	Leaf	2	<i>Cardamine flexuosa</i> × <i>C. pratensis</i> , <i>Drosera intermedia</i> × <i>D. rotundifolia</i>

The table includes all 234 clonal perennials, rather than the 222 listed in Table 6 for which all characters listed in Table 5 are available.

perhaps accidentally as a weed. Several mints, including *Mentha arvensis* × *M. spicata*, occur both as spontaneous hybrids and as escapes from cultivation (there are both glabrous and hairy variants; the hairy plants are probably usually spontaneous hybrids and the glabrous variants are the garden escapes). There is no such obvious reason for the distribution of such hybrids as *Elytrigia atherica* × *E. repens*, *Equisetum hyemale* × *E. variegatum* and *Potamogeton gramineus* × *P. perfoliatus* in areas from which their parents are absent. More or less sterile hybrids with a more extreme degree of independence (I = 3) include the same mixture of distributions that appear to be natural, such as *Carex saxatilis* × *C. vesicaria*, *Circaea alpina* × *C. lutetiana* and *Potamogeton berchtoldii* × *P. coloratus*, and those where the hybrids owe at least part of their presence beyond the range of overlap of the parents to human introduction of the hybrid (e.g. *Ammophila arenaria* × *Calamagrostis epigejos*, *Polygonatum multiflorum* × *P. odoratum*). *Spartina alterniflora* × *S. maritima* is a hybrid between one native and one alien species and *Mimulus guttatus* × *M. luteus* a hybrid between two alien parents; both have subsequently been spread in part by human agency. The most extreme examples of isolated hybrids are three apparently native hybrids with one parent that

is absent as a native from Britain and Ireland: two hybrids of *Equisetum ramosissimum* (with *E. hyemale* and *E. variegatum*) and one of *Potamogeton vaginatus* (with *P. pectinatus*). Rumsey & Spencer (2012) have argued that *E. ramosissimum* may be native in Britain but even they do not regard the evidence as compelling and in any event the recorded localities of this species bear little relation to those of its hybrids.

The final category of clonal perennials are those that combine at least a moderate degree of fertility (F = 2, 3) and independence (I = 2, 3). Hybrids with apparently natural ranges include *Nuphar lutea* × *N. pumila*, *Sagina procumbens* × *S. saginoides* and *Saxifraga hirsuta* × *S. spathularis* (in Ireland). *Hypericum maculatum* × *H. perforatum* has perhaps spread naturally along railways, and by human introduction, *Rorippa microphylla* × *R. nasturtium-aquaticum* has certainly been introduced in some localities and *Ulmus glabra* × *U. minor* may also have been spread as an introduction but the history of elms is obscure. *Ranunculus reptans* appears to be introduced periodically to northern lake shores in Britain, perhaps as seeds carried by migrant geese; it often fails to persist but it leaves behind populations of the fertile hybrid *R. flammula* × *R. reptans*. This hybrid has even been recorded

from Ireland, where *R. reptans* has not been confirmed.

FREQUENCY OF HYBRIDS

Hybrids tend to be rare, if rarity is measured by the number of 10-km squares in which they are recorded. If spontaneous hybrids are considered, only 137 of 694 spontaneous hybrids are found in 50 or more of the 2852 hectads in Britain for which botanical records are available; the remaining 557 hybrids are recorded in 1–49 hectads and 306 of these are found in only 1–5 hectads. Furthermore, these hybrids are almost all much less frequent than what might be naively described as their ‘potential distribution’, the number of hectads that supports both parents (Figs 6 and 7). (The 694 hybrids are those occurring in Britain for which data on their range and the ranges of both parents are available, so that hybrids confined to Ireland and some triple hybrids are excluded.) The six hybrids that are conspicuously more frequent than would be expected (Fig. 7) include five that, although they occur spontaneously, owe their frequency to the spread of the hybrid in horticulture (*Hyacinthoides hispanica* × *H. non-scripta*, *Mentha spicata* × *M. suaveolens*, *Mimulus guttatus* × *M. luteus*, *Polygonatum multiflorum* × *P. odoratum*, *Tilia cordata* × *T. platyphyllos*) plus *Circaea alpina* × *C. lutetiana*, a hybrid that has a native distribution that is much more

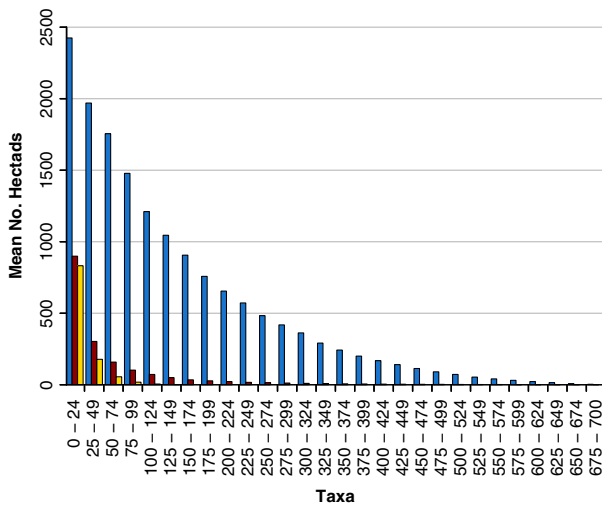


Figure 6. The number of hectads in which spontaneous hybrids (red), the parents of spontaneous hybrids (blue) and introduced hybrids (yellow) are all recorded. Taxa have been ranked by their frequency; mean values for successive groups of 25 taxa are shown. The values for the parents are the numbers of hectads that support both parents of each hybrid combination.

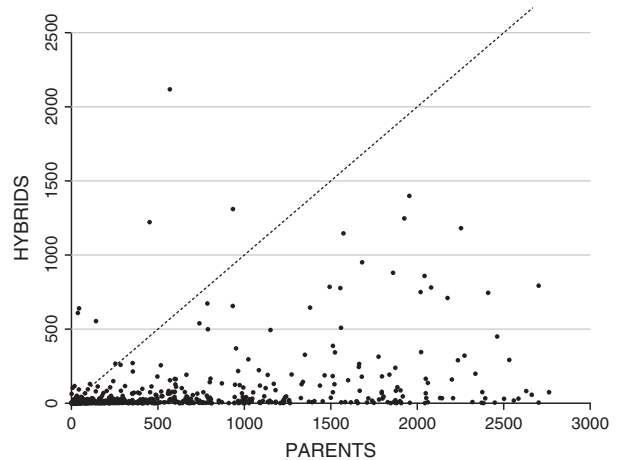


Figure 7. The number of hectads in which spontaneous hybrids have been recorded, plotted against the number of hectads that support both parents of that hybrid combination. The dotted line indicates the 1:1 ratio.

widespread than that of the rarer parent, *C. alpina*. Raven (1963) suggests that *Circaea alpina* has declined in postglacial times, leaving populations of the hybrid that may then have spread by means of their vigorous rhizomes.

The 148 introduced hybrids for which British hectad counts are available have a similar range of frequencies to the spontaneous hybrids (Fig. 6), except that the extremely long ‘tail’ of very rare hybrids is absent. There are 63 introduced hybrids in 50 or more hectads and 85 in 1–49 hectads, of which 38 hybrids are found in only 1–5 hectads. However, as noted above, the distinction between spontaneous and introduced hybrids is not absolute and some populations treated as spontaneous actually owe their presence in the wild to a combination of spontaneous and introduced populations. The difference in the length of the ‘tail’ of the distribution probably reflects a greater concentration on the native flora, and a difference in the criteria for the inclusion of spontaneous and introduced hybrids. All spontaneous hybrids between native species are mentioned by Stace (2010) and treated by Stace *et al.* (2015), even those that have been found as a single individual only once. However, introduced hybrids are included only if they are established in the wild or recorded relatively frequently as casuals. Some alien hybrids that have been recorded only rarely are mentioned by Stace *et al.* (2015) but not treated in full. Brief notes are provided on others that may occur in the wild but have not been reliably recorded because of the frequent problem of distinguishing hybrids and their parents in genera in which the species have been extensively hybridized in cultivation. The number of rare introduced hybrids is therefore more than is apparent from Figure 6.

The frequency of hybrids, measured by the number of hectads in which they are recorded in Britain, is related to perennation and fertility in Table 8. Annuals and biennial hybrids are clearly recorded less frequently than perennials (annuals mean 22 ± 5 , perennials mean 68 ± 8). Annuals and biennials of low fertility ($F = 0, 1$) are recorded in an average of 11 ± 3 hectads, compared with 28 ± 7 for those of higher fertility ($F = 2, 3$). The same difference is shown by non-clonal perennials (low fertility mean 41 ± 9 hectads, higher fertility 104 ± 21). However, the difference is much less marked for the clonal perennials, 65 ± 16 hectads as opposed to 73 ± 15 . Sterile hybrids ($F = 0$) are recorded less frequently (mean 32 ± 7 hectads) than more fertile hybrids ($F = 1-3$, mean 74 ± 9 hectads) when all perennation classes are considered together.

DISCUSSION

LIMITATIONS OF THE APPROACH

In this paper we have attempted to provide an overview of the occurrence of hybrids in Britain and Ireland. The definition of a hybrid we have adopted is a taxonomic one, and the picture we present is therefore dependent on the taxonomy adopted by Stace (2010), which we follow. Different decisions about the delimitation of species would affect the details of the picture, and if a radically different taxonomic approach was taken to the genus *Euphrasia*, which provides most annual hybrids, the differences might be quite substantial.

The classification of hybrids into categories for fertility, vegetative reproduction and independence of the parents has been largely based on the summary accounts presented by Stace *et al.* (2015). It has

inevitably involved some simplification, especially for fertility. The fertility of F_1 hybrids can vary between individuals, and later generations are often more fertile than F_1 s. The amount of evidence available for different hybrids also differs greatly: in some hybrids, for example, pollen stainability and seed-set has been studied in both natural and artificial hybrids, whereas the only description of the fertility of others may be a description of the hybrid as sterile. There may also be variation between individuals of the same hybrid in the presence or absence of rhizomes or stolons. The independence of hybrids might in theory be calculated from the available distributional data, but in practice we have taken into account what we know about the adequacy with which the hybrids and their parents are recorded. Many species of *Rosa*, for example, are less well recorded than most other vascular plant species, so a hybrid might not be as independent of its parents as it appears from a distribution map. In such cases we have given emphasis to the distribution patterns in areas where species and hybrids are known to have been well recorded. Tables 6 and 8 exclude hybrids for which the required information is not available. The most serious consequence of this restriction is to exclude 21% of *Euphrasia* hybrids, 60% of *Salix* hybrids and 63% of orchid hybrids, chiefly because of the lack of information on their fertility. Our measure of the frequency of a hybrid shown in Table 8, the number of hectads in which it is recorded in Britain, is clearly very imperfect, because of the difficulties of recording hybrids discussed earlier in this paper.

SIGNIFICANCE OF HYBRIDS IN THE WILD

Despite the limitations of the approach outlined above, it is possible to draw some outline conclusions

Table 8. The number of British hectads in which hybrids are recorded, shown in relation to their perennation and fertility

Perennation	Fertility				Total
	F0	F1	F2	F3	
Annuals	15 ± 8 ($N = 20$)	5 ± 2 ($N = 8$)	20 ± 9 ($N = 9$)	28 ± 8 ($N = 62$)	23 ± 5 ($N = 99$)
Biennials	9 ± 3 ($N = 20$)	4 ($N = 1$)	10 ± 4 ($N = 3$)	94 ± 86 ($N = 2$)	15 ± 7 ($N = 26$)
Non-clonal perennials	34 ± 15 ($N = 78$)	50 ± 10 ($N = 62$)	102 ± 27 ($N = 57$)	105 ± 32 ($N = 56$)	69 ± 11 ($N = 253$)
Clonal perennials	39 ± 11 ($N = 98$)	120 ± 42 ($N = 46$)	59 ± 17 ($N = 45$)	102 ± 31 ($N = 23$)	68 ± 12 ($N = 212$)
Total	32 ± 7 ($N = 216$)	74 ± 18 ($N = 117$)	76 ± 15 ($N = 114$)	71 ± 14 ($N = 143$)	58 ± 6 ($N = 590$)

Figures are the mean number of hectads \pm standard error, with the number of hybrids in the category, N . The table is based on 590 spontaneous hybrids occurring in Britain for which perennation and fertility scores are available. For the explanation of the Fertility scores, see Table 5. We have excluded 13 hybrids because they have ranges that have been substantially increased by introductions (e.g. *Polygonatum multiflorum* \times *P. odoratum*, *Tilia cordata* \times *T. platyphyllos*).

about the significance of hybrids in the British and Irish flora. The first point to make is the great variability of hybrids – the fact that a taxon is a hybrid actually tells you little information about its biology and ecology. There is perhaps a parallel to be drawn between ‘hybrid’ as a descriptor of the genetic origin of a taxon and ‘alien’ as a term describing a plant’s geographical origin. In both cases the terms summon up a popular stereotype, hybrids sterile and transient, aliens established, vigorous and competitive, stereotypes that are at variance with the range of behaviour actually observed.

When the perennation, fertility and independence of hybrids are considered together, certain conclusions are clear. With the very marked exception of *Euphrasia* hybrids, there are relatively few annual and biennial hybrids and they tend to be rare and to be found in association with their parents. The *Euphrasia* hybrids are numerous and sometimes very fertile; the fertile hybrids may show considerable independence and such hybrids have been described as ‘incipient species’. Perennial hybrids that can reproduce by seed or vegetatively may also show considerable independence, and these hybrids tend to be more frequent than the non-clonal perennials that are sterile or have very low fertility. The association of increased independence and frequency with some means of reproduction make clear biological sense, and suggests that our main conclusions may be well founded despite the limitations of the study outlined above.

Although we have argued that hybridization is not solely a result of human interference with natural habitats, there is no doubt that human activities have greatly increased the number of hybrids in the British and Irish flora. This situation has happened by: (1) the increase in the range of some spontaneous hybrids between native species by planting or escapes from cultivation; (2) the introduction of alien species that have hybridized with natives; and (3) the accidental or deliberate hybridization of garden plants with the subsequent cultivation and escape into the wild of their hybrids.

FUTURE RECORDING

There is clearly still much scope for the improved recording of hybrids by traditional methods. Most hybrids that can be identified by the normal techniques of the field botanist are under-recorded. We hope that the publication of the new *Hybrid Flora* will help improve the recording of hybrids, both by providing the detailed information needed for their identification and more generally by stressing the importance of hybrids, and thus discouraging the view still taken by some recorders that they are

happy to record species but ‘don’t do hybrids’. Thirty years ago it was commonplace to hear recorders say that they were happy to record native species but not aliens, an attitude that has now all but disappeared. We should aim to expand the repertoire of the next generation of recorders to include hybrids. In addition, the specimens of hybrids in many herbaria have not been revised in the light of the great increase in our knowledge since 1975; expert revision of this material and incorporation of the confirmed records into the appropriate databases is also a desideratum.

In addition to including hybrids in routine recording, there is an almost unlimited scope for detailed studies designed to investigate the fertility of hybrids in the wild, or the relationship of their distributions to those of their parents. A few hybrids have been studied in detail, but many have scarcely been studied at all.

Lawson Handley (2015) has emphasized the potential of molecular methods to revolutionize biological recording. Although this is certainly true for some taxa, such methods are very unlikely to have a rapid revolutionary effect on our study of plant hybrids. Ideally, one would like such methods to be used to elucidate the taxonomy of hybrids and their parents, followed (if necessary) by the provision of molecular tools to facilitate the identification of individual specimens of those hybrids that cannot be identified with confidence by morphological methods alone. However, current methods (e.g. DNA barcoding) do not provide a universal identification system that can be used to distinguish all plant species, let alone hybrids, so that in practice each problematic genus needs to be tackled individually. The investigation of the world’s *Potamogeton* species and hybrids by traditional and molecular methods has been the main research priority of Zdenek Kaplan (Czech Republic) for at least a decade, and other groups have contributed to the research that has established our current knowledge of the European taxa. In Britain there have been substantial contributions from four research students or post-doctoral workers (Jeremie Fant, Peter Hollingsworth, Andy King, John McMullan), working in collaboration with CDP and Richard Gornall (Leicester) or John Barrett (Cambridge). Thus a considerable research effort has been devoted to a genus that in European terms is not especially large (23 species), and represents a relatively straightforward set of problems as its hybrids are naturally occurring, usually highly sterile, have ranges that are unaffected by escapes from cultivation and have proved amenable to molecular study. It will require a massive financial and intellectual investment to investigate some of the other genera

with numerous hybrids, despite the decreasing cost of the laboratory procedures. Of all the hybrid-rich genera in Britain, *Salix* is perhaps most in need of cytological and molecular studies. This is a much larger genus than *Potamogeton* in Europe, with 65 species recognized by *Flora Europaea* (Tutin *et al.*, 1993), its hybrids are often fertile, and its lowland species and hybrids have been cultivated and spread by basket-makers, probably since prehistory. Attempts to identify the species rapidly by barcoding have been a 'spectacular failure' (Percy *et al.*, 2014) and more detailed molecular studies have only just begun (Scottish Montane Willow Research Group 2005).

Even if it proves possible to set up the necessary collaborations between field and laboratory workers to investigate the British and Irish hybrids by molecular techniques, and to obtain the necessary money from funding bodies who do not regard the elucidation of the taxonomy and distribution of hybrids as sufficient justification for funding but require it to be tied in to broader, more theoretical questions, we cannot assume that all genera will be as amenable to molecular study as *Potamogeton*. *Platanthera* is an orchid genus with just two British species but they are so similar at the molecular level that markers to distinguish them have not yet been discovered, perhaps because they are at an early stage of speciation (Bateman, James & Rudall, 2012). Molecular confirmation of putative hybrids in other genera has proved to be impossible using a small number of nuclear and plastid markers. *Dactylorhiza*, a notoriously critical orchid genus, has been subjected to much molecular research but the extensive data accumulated over the last decade on allozymes, chloroplast haplotypes and semi-quantified ITS allele frequencies are not sufficient to allow the reliable identification of most hybrid combinations, due to the diversity observed in the tetraploids and to the fact that in diploid-tetraploid hybrids the former are often part-parental to the latter (Stace *et al.*, 2015). Thus we are currently handicapped by the very importance of hybridization in plant speciation. The tools for solving these problems may well become available, but we will still need to find funding to realize the potential of molecular methods. Although molecular studies will certainly make further valuable contributions to our understanding of the taxonomy of plant hybrids in future years, they are not likely to provide rapid solutions to all identification problems. In many cases we will continue for the foreseeable future to depend for most of our information on British and Irish hybrids on volunteer recorders, working with more or less traditional techniques.

ACKNOWLEDGEMENTS

This paper is based on the *Hybrid flora of the British Isles*, which has been written jointly with Professor Clive Stace. We are grateful to all those who have contributed records and other information for this flora, to Steph Rorke (BRC) for her work on the resulting database and for preparing the distribution maps for this paper, to Colin Harrower for plotting the other figures, to Dr Mark Hill for statistical advice and to Björn Beckmann, Dr Oli Pescott and Paul Westley for other help. Professor Harald Niklfeld kindly advised us on the Austrian record of *Carex ericetorum* × *C. montana* and we have benefitted from discussing the application of molecular methods to the study of plant hybrids with Professor Peter Hollingsworth. Oli Pescott and Dr Helen Roy kindly commented on a draft of the paper and two reviewers provided rapid and helpful comments. The Biological Record Centre receives support from the Joint Nature Conservation Committee and the Natural Environment Research Council (via National Capability funding to the Centre for Ecology and Hydrology, project NEC04932).

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