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Hybridisation and hybrid speciation under global change

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Summary

An unintended consequence of global change is an increase in opportunities for hybridisation among previously isolated lineages. Here we illustrate how global change can facilitate the breakdown of reproductive barriers and the formation of hybrids, drawing on the flora of the British Isles for insight. Although global change may ameliorate some of the barriers preventing hybrid establishment, for example by providing new ecological niches for hybrids, it will have limited effects on environment-independent post-zygotic barriers. For example, genic incompatibilities and differences in chromosome numbers and structure within hybrid genomes are unlikely to be affected by global change. We thus speculate that global change will have a larger effect on eroding pre-zygotic barriers (eco-geographic isolation, phenology) than post-zygotic barriers, shifting the relative importance of these two classes of reproductive barriers from what is usually seen in naturally produced hybrids where pre-zygotic barriers are the largest contributors to reproductive isolation. Although the long-term fate of neo-hybrids is still to be determined, the massive impact of global change on the dynamics and distribution of biodiversity generates an unprecedented opportunity to study large numbers of unpredicted, and often replicated, hybridisation "experiments", allowing us to peer into the birth and death of evolutionary lineages.

Keywords: alien; allopolyploidy, genome duplication, global change, hybrid, invasive species, reproductive isolation, speciation.

I. Introduction

'Global change', the term often used to describe the combination of planetary change and human societal change, is having a profound effect on biodiversity across the globe. Climate change, industrialization, environmental degradation, and global trade and travel have moved plants and animals around the planet, breaking down previous geographic barriers to gene flow between closely related species (Mooney & Cleland 2001). The loss of ecological and geographic barriers that historically kept closely related species apart is creating unprecedented new opportunities for hybridisation (Mable 2013; Chunco 2014, Brennan *et al.,* 2015; Taylor *et al.*, 2015), which could potentially have a profound impact on biodiversity and ecosystems worldwide.

Hybridisation has been defined in many different ways, from crosses between genetically distinct populations (Abbott *et al.,* 2013), to crosses between genetically distinct taxa resulting in the production of viable offspring (Mallet 2007), thus occurring both within and between species (Rieseberg & Carney 1998). Here we focus on inter-specific hybridisation. Interspecific hybridisation is a regular natural phenomenon and it is estimated that as many as 25% of plant species and 10% of animal species hybridise naturally (Mallet 2007). Hybridisation has long attracted the interest of evolutionary biologists, in part because it seems to undo the very process responsible for the generation of species diversity (Dobzhansky 1937, Mayr 1942, Stebbins 1959, Grant 1971, Abbott *et al.,* 2013). However, the consequences of hybridisation between genetically distinct lineages can result in a variety of outcomes that may influence diversity, including gene flow from one taxon to another (introgression) (Rieseberg & Wendel, 1993), the displacement and/or extinction of one or both parental taxa (Ellstrand & Elam, 1993), the fusion of previously divergent taxa (Grant & Grant, 2014), or the creation of new, stable hybrid taxa and, ultimately, speciation (Mallet 2007, Abbott *et al.,* 2013, Thomas 2015). Hybridisation and its consequences have been best studied in plants (Grant, 1971; Arnold, 1997; Rieseberg & Carney, 1998; Abbott *et al.*, 2013), but the biological features and evolutionary mechanisms that contribute to the variation in the occurrence, persistence, and evolution of hybrids are relatively little understood in both plants and animals.

Whether the incidence of hybridisation at a global scale is changing, and if so at what rate, is still unclear, yet analyses of well-studied floras, such as the British Isles, indicate that a significant fraction of hybrid taxa may involve introduced taxa (Stace *et al.,* 2015, Stace & Crawley 2015). Among the flora of Britain and Ireland hybridisation involving introduced (non-native) taxa is well documented (Stace *et al.,* 2015, Stace & Crawley 2015, Table 1), and a recent survey revealed that 33% of hybrid taxa (301/909) involve introduced (non-native) taxa (Preston & Pearman 2015). Approximately half of these non-native hybrids have arisen spontaneously in the wild, while the remainder were introduced as hybrids. Studying the origin and fate of these hybrids is timely and

important if we are to understand the consequences of ongoing changes in the distribution of global biodiversity.

Because hybrid formation does not equate to hybrid success, the long term consequences of contemporary hybridisation under global change are hard to predict. Here we present an overview of the consequences of this new era of increased hybridisation opportunities drawing on the flora of Great Britain and Ireland because it is probably the best documented hybrid flora in the world. Specifically, our review addresses the following questions: How does global change alter the likelihood of hybrid formation? Does global change alter the relative importance of prezygotic and postzygotic barriers in maintaining species apart? What is the incidence of human-made hybrids in current floras and is likely to increase or decrease under global change? What are the biological characteristics that make some hybrids more likely to become established than others? Why are recently formed hybrids relatively common, but their allopolyploid derivatives rare? We suggest that global change is clearly increasing opportunities for hybridisation, for example directly by moving species around the world or indirectly by eroding phenological and ecological barriers. Human-made hybrids, created for example for horticultural purposes, can also significantly contribute to current floras as exemplified in the naturalised flora of Britain and Ireland. We speculate that this new scenario is shifting the relative importance of prezygotic and postzygotic barriers from what is generally seen in natural systems, and therefore the consequences of secondary contact in this changing world may depend more heavily on postzygotic than on prezygotic barriers. The persistence of newly formed hybrids, and their evolutionary fate, will hinge on mechanisms that stabilise hybrids including asexual reproduction, selection for increased fertility, polyploidy, and ecological niche diversification, among others. In the next sections, we take a comprehensive approach to understand the processes and mechanisms leading to: (1) hybrid formation, (2) the establishment of hybrids, and (3) the ecological and evolutionary outcomes of hybridisation.

II. Hybrid formation

Understanding hybridisation and the potential for global change to alter its incidence requires analysis of the conditions that allow hybrid formation and establishment. Speciation involves the origin of barriers preventing gene flow between incipient species (Coyne & Orr 2004, Baack *et al.,* 2015), but hybridisation bypasses these barriers. Isolating barriers are traditionally classified as those acting before (pre-zygotic) and after zygote formation (post-zygotic) (reviewed in Coyne & Orr 2004) (Fig. 1). In plants, pre-zygotic barriers include: (i) Pre-pollination barriers such as geographical and ecological barriers (e.g. habitat preferences), flowering phenology and pollinator preference and behaviour, which prevent or reduce the likelihood of interspecific mating; and (ii) post-pollination

barriers which act before zygote formation, such as unilateral interspecific incompatibility (Hiscock *et al.*, 1998), and gametophytic selection, in which conspecific pollen is favoured over heterospecific pollen (Rieseberg & Willis 2007). The breakdown of geographic isolation is usually treated separately from other isolating barriers (Coyne & Orr 2004) as it may reflect both biological differences in habitat preference and non-biological and historical features causing species to occur in different geographic locations (Dobzhansky 1937). However, we include geographic isolation in our discussion because global change, including the movement of species around the globe, has had a direct impact in increasing the opportunities for secondary contact between previously isolated taxa.

Although the potential for human-induced environmental change to influence the rate of hybridisation has long been recognised (e.g., Anderson 1948), the evidence to support this view is only just beginning to accumulate (Walther *et al.,* 2009, Garroway *et al.,* 2010, Hoffmann & Sgrò 2011, Campbell & Wendlandt 2013, Chunco 2014, Chown *et al.,* 2015). In this section, we discuss how hybrids may overcome pre-zygotic isolating barriers and geographic isolation, paying attention to those barriers that are likely to be affected by global change.

1. Breakdown of geographic isolation

The breakdown of geographic isolation when species increase their range, either as a consequence of climate change (e.g. during periods of glaciation), or through anthropogenic dispersal, provides historically isolated taxa with new opportunities for hybridisation. Human-mediated transport of species, either accidental or deliberate, is the most dramatic of these and has been going on for thousands of years, but has been accelerating rapidly in Europe and North America (Hulme *et al.,* 2008). Increased international trade and travel in the current era of globalisation means that the spread of non-native species is likely to increase (Hulme *et al.,* 2008). The pathways of human-assisted dispersal are varied, and include accidental long-distance dispersal events that result in translocation of terrestrial plant species across oceanic barriers, facilitated dispersal (e.g., along roadsides and railroads), and intentional introductions (e.g., horticultural trade). Although long distance dispersal events occur with low probability, theoretical analyses have shown that these events can accelerate migration rates in plants by an order of magnitude (Higgins & Richardson 1999), greatly increasing opportunities for secondary contact.

Long distance dispersal where propagules are transported as contaminants of commodities (e.g., grains, timber, and wool) and in ships' ballasts is well documented (Stace & Crawley 2015). For instance, in the early 20th century, the River Tweed in the English-Scottish border hosted 384 introduced plant species growing along its banks (Myers & Bazely 2003). Many of these plants originated in Europe, Asia, Australasia, and the Americas and were brought as wool contaminants, which were then washed into local rivers during the cleaning process (Silvertown 2011). In addition,

anthropogenic activities can also facilitate range expansion by creating dispersal routes that can then be exploited by natural means. Roads and railways provide corridors that can act as dispersal routes allowing species to spread rapidly to new areas. The introduced hybrid *Senecio squalidus* (Oxford ragwort, Asteraceae), originally from Mount Etna, Sicily, escaped from cultivation in the Oxford Botanic Garden in the late 18th century, but it was not until the development of railway lines in the 1800's that it began spreading throughout the British Isles (Abbott *et al.,* 2009). The spread of *S. squalidus* in the British Isles has resulted in novel hybridisation events with native *Senecio* species. Crosses between *S. squalidus* and *S. vulgaris* have given rise to three new fertile hybrid taxa via a sterile triploid intermediate ('bridge') *S. x baxteri*: the tetraploid introgressant 'radiate goundsel', *Senecio vulgaris* var. *hibernicus*, the allohexaploid *S. cambrensis* (Welsh groundsel), and the tetraploid *S. eboracensis* (York radiate groundsel, Abbott & Lowe 2004). Additionally, hybridization between *S. squalidus* and native *S. viscosus* has given rise to the sterile triploid *S. subnebrodensis* (Lousley 1946).

In addition to facilitating long distance dispersal events, global change in the form of climate change can increase previously existing areas of sympatry among species, or bring previously isolated taxa together through shifts in their range (Hoffmann & Sgrò 2011, Brennan *et al.,* 2015). For example, changes in temperature or precipitation can result in increased range overlap, and the creation or expansion of hybrid zones (Campbell & Wendlandt 2013, Taylor *et al.,* 2015). Because hybrid zones often occur at the range limits of the parental species, changes to the geographic boundaries where these species occur should have a particularly strong impact on the location and extent of hybrid regions (Chunco 2014). There are a number of historical examples of this within the British flora. For instance, the hybrid waterlily *Nuphar x spenneriana* (Nymphaeaceae) is postulated to have arisen during the Late Glacial period ~10,000 years ago when the ranges of its parental species *N. pumila* (tolerant of cold water) and *N. lutea* (preferring warmer water) overlapped (Preston and Croft 1998). *N x spenneriana* then subsequently displaced *N. lutea* at its more northerly locations due to its competitive advantage in tolerating cooler water. A similar story may account for the current distribution of *Circaea x intermedia* (Onagraceae), a hybrid between *C. alpina* and *C. lutetiana* which has all but displaced its cold-loving parent *C. alpina* in northern Britain since the ice retreated (Marren 1999).

Climate change can also facilitate the spread of invasive populations which can then contribute to hybridisation events either with native species, or with other invasive taxa. For example, warmer climates may allow the migration of species from warmer regions into regions that were formally too cold for their long-term survival as well as allowing introduced species from warmer regions to overwinter more successfully and extend the growing season, thus facilitating the establishment and

spread of non-native taxa (Walther *et al.,* 2009).The increases in populations of *Orchis simia* and *O. purpurea* in Kent and their spread north into other counties of southern England provides a good example of the former scenario (Fay 2015). Despite the expected importance of climate change on increasing hybridisation rates (Chunco 2014, Brennan *et al.,* 2015), most evidence in plants remains indirect (e.g., perceived changes on the extent of hybrid zones) or correlative (e.g., comparisons of number of hybrids at different time points), and more detailed case studies are needed (e.g., Campbell & Wendlandt 2013).

2. Erosion of ecological isolation barriers

The production of hybrids may be prevented by pre-zygotic, ecological barriers that have evolved as by-products of adaptation to their local environments (Coyne & Orr 2004, Baack *et al.,* 2015) (Fig. 1). For example, broadly sympatric species may still display ecological preferences for different habitats (e.g., mesic vs. arid habitats and forested vs. open habitats), or be reproductively isolated by virtue of flowering at different times. Habitat modification, including increased disturbance and fragmentation, can erode ecological barriers and facilitate hybrid formation (Anderson 1948, Stebbins 1950, Buggs 2007). Moreover, altered and disturbed habitats, e.g., arising as a consequence of agricultural practices or urbanisation, can provide hybrids with new environments where they can establish. Among the British flora *Silene dioica x S. latifolia (= S. x hampeana,* Caryophyllaceae) (Marren 1999) provides a good example of how habitat modification may facilitate hybridisation, while *Senecio squalidus* and *S. cambrensis* (Asteraceae) are examples of how hybrids can establish in new environments (Abbott *et al.*, 2009). Human-induced breakdown of ecological isolation has also been implied in hybridisation between *Centaurea erythraea* and *C. littorale* (Gentianaceae). These two species generally occur in different habitats, but human disturbance in sand dune systems is thought to have resulted in mixed populations (Ubsdell 1979), which can be found in coastal regions in England and mainland Europe (Brys *et al.,* 2014). Some of these populations harbour nearly sterile F1 hybrids and backcrosses, which appear to differ in fertility (Ubsdell 1979). Nevertheless, differences in floral morphology and mating system are efficient in reducing hybridisation, at least in mixed populations in Belgium, where established hybrids occur at a frequency of approximately 1% (Brys *et al.,* 2014). Ultimately, the outcome of habitat alteration on hybridisation may be dependent on phylogenetic relationships between taxa. For instance, Brennan *et al.*, (2015) suggest that habitat alteration may be more important for hybridisation between younger taxa, as they are expected not yet to have accumulated strong genetic barriers.

Climate change affects the phenology of many species (Cleland *et al.,* 2007), for instance by causing plants to flower earlier. Changes in the timing of reproductive events, such as flowering, can directly alter the level of reproductive synchronisation between sympatric species, breaking down

temporal isolation barriers, and facilitating hybridisation. For temperature or precipitation changes to increase hybridisation opportunities, it is necessary for one species to change its phenology while the other remains stable or changes more slowly (Chunco 2014). Experimental data shows that this situation may not be uncommon. For instance, artificial warming of experimental plots results in more reproductive overlap among grassland species (Sherry *et al.,* 2007). The breakdown of temporal isolation may be particularly important in sympatric species where phenological isolation is an important reproductive barrier.

A further potential barrier to hybridisation in sympatric populations is isolation resulting from pollinator preference (Ramsey *et al.,* 2003). If global change affects the distribution of pollinators and/or their behaviour, we can predict that hybridisation could be facilitated by a breakdown of pollinator isolation barriers (Campbell & Wendlandt 2013). Recent studies show that the distribution of certain species of butterfly in the British Isles and Europe is changing and that their choices of host (brood) plants are changing as a consequence (Bridle *et al.,* 2013). If these changes mean that pollinators visit a broader range of species, it is conceivable that this creates new opportunities for hybridization. Paradoxically, changes in visitation preferences could hypothetically reduce hybridisation, for instance if generalist pollinators change their preference to ignore rarer plant species, thereby resulting in a reduction in heterospecific pollen transfer. In addition to changes in visitation preferences, loss of pollinator diversity may also alter opportunities for hybridization. For example, if pollinators that are specialised on individual plant species are lost, pollen transferred by generalist pollinators may deposit a proportionally higher fraction of heterospecific pollen on stigmas. Clearly, the consequences of changes in pollinator distribution, diversity and abundance can have complex repercussions on hybridization, and these may depend on the particular assemblage of plant and pollinator species. Future studies, akin to that of Bridle *et al.*, should seek to address these questions.

3. Artificial hybridisation

Traditionally, artificial hybridisation is not considered in discussions of the ecological and evolutionary significance of hybrids (Rieseberg 1995, Arnold 1997). However, hybrids can be produced artificially and then become part of the natural environment. In the context of global changes to species distribution, the importance of artificial hybrids may be substantial, at least at ecological levels. For example, in the flora of the British Isles, approximately 17% (152/909) of hybrids were introduced as hybrids (Preston & Pearman 2015). Moreover, some of these are deliberate introductions of hybrids of agricultural or horticultural interest such as *Mentha* (Lamiaceae), *Mimulus* (Phrymaceae), and *Verbascum* (Scrophulariaceae). Although most horticultural varieties do not persist outside cultivation (Mack 2005), horticultural introductions do

contribute to the non-native component of many floras, including the British Isles (Clement & Foster 1994, Stace 2010).

Artificial hybrids may have a disproportionate contribution to hybrid floras, as artificial hybridisation can bypass other pre-zygotic barriers such as pollinator isolation, phenology, habitat isolation and geographic isolation. Furthermore, artificial selection on horticultural hybrids may coincidentally increase their probability of establishment and spread (Ellstrand & Schierenbeck 2000). For example, horticultural varieties are often selected on the basis of traits such as hardiness and cold-tolerance (Milne & Abbott 2000), or ease of propagation and large plant size, which may allow the establishment of cultivars beyond the ecological range of their wild parental species (Mack 2005). Indeed, it would be interesting to investigate whether artificial hybrids deliberately introduced through the horticulture trade have a larger range than those that originated spontaneously. Artificial crosses from both the horticultural trade and botanic gardens are a relatively unappreciated source of plant hybridisation (Knobloch 1972, Ellstrand & Schierenbeck 2000), but the contribution of artificial hybrids to ecological and evolutionary phenomena is likely to increase in an era of global change.

4. Weakening of gametic barriers

In some cases, pre-zygotic, post-pollination 'gametic' barriers must also be overcome for hybrid formation. This type of post-pollination barrier can arise from gametophytic incompatibilities and conspecific pollen precedence (Hiscock *et al.,* 1998, Howard 1999, Husband *et al.,* 2002). Gametic/gametophytic barriers should be little affected by processes associated with global change, unless these affect the relative receipt of heterospecific pollen (e.g., by increasing the number of heterospecific matings). Because conspecific pollen precedence often depends on the relative amounts of conspecific and heterospecific pollen received on stigmas (Howard 1999), an increase in heterospecific pollen receipt may translate to higher rates of hybrid production. This could be the case if an introduced species becomes invasive and comes to dominate a particular habitat where related native species occur (Morales & Traveset 2009). Pollinators would then carry an increased pollen load of the alien species with corresponding increased chance of cross-pollinating the native species. Thus we predict that the main consequence of global change on pre-zygotic, post-pollination barriers will be through increasing the deposition of heterospecific pollen as non-native species become more abundant, thereby weakening conspecific pollen precedence and facilitating hybridization.

In summary, global change is clearly altering the opportunities for hybrid formation, and we would expect the incidence of hybridization to continue increasing. Increased opportunities for hybrid formation may result as a consequence of multiple and not mutually exclusive processes,

312 such as the global re-shuffling of species through human-mediated dispersal, shifting species
313 distributions and phenology as a consequence of climate change, the erosion of ecological barriers,
314 including the "hybridisation of the habitat", changes in pollinator preference and diversity, the
315 expansion of non-native species, and the artificial production and spread of hybrids. Although we
316 think that hybrid formation is likely to increase, an alternative view may be that we have reached
317 "peak" hybridisation, and the rate of hybridisation is slowing down. For example, it may be argued
318 that both species introductions and invasions reduce local biodiversity, and fewer species should
319 mean fewer hybridisation opportunities. Similarly, loss of habitat may reduce contact zones between
320 potentially hybridising taxa. However, we think that the effect of global change in promoting
321 hybridisation through the mechanisms reviewed in this section will by far exceed any hypothetical
322 reduction in hybridisation opportunities. As our records of local floras continues improving,
323 monitoring the temporal patterns of hybridization in floras around the world becomes feasible. Of
324 particular interest will be to monitor floras in developing countries where expansion of international
325 trade, and colossal changes in land use as economies grow, may fast-track the upward trend in the
326 formation of hybrids.

327III. Hybrid establishment: Overcoming intrinsic and extrinsic post-
328 zygotic barriers

329 After hybrids are formed, their short-term fate is partly determined by their ability to overcome both
330 intrinsic (e.g., environment-independent low viability and sterility), and extrinsic (e.g., ecological
331 selection) post-zygotic isolation barriers (Coyne & Orr 2004) (Fig. 1). In natural settings, pre-zygotic
332 barriers may contribute more to total reproductive isolation than post-zygotic barriers (Lowry *et al.,*
333 2008, Baack *et al.,* 2015). However, given the potential for global change to by-pass pre-zygotic
334 barriers and geographic isolation, as argued in the previous section, we speculate that post-zygotic
335 isolation may be the most important hurdle to overcome in the early stages of neo-hybridisation.
336 Intrinsic post-zygotic isolation barriers have been relatively well characterised at the genetic level, in
337 comparison to pre-zygotic barriers (Lowry *et al.,* 2008, Widmer *et al.,* 2009, Rieseberg & Blackman
338 2010). As in animal systems, post-zygotic isolation barriers are expected to increase as a function of
339 genetic divergence (Coyne & Orr 2004), although evidence of this from plant systems is limited
340 (Moyle *et al.,* 2004, Scopece *et al.,* 2007).

341 5. Escaping hybrid inviability and sterility

342 Hybrids are not uniformly unfit (Arnold & Hodges 1995, Rieseberg & Carney 1998), and within a
343 single hybrid taxon (or sometimes a single hybrid cross) it is possible to find individuals with lower,
344 similar or higher fitness relative to their parents (Taylor *et al.,* 2009). Nevertheless, many hybrids

345 have to overcome severe intrinsic post-zygotic barriers before they can become established (Lowry
346 *et al.,* 2008).
347 Post-zygotic barriers include intrinsic hybrid inviability and sterility (Fig. 1), and may be
348 caused by a variety of mechanisms (Rieseberg & Blackman 2010, Baack *et al.,* 2015), including
349 differences in chromosome structure and ploidy level (Stebbins 1971, Rieseberg 2001, Levin 2002),
350 nuclear-nuclear and nuclear-cytoplasmic genic incompatibilities (Lowry *et al.,* 2008), and parental
351 genomic conflict during seed development (Köhler *et al.,* 2010) (Fig. 1). Genic incompatibilities
352 associated with reduced hybrid fertility and viability have been extensively studied at the genetic
353 level in many plant hybrids (Lowry *et al.,* 2008). The most widely accepted model for the
354 accumulation of such hybrid incompatibilities is the Dobzhansky-Muller (DM) model, in which
355 allopatric populations fix different (and mutually incompatible) alleles at one or more loci (Rieseberg
356 & Willis 2007, Baack *et al.,* 2015). An example of a post-zygotic hybridisation barrier that arises
357 through genic incompatibilities is hybrid necrosis, which resembles plant responses to stress
358 including pathogens (Bomblies & Weigel 2007). Hybrid necrosis can be debilitating or lethal, and
359 generally acts in early (F_1 and sometimes F_2) hybrid generations (Bomblies & Weigel 2007). Other
360 examples of genic-based, intrinsic post-zygotic barriers in inter-specific crosses include hybrid
361 inviability in *Iris* (Iridaceae) (Martin *et al.,* 2008), and hybrid sterility in *Mimulus* (Phrymaceae)
362 (Fishman & Willis 2001) and *Solanum* (Solanaceae) (Moyle & Graham 2005). Postzygotic barriers can
363 thus affect hybrids at different stages (e.g., immediately after zygote formation or in later hybrid
364 generations) and with different consequences (e.g., killing or debilitating hybrids, or rendering them
365 partially or completely sterile).
366 Among the strongest postzygotic barriers are those due to differences in the structure and
367 number of chromosomes of hybridising species (Levin 2002, Husband 2004, Karlsdóttir *et al.,* 2008,
368 Chapman & Abbott 2010). Hybrid viability can be severely affected by differences in the number of
369 chromosomes between hybridising species, especially in interploidy crosses (Stebbins 1958).
370 Hybridisation between a diploid and a tetraploid is often associated with endosperm failure, a
371 phenomenon known as triploid block (Bretagnolle & Thompson 1995, Köhler *et al.,* 2010). However,
372 triploid block may represent a porous hybridisation barrier (Scott *et al.,* 2013). For example, hybrid
373 inviability associated with triploid block is often asymmetric, meaning that the viability of the hybrid
374 depends on whether a given taxon is the maternal or paternal parent (Ramsey & Schemske 1998). In
375 the British Isles a good example of this asymmetry is *Nasturtium x sterile* (2n = 48 (45-58),
376 Brassicaceae), where attempts to produce this well-established hybrid through artificial crosses are
377 successful only if *N. microphyllum* (2n =64) is used as the maternal parent and *N. officinale* (2n = 32)
378 as the paternal (Howard & Manton 1946, Stace *et al.,* 2015). The British flora has many examples of

young, established hybrids produced from parents of different ploidy, including a number of species of recent origin, in which at least one of the parents is a non-native taxon such as *Anchusa ochroleuca x A. officinalis* (Boraginaceae)*, Brassica napus x B. rapa* (Brassicaceae)*, Fallopia baldschuanica x F. japonica* (Polygonaceae)*, Gaultheria mucronata x G. shallon* (Ericaceae)*, Mimulus guttatus x M. luteus* (Phrymaceae)*, Rorippa austriaca x R. sylvestris* (Brassicaceae)*, Rumex crispus x R. frutescens/R. obovatus, Rumex cristatus x R. palustris* (Polygonaceae)*, Senecio squalidus x S. vulgaris* (Asteraceae)*, Spartina alterniflora x S. maritima* (Poaceae)*,* and a number of *Verbascum* (Scrophulariaceae) hybrids (Stace *et al.,* 2015). These taxa provide excellent opportunities to further investigate how inter-ploidy hybrids overcome viability barriers such as triploid block, and to what extent natural hybrid populations have an asymmetric origin.

Once a viable hybrid has been produced, a subsequent major challenge is to overcome partial or complete sexual sterility. Interploidy hybrids are often sterile (or have strongly reduced fertility), as a consequence of problems in chromosome pairing during meiosis, leading to unbalanced aneuploid gametes, which are often non-functional (Ramsey & Schemske 1998, Comai 2005)(Fig. 2). This pairing problem is expected to be most conspicuous in triploids and hybrids with an odd-number set of chromosomes (Griffiths *et al.,* 2000, Comai 2005), but may also arise in other hybrids in which meiotic pairing results in univalents or odd-numbered multivalents (De Storme & Mason 2014). However, occasionally, interploidy hybrids, such as triploids, produce viable gametes (Ramsey & Schemske 1998, Husband 2004, De Storme & Mason 2014) (Fig. 2). Viable gametes could be produced through multiple routes (Fig. 2), including the production of gametes with the somatic number of chromosomes (unreduced gametes; Köhler *et al.,* 2010, De Storme & Mason 2014, Mason & Pires 2015). Although unreduced gametes are produced at a low rate in non-hybrids (0.0056), their rate of production in hybrids is 50 times higher (0.275) (Ramsey & Schemske 1998). This difference in the rate of production of unreduced gametes is consistent with the observation that polyploids are more common in interspecific hybrid crosses than in crosses within species (Ramsey & Ramsey 2014). Incidentally, the production of unreduced gametes may also help hybrids to bypass the triploid block. For example, mating between the unreduced gametes of a diploid and a tetraploid would produce a hexaploid zygote, without the need to go through a triploid stage. Interestingly, it has been suggested that environmental stress, such as extremes of temperature, may increase the rate at which unreduced, and potentially viable, gametes are formed (De Storme & Mason 2014). Together, this leads to the tantalising idea that global change could facilitate hybridization between diploids and tetraploids—with or without triploids stages—that in the absence of extreme weather events would have remained reproductively isolated.

412 Even in species with the same number of chromosomes, hybrid fertility can be negatively
413 affected by structural differences between parental species including chromosomal re-arrangements
414 (e.g., fusions, fissions, deletions, insertions and inversions) (Rieseberg 2001), and differences in the
415 size of homologous chromosomes (Levin 2002). Reduced fertility among species with structural
416 chromosomal differences is often caused by pairing irregularities during meiosis, which result in
417 unbalanced, and unviable, gametes (Rieseberg 2001, Levin 2002). The strength of this type of
418 chromosomal barrier thus depends on the level of differentiation between the hybridising genomes,
419 and the extent to which these differences cause pairing irregularities (Levin 2002). Bivalent pairing
420 during meiosis may partly reflect structural similarity of the hybridising genomes, although recent
421 work in both auto- and allopolyploid systems suggests that it may also be under the control of a few
422 genes (Hollister 2015). Chromosomal re-arrangements have been shown to contribute to hybrid
423 sterility in many plant groups (Rieseberg & Carney 1998), and they may be particularly important in
424 mediating secondary contact between previously allopatric species (Rieseberg 2001). However,
425 artificial selection on fertility of initially near-sterile hybrids has shown that increased chromosome
426 pairing and more stable meiosis can evolve very rapidly and drastically improve hybrid fertility
427 (Grant 1966). Indeed, some hybrid derivatives between species with divergent chromosome
428 structure have overcome initial reductions in fertility, and formed evolutionarily stable lineages
429 (Rieseberg *et al.,* 1996).

430 6. Persistence of viable but sexually sterile hybrids

431 Hybrids may prevail even when the initial F1 is highly sterile, if they are able to propagate by other
432 means (clonally, apomictically, Fig. 3; Table 1) or by evolving higher sexual fertility (Grant 1966). In
433 addition, polyploid derivatives produced via unreduced gametes (Fig. 2) or somatic mutation can
434 have increased fertility (Rieseberg 2001, Stathos & Fishman 2014); the evolutionary fate of these
435 neo-polyploids is discussed in the *Allopolyploid speciation* section.
436 When sexual reproduction is severely impaired, asexual reproduction can allow individuals
437 to persist and spread (Grant 1971). In the British Isles, perennial hybrids that can propagate through
438 clonal reproduction are more widespread than those that cannot (Preston & Pearman 2015; Table
439 2), showing that the capacity for vegetative reproduction is correlated with spatial coverage.
440 Furthermore, analysis of introduced taxa in the recently published alien flora of the British Isles
441 (Stace & Crawley 2015) indicates that approximately 20% of introduced hybrid taxa reproduce
442 exclusively via clonal propagation, compared to only 8% of non-hybrid introduced taxa (Table 2).
443 Examples of sterile hybrid lineages that persist through vegetative propagation include *Circaea x*
444 *intermedia* (Onagraceae)*, Drosera x obovata* (Droseraceae) and *Stachys x ambigua* (Lamiaceae)
445 (Stace *et al.*, 2015). Some of these sterile lineages, for instance the triploid hybrid *Spartina x*

446 *townsendii* have not spread widely (Strong & Ayres 2013). In contrast other clonal taxa such as the
447 sterile triploid hybrid *Mimulus x robertsii* have spread more extensively (Preston *et al.,* 2002, Vallejo-
448 Marín & Lye 2013; Box 2). The ability to disperse over larger geographic areas through vegetative
449 propagation alone, may depend on the characteristics of the habitat. For instance, hybrids growing
450 along dynamic habitats (e.g., rivers and streams) may disperse clonal propagules more extensively
451 than those where dispersal relies on clonal growth on solid ground. For hybrids exploiting dynamic
452 riparian habitats such as those occupied by introduced *Mimulus* populations in the British Isles,
453 global change may facilitate their spread. For example, if extreme weather events result in more
454 intense or frequent flooding, changes in water flow regimes could help spread clonal propagules
455 further. Thus clonal propagation provides a (temporary) escape route to sexual sterility in hybrids,
456 and extreme weather events brought by global change may amplify its effects on the spatial spread
457 of some hybrids.
458 Another way in which asexuality can bypass sexual failure is through the evolution of
459 agamospermy, i.e., the production of seeds without sex (Fig. 3). Agamospermy (often referred to as
460 apomixis, Whitton *et al.,* 2008) is frequently associated with polyploidy and to a lesser extent
461 hybridisation (Grant 1971, Briggs & Walters 1997, Otto & Whitton 2000). Seeds produced through
462 apomixis are genetically identical to the parental plant, and because there is no sexual reproduction
463 they are reproductively isolated from progenitor taxa, so act as 'good' biological species. For this
464 reason, collections of similar apomictic lineages are sometimes called microspecies, agamospecies,
465 agamocomplexes or syngameons (Briggs & Walters 1997). The flora of the British Isles includes
466 numerous examples of cryptohybrids (ancient hybrids stabilised by apomixis) including syngameons
467 in the genera *Euphrasia* (Orobanchaceae)*, Sorbus* (Rosaceae; see Box 1)*, Rubus* (Rosaceae)*,*
468 *Hieracium* (Asteraceae)*, Taraxacum* (Asteraceae) and *Rosa* (Rosaceae), all of which are relatively
469 understudied. However, apomixis does not necessarily result in the complete loss of sex. Many
470 facultative apomictic species, such as *Sorbus* (Box 1), display sexual 'leakiness', and produce viable
471 pollen and ovules that can contribute to subsequent hybridisation events (Ludwig *et al.*, 2013). A
472 further example of variation in reproductive system in apomicts is *Hypericum perforatum*
473 (Hypericaceae). This species is a facultative agamospermous tetraploid (2n = 32), where sexual
474 reproduction results in diploid offspring, and agamospermy results in tetraploid and hexaploid plants
475 (Barcaccia *et al.*, 2006). *H. perforatum* hybridises with other taxa, including diploid and tetraploid *H.*
476 *maculatum* (2n = 16, 32) with which it produces 3x, 4x, and 5x hybrids, which show variable levels of
477 pollen and seed fertility. Yet, it is not known whether these hybrids reproduce sexually,
478 apomictically, or using a combination of both. An unusual form of reproduction via seeds that has
479 evolved in hybrids with odd-numbered chromosomes, occurs in species such as *Rosa canina* (2n = 5x

480 = 35). The *R. canina* complex contains a large number of species in which a permanent state of odd-
481 ploidy is maintained by fusion of gametes with complementary genomes (Grant 1971). Permanent
482 chromosomal heterozygosity results from fertilisation and syngamy between pollen with 7
483 chromosomes and ovules with 28 chromosomes (Grant 1971). Determining the incidence and
484 genetic consequences of occasional bouts of sexuality and recombination in hybrids with facultative
485 apomixis and other unusual forms of reproduction is of key importance to understand their fate, as
486 lack of sex can have both potential benefits and costs for the maintenance of hybrids at ecological
487 and evolutionary timescales.

488 One of the potential benefits that arises from bypassing regular sexual reproduction is that the
489 genetic constitution of the hybrids can be preserved ('fixed heterozygosity'), since gene
490 combinations are not broken down by meiosis and recombination. Viable F1 hybrids have the
491 capacity to show increased vigour (heterosis) relative to their parents (Barton 2001), and this hybrid
492 vigour can be maintained in the absence of sex and recombination. Therefore, clonality and apomixis
493 may be important not only for the persistence of hybrids, but also as a mechanism to maintain
494 hybrid vigour. In the context of global change, the advantages of asexual reproduction, including
495 fixed heterozygosity, may be balanced by a limited ability to deal with rapidly changing
496 environments due to low genotypic diversity. Yet, in recently formed asexual hybrid populations,
497 genotypic diversity may still occur as remnants of the initial hybridisation event (e.g., in hybrids
498 formed from diverse parental stock) or as a consequence of multiple origins of the same hybrid
499 (*Mimulus x robertsii*; Vallejo-Marin and Lye 2013), which may provide enough raw material for short-
500 term evolutionary change through genotypic selection. Moreover, many highly asexual populations
501 can preserve significant levels of genetic and genotypic diversity (Vallejo-Marín *et al.*, 2010), as even
502 rare bouts of sexual reproduction can significantly increase genetic variation (Bengtsson 2003).
503 Populations of asexual hybrids may also be able to deal with rapid environmental change through
504 phenotypic plasticity (Nicotra *et al.*, 2010). Additionally, epigenetic variation can also contribute to
505 rapid adaptation to environmental challenges, as suggested by the ecologically differentiated
506 populations of the invasive species *Fallopia japonica* which display abundant epigenetic diversity,
507 despite genetic uniformity (Kilvitis *et al.*, 2014). The variety of mechanisms available to asexual
508 hybrid populations to adapt to different environments may make hybrids more resilient to the rapid
509 modifications brought by global change.

510 7. Ecological inviability

511 Hybrids may suffer from low fitness when they are unable to find a suitable ecological niche, even if
512 they are not affected by intrinsic developmental problems (Coyne & Orr 2004). For instance, hybrids
513 which have intermediate phenotypes might be selected against in parental habitats, resulting in

514 ecological hybrid inviability (Baack *et al.,* 2015). A potential example of such an extrinsic barrier to
515 hybridisation in the British Isles flora is the hybrid between *Geum urbanum* and *G. Rivale,* (*G. x*
516 *intermedium* (Rosaceae). Although the parents of *G. x intermedium* have broadly overlapping
517 distributions they occupy slightly different habitats: *G. urbanum* occurs in well-drained soils, in areas
518 partially shaded or sometimes in open disturbed habitats, while *G. rivale* is usually found in wetter
519 soils and more open habitats (Stace *et al.*, 2015). Experimental crosses have shown that F1 hybrids
520 are viable and fertile, and that seeds produced in zones of contact contain a variety of hybrid
521 genotypes (Ruhsam *et al.,* 2013). Yet, among adult plants only F1s and backcrosses to *G. rivale* are
522 observed (Ruhsam *et al.,* 2011). Using an experimental garden, Ruhsam *et al.* (2013) showed that
523 hybrids have no intrinsic low fitness, raising the possibility that ecological selection may be filtering
524 out certain hybrid classes (Ruhsam *et al.,* 2013). The agent of selection is unknown, but it is possible
525 that the intermediate morphology of hybrids makes them poorly suited for establishing in parental
526 environments, and explain why some advanced generation hybrid are rare despite obvious intrinsic
527 post-zygotic barriers. The role that ecological barriers play in preventing the establishment of
528 recently formed hybrids remains a relatively unexplored.

529 IV. Outcomes of hybridisation

530 The long term outcomes of hybridisation can vary from genetic homogenisation of the parental taxa
531 (genetic swamping; Rieseberg & Ellstrand 1993, Wolf *et al.,* 2001), transfer of neutral and adaptive
532 genetic variation across species (introgression and genetic rescue; Rieseberg & Wendel 1993,
533 Ellstrand & Schierenbeck 2000, Baskett & Gomulkiewicz 2011, Gomulkiewicz & Shaw 2013, Hamilton
534 & Miller 2016), and the evolutionary persistence of hybrids as autonomous entities (with or without
535 speciation; Abbott *et al.,* 2013). The persistence of hybrids over evolutionary time can be achieved
536 through four different, non-mutually exclusive pathways: (1) the stabilisation of hybrid zones (Barton
537 & Hewitt 1989, Baack & Rieseberg 2007), (2) spatial displacement of parental taxa, (3) the expansion
538 of hybrids into new ecological niches (hybrids by virtue of transgressive segregation may be pre-
539 adapted to more extreme habitats, Rieseberg 1991, Rieseberg *et al.,* 1999), and (4) hybrid speciation
540 (Rieseberg & Willis 2007, Abbott *et al.,* 2013) (Fig. 3).

541 Global change through its effects on habitat modification, change in climate, and alterations
542 in ecological interactions, has the potential to alter the outcomes of hybridisation (Campbell &
543 Wendlandt 2013, Chunco 2014). Probably the most obvious example of such an effect is the
544 facilitation of hybrid persistence through "hybridisation of the habitat" in which parents occupy
545 different ecological niches and hybrids a third, intermediate, niche (Anderson 1948, Arnold *et al.,*
546 2012). Under the bounded hybrid superiority model, in which hybrids enjoy a higher fitness in
547 intermediate habitats but suffer from lower fitness in parental ones (Moore 1977, Barton & Hewitt

548 1985), the creation and distribution of these intermediate habitats should influence not only hybrid
549 formation, but also their persistence. Despite the intuitive appeal of the effects of global change on
550 plant hybridisation outcomes, there are few good examples from the British Isles flora. Nevertheless,
551 one tantalizing case for the potential of hybridisation to result in adaptive introgression comes from
552 hybridisation between non-native species of *Rhododendron* (Ericaceae). *Rhododendron ponticum* is
553 widespread in the British Isles and displays the signature of hybridisation with other species,
554 including the more cold-tolerant *R. catawbiense* (Milne & Abbott 2000). Introgression from *R.*
555 *catawbiense* to *R. ponticum* is more prevalent in colder regions in eastern Scotland than elsewhere
556 in Britain. Given this, Milne and Abbott (2000) raised the possibility that gene flow may confer
557 increased cold-tolerance. However, the hypothesis that hybridisation results in increased cold
558 tolerance in *R. ponticum*, and that selection (either natural or artificial) is responsible for the
559 geographic distribution of introgression patterns remains to be tested. The success of hybrids under
560 the novel ecological conditions brought by global change will depend on both the availability and
561 type of new habitats and ecological niches, and on whether hybrids are better equipped to deal with
562 these new environments, either via the ability to thrive in "intermediate" habitats or through the
563 expression of new adaptive phenotypes, e.g., due to transgressive segregation in hybrids.

564 8. Hybrid speciation

565 Although hybridisation may result in the reversal of speciation ("speciation undone", Grant & Grant
566 2014, Taylor *et al.,* 2006), in some cases new species can be formed following hybridisation events
567 (Mallet 2007, Abbott *et al.,* 2013). Hybrid speciation can occur with or without whole genome
568 duplication (allopolyploid or homoploid speciation, respectively) (Soltis & Soltis, 2009). The use of
569 genetic and genomic tools has helped to dramatically increase our understanding of hybrid
570 speciation at both homoploid (Rieseberg 1991, 1997, 2006, Gross *et al.,* 2007) and allopolyploid
571 levels (Hegarty & Hiscock, 2008, Soltis *et al.,* 2014a). Below we present a brief overview of these two
572 modes of hybrid speciation, focusing on those speciation events that have been facilitated by the
573 breakdown of reproductive barriers due to global change, particularly the introduction of non-native
574 species into the British Isles flora.

575 (a) Allopolyploid hybrid speciation

576 The origin of a new species through hybridisation and polyploidisation can occur rapidly, as taxa with
577 different chromosome numbers are usually characterised by post-zygotic reproductive barriers
578 (Stebbins 1971). In principle, a hybrid can give rise to a new species in a single generation via
579 polyploidisation (Ramsey & Ramsey 2014) leading to a "cataclysmic origin of species" (Dobzhansky
580 1937, p. 192). Such abrupt speciation is well documented for new British allopolyploid species in the

genera *Senecio*, *Spartina,* and *Mimulus*, all of which have evolved in the last 200 years (Ainouche *et al.,* 2004, Hegarty *et al.,* 2012, Vallejo-Marín 2012), and all of these cases involve hybrids that owe their origin to global change.

The genus *Senecio* (ragworts and groundsels) provides some of the best examples of recent hybrid speciation and 'evolution in action' among the British Flora. Within the last 100 years three new polyploid taxa have arisen in the UK as a consequence of hybridization between native tetraploid *Senecio vulgaris* (common groundsel) and the introduced invasive diploid species *S. squalidus* (Abbott & Lowe 2004, Hegarty *et al.*, 2012), providing one of the first examples of hybridization induced by global change. Hybridisation between these two species gave rise to three allopolyploid taxa - allohexaploid *S. cambrensi*s (Welsh groundsel) tetraploid *S. eboracensis* (York radiate groundsel) and tetraploid *S. vulgaris* var. *hibernicus* (radiate groundsel, a stabilized introgressant form of *S. vulgaris*). The latter of these hybrid taxa occurs sporadically throughout the UK, but *S. eboracensis*, first discovered in a York car park, is now probably extinct (Lowe & Abbott 2000, 2003, Abbott *et al.,* 2009). *Senecio cambrensis*, which was discovered in North Wales in 1948 (Rosser 1955) is locally common in North Wales (Hegarty *et al.*, 2012) and most likely arose following a genome duplication event in the sterile triploid hybrid *S. x baxteri*, as hexaploid plants with similar morphology to the wild form of *S. cambrensis* can be produced by treating synthetic triploid *S. vulgaris* x *S. squalidus* hybrids with colchicine (Weir & Ingram 1980, Hegarty *et al.*, 2005). In 1982 *S. cambrensis* was found growing in Edinburgh (Abbott *et al.*, 1983) and subsequent molecular marker analyses revealed that this represented an independent second origin in Scotland (probably during the 1970s) rather than dispersal from Wales (Ashton & Abbott 1992, Harris & Ingram 1992). Unfortunately, the Edinburgh lineage may now be extinct as the species has not been recorded in Edinburgh since 1993 (Abbott & Forbes 2002). Independent origins of recently formed allopolyploids are common as has been shown for the allotetraploid *Tragopogon* of the USA (Soltis *et al.,* 2004) – themselves another example of hybridization facilitated by global change.

Another recently discovered example of rapid allopolyploid speciation in the British Isles is *Mimulus peregrinus,* which has evolved at least twice, independently in southern Scotland and the Orkney Isles (Vallejo-Marín *et al.,* 2015; Box 2). As in the case of *Senecio*, *M. peregrinus* owes its origin to global change bringing together previously isolated species. This species is derived from a sexually-sterile triploid hybrid (*M. x robertsii*), which is the product of hybridisation between two non-native species: diploid *M. guttatus* (native to North America) and tetraploid *M. luteus* (native to South America). The triploid hybrid persists in the wild and can form large, naturalised populations where it reproduces clonally (Vallejo-Marín & Lye 2013). Unlike the triploid, the allohexaploid derivatives are pollen and seed fertile (Vallejo-Marín 2012). The mechanism for the formation of the

allohexaploid from triploid hybrids is unknown, but one likely route is through mating between unreduced gametes (Husband 2004, Mason & Pires 2015). *Mimulus peregrinus* is an example of how a sterile hybrid taxon has escaped the sterility barrier through genome duplication to form a fertile species.

Given the young age (<200 years) of allopolyploids such as *Senecio cambrensis* (Hegarty *et al.,* 2012)*, Spartina anglica* (Ainouche *et al.,* 2004)*,* and *M. peregrinus* (Vallejo-Marín 2012)*,* their long term persistence is still uncertain. Allopolyploid species often go through severe bottlenecks during their formation (Soltis *et al.,* 2014a), as potentially a single allopolyploid hermaphroditic individual can give rise to a new allopolyploid taxon. This initially low population size may impose severe ecological barriers, such as costs due to matings between individuals with different ploidies (minority cytotype exclusion, Levin 1975; Figure 3), as well as simple stochastic extinction. Yet allopolyploids tend to be formed recurrently, and most allopolyploid species have multiple origins (Soltis *et al.,* 2014a). To the extent that these independently originated allopolyploids are inter-fertile (Modliszewski & Willis 2012), interpopulation crosses could, in principle, increase genetic and phenotypic variation in nascent lineages, as appears to have been the case in *S. cambrensis* (Abbott *et al.*, 2007). Indeed, inter-population crosses between accessions from the two known localities for *M. peregrinus* produce viable and fertile offspring (Vallejo-Marín *et al.*, *unpublished*), although whether this results in increased phenotypic diversity remains to be established. Determining the degree of phenotypic and ecological diversity of recently allopolyploids seems fundamental to predict their long term fate, particularly as global change continues to alter environments and presents novel challenges to their long term survival.

It has long been recognised that hybridisation and polyploidy have the potential to generate ecological novelty (Levin 1983, Otto 2007, Soltis *et al.,* 2014a). The development of genomic tools for recently formed allopolyploids opens the opportunity to take these early hypotheses and investigate the underlying genetic changes associated with ecological innovation. Unlike the case of homoploid hybrids, which have been subject of intense scrutiny at the interphase between ecology and genomics (Yakimowski & Rieseberg 2014), genomic approaches have been rarely used to study the ecology of natural populations of allopolyploids (Ramsey & Ramsey 2014, Soltis *et al.,* 2014b). A rare example of such a study from the British flora is a recent study of the allopolyploid species complex *Dactylorhiza majalis, D. traunsteinerii,* and *D. ebudensis* (Orchidaceae) by Paun *et al.*, (2011). Analysis of genome-wide markers (cDNA-AFLPs) showed that these allopolyploids have higher variation in gene expression than their diploid relatives. Paun *et al.,* (2011) suggest that variable gene expression, and potentially having more plastic phenotypes, have facilitated the colonisation of different ecological niches by these three allopolyploid orchids. A similar situation may be

649 responsible for the success of *S. cambrensis* which also shows altered patterns of gene expression
650 relative to its parents (Hegarty *et al.*, 2006) and also changed patterns of DNA methylation (Hegarty
651 *et al.*, 2011) suggesting the possibility of an epigenetic element to the generation of phenotypic
652 novelty in allopolyploids. Studying the genomic basis and evolution of ecological novelty in
653 polyploids is particularly timely, as we have increasing access to genomic tools for non-model
654 organisms, and because understanding ecological adaptation becomes urgent as populations face
655 the challenge to adapt or perish in the new environments brought by global change.
656 Beyond the earliest stages of allopolyploid speciation, the British Isles flora contains several
657 examples of older allopolyploid taxa, including *Mentha spp., Rubus, Euphrasia, Rorippa,* and
658 *Nasturtium* to name just a few (Stace *et al.,* 2015). A particularly intriguing case is the rare Scottish
659 primrose, *Primula scotica* (2n = 6x = 54, Section *Aleuretia*), endemic to the north of Scotland and
660 Orkney Isles. Early genetic work showed clear evidence that *P. scotica* was formed through an
661 allopolyploidisation event (Glover & Abbott 1995). Furthermore, *P. scotica* is thought to have given
662 rise to another allo-octopolyploid species, *P. scandinavica* (2n = 8x = 72), through a hybridisation
663 event with *P. farinosa* (Guggisberg *et al.,* 2009), and it may even be involved in the origin of the 14x-
664 polyploid *P. stricta* (Guggisberg *et al.,* 2006). Currently, the distribution of *P. scotica*'s putative
665 parents, *P. farinosa* and *P. halleri* (Guggisberg *et al.,* 2009), and its potential derivatives *P.*
666 *scandinavica* and *P. stricta*, does not overlap with *P. scotica*, suggesting that they may occupy
667 different ecological niches, a hypothesis that could be tested using ecological niche modelling (e.g.,
668 McIntyre 2012). Recent work on polyploid taxa in *Primula* Sect. *Aleuretia* has shown that polyploids
669 in this section tend to have a smaller distribution and narrower niche breadths than diploids
670 (Theodoridis *et al.,* 2013), which could indicate that genome duplication is associated with habitat
671 specialisation. *Primula scotica* and other taxa in Section *Aleuretia* are wonderful examples of how
672 allopolyploid taxa can not only persist over evolutionary time, but also continue to speciate and
673 diversify. The development of genomic tools in *Primula*, including a draft reference genome for *P.*
674 *veris* (Nowak *et al.,* 2015), has the potential to elevate this group as a system for the study of
675 evolutionarily established allopolyploids. Notably, the timing of the formation of some of these
676 *Primula* allopolyploids seems to coincide with large-scale environmental changes brought by
677 historical climate change (e.g., end of glacial maxima), which spurs further speculation on the
678 incidence and importance of allopolyploid speciation in times of environmental upheaval.
679 Recently formed hybrids, including those potentially associated with global change, are
680 much more common than the new allopolyploid species they have generated (Stace *et al.,* 2015,
681 Thomas 2015), posing the question, why? Polyploids are thought to be most commonly formed by
682 fusion of unreduced gametes (Levin 2013), and the rate of unreduced gamete formation in hybrids

683 can be extremely high in some plant groups (> 25%, Ramsey & Schemske 1998), indicating ample
684 opportunities for their formation. In the case of sterile hybrids, one key hurdle to overcome in order
685 for an allopolyploidisation event to result in a new taxon is the restoration of sexual fertility. In some
686 cases, genome duplication can restore fertility when sterility arises from structural or numeric
687 differences in the parental chromosome sets (Stebbins 1958, Coyne & Orr 2004). However, if sterility
688 is rooted in genic incompatibilities between the parents, genome duplication alone will not be
689 sufficient for fertility restoration. Thus one would expect that those hybrids that have produced
690 allopolyploid species should tend to show few or no genic incompatibilities. This hypothesis can be
691 experimentally tested by inducing polyploidy in sterile hybrids (Hegarty *et al.,* 2013) and assessing
692 their level of fertility (Stathos & Fishman 2014). If synthetic polyploids are as sterile as their parents,
693 then genic incompatibilities can be inferred (Coyne & Orr 2004). If polyploidy restores fertility, the
694 absence of allopolyploids in nature could be explained by ecological or perhaps stochastic causes.
695 Ultimately, determining why allopolyploids are rarer than their hybrid ancestors remains an
696 open question. Their absence is puzzling given the high rate of unreduced gamete production in
697 hybrids (Ramsey and Schemske 1998). Beyond the barrier of overcoming sexual sterility in
698 allopolyploids, other extrinsic post-zygotic mechanisms such as minority cytotype disadvantage
699 (Levin 1975), and ecological competition with their hybrid ancestors, may pose significant barriers to
700 the establishment of recently formed allopolyploids. It is also possible that our records of neo-
701 allopolyploids will continue to accumulate as more recently formed hybrids come of age (Thomas
702 2015). Recently formed allopolyploids may be difficult to spot in botanical surveys, particularly in the
703 initial stages when they are quite rare. Large-scale searches for cryptic allopolyploids among recently
704 formed hybrids, using direct or indirect measurements of genome size such as flow cytometry (e.g.,
705 Castro *et al.*, 2012), and pollen and stomata size, may provide an effective way to establish if recent
706 allopolyploids are indeed as rare as they appear to be.

707 (b) **Homoploid hybrid speciation**

708 In contrast to allopolyploid speciation, homoploid hybrid speciation appears less common, although
709 the number of confirmed cases of homoploid hybrid speciation is increasing (Gross & Rieseberg
710 2005, Abbott *et al.,* 2013, Schumer *et al.,* 2014). This apparent rarity of homoploid speciation may
711 therefore simply reflect the difficulty in detecting it (Abbott *et al.,* 2013). Homoploid hybrid
712 speciation requires the evolution of a hybrid that is reproductively isolated from its parents in the
713 absence of differences in ploidy level (Gross & Rieseberg 2005, Yakimowski & Rieseberg 2014).
714 Reproductive isolation between parental and hybrid taxa could thus be based on differences in
715 chromosome structure, ecological divergences, spatial isolation, or a combination of the above
716 (Rieseberg 1997). In the British Isles flora, the only confirmed case of recent homoploid hybrid

717 speciation is *Senecio squalidus* (Oxford ragwort) although the place of origin of the hybrid plants was
718 Sicily (reviewed in Abbott *et al.,* 2013). *S. squalidus* is a recent homoploid hybrid species, which
719 evolved in the UK following its introduction from a *S. aethnensis* x *S. chrysanthemifolius* hybrid zone
720 on Mt Etna ~300 years ago.

721 *Senecio aethnensis* is endemic to of high altitudes of Mt Etna, whereas *S. chrysanthemifolius*, a
722 native of Sicily, is more widespread at lower altitudes. At mid altitudes on the volcano the
723 distribution of the two species frequently overlaps leading to the formation of stable hybrid zones
724 around the circumference of the volcano (Brennan *et al.,* 2009). Material from this hybrid zone was
725 introduced to the Oxford Botanic Garden in the early 1700s from where plants subsequently
726 escaped and colonized the masonry of college walls and roadsides. During the industrial revolution
727 the clinker beds of the expanding railway network provided an ideal habitat (akin to the volcanic
728 slopes of Mt Etna) for *S. squalidus* to thrive and spread. During the next 300 years *S. squalidus*
729 diverged phenotypically and to a lesser extent genetically in allopatric isolation from its parental
730 species, such that it now meets the criteria for a new homoploid species (James & Abbott 2005,
731 Abbott *et al.,* 2013). *S. squalidus* and its parental species are divergent in their morphology,
732 flowering phenology, and in ecologically important traits even though they are genetically very
733 similar and completely interfertile (Chapman *et al.,* 2013, Osborne *et al.,* 2013). Nevertheless, the
734 ~300 years of allopatric isolation have allowed *S. squalidus* to adapt to the cooler climate and non-
735 volcanic soils of the UK, resulting in the ecological and phenotypic divergence seen today.

736 Other potential candidates for homoploid hybrids in the British flora are found in the complex
737 assemblage of interspecific hybrids in annual, hemiparasitic *Euphrasia*. Species of *Euphrasia* in the
738 British Isles include both diploid and tetraploid taxa, which are strongly reproductively isolated
739 across ploidy levels (Yeo 1968). However, hybrids within ploidy levels are often fertile (Stace *et al.,*
740 2015), and Yeo (1968) suggests that some of these hybrids may have produced new hybrid taxa. The
741 high fertility of within-ploidy hybrids means that for homoploid speciation to occur, reproductive
742 isolation between parental and hybrid taxa will depend on ecological divergence and spatial isolation
743 (Yeo 1968, Rieseberg 1997). Future studies of *Euphrasia* will determine whether the hypothesis of
744 homoploid hybrid speciation holds for this group.

745 Taken at face value, homoploid hybrid speciation seems to be rarer than polyploid hybrid
746 speciation (Abbott *et al.*, 2013). The apparent higher facility of allopolyploids to form and establish
747 may be linked, in part, to the reproductive isolation barriers introduced by differences in ploidy level
748 between derivative and parental taxa. But allopolyploid taxa also have the added feature of
749 genome-wide redundancy conferred by polyploidisation (Soltis *et al.*, 2014a). It is tempting to
750 speculate that genomic redundancy is causally linked to evolutionary success in allopolyploids, for

751 example by allowing duplicated subgenomes to differentiate and specialise in different functions
752 (subfunctionalisation and neofunctionalisation; Ohno 1970; Soltis *et al.*, 2014b). This higher
753 evolutionary potential of allopolyploids may not be immediately realised upon genome duplication
754 (or seen in synthetic allopolyploids; Hegarty *et al.*, 2006), but instead may accumulate as lineages
755 diverge. The higher incidence of allopolyploids *vs.* homoploid hybrid species may thus reflect an
756 evolutionary advantage over the longer term in taxa with highly redundant and malleable genomes.
757 Whether recently formed allopolyploids can keep up with rapid global change remains to be seen.

758 V. Outlook

759 Hybridisation and hybrid speciation permeates the evolutionary history of plants, and is certainly not
760 a novel phenomenon. However, the accelerating transformation of the world's biota brought about
761 by global change make the study of hybridisation both current and urgent if we are to understand
762 the consequences of eroding reproductive barriers between evolutionarily distinct lineages. For
763 instance, hybridisation can threaten the conservation of local biodiversity by altering the genetic
764 integrity of native species through introgression, and genetically swamp rare ones (Vilà *et al.,* 2000,
765 Wolf *et al.,* 2001, Brennan *et al.,* 2015, Chown *et al.,* 2015, Taylor *et al.,* 2015). Changes to ecological
766 communities due to hybridisation involving non-native species can also change ecological
767 communities, and hybrids can compete for pollination services and fruit dispersers (Vilà *et al.,* 2000).
768 Moreover, hybrids themselves can become significant invasive pests (Ellstrand & Schierenbeck 2000)
769 with negative effects for local economies and biodiversity. On the other hand, the consequences of
770 hybridisation and its effects on biodiversity need not necessarily always be negative since
771 hybridisation can spur accelerated rates of speciation and thus increase biodiversity (Thomas 2015).
772 More studies are needed to gauge whether the balance of neo-hybridisation is positive or negative.
773 Although the ecological and evolutionary consequences of recently formed hybrids are hard to
774 predict, many hybrids are probably innocuous to local ecosystems as we know them. Regardless of
775 their perceived costs and benefits, recently formed hybrids provide us with the unique opportunity
776 to study, in real time, the breakdown of reproductive barriers and the processes allowing newly
777 formed hybrids to become established, and in some cases speciate (Mallet 2007, Abbott *et al.,*
778 2013). The dynamic and rapidly changing nature of our planet's biota has created a global
779 experiment on hybridisation. We now have the timely opportunity to use this unplanned experiment
780 to study the basic biological phenomena responsible for the birth and death of species. Capitalizing
781 on this opportunity needs a multidisciplinary approach, combining classic taxonomic studies and
782 catalogues of hybrid floras (Stace *et al.,* 2015) with ecological experiments, phylogenetic analysis,

783 quantitative genetics, and bioinformatics to exploit the new genomic resources available for non-
784 model organisms.

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1193 ## Figure Legends

1194

1195 **Figure 1.** Reproductive isolation barriers preventing the formation and establishment of hybrids.
1196 Reproductive isolation barriers are usually divided in pre-zygotic and post-zygotic. Notice that in
1197 plants, some barriers such as pollen precedence act after mating (pollination) but before zygote
1198 formation.

1199

1200 **Figure 2.** Meiosis in hybrids is adversely affected by differences in chromosome number and
1201 structure between parental species. The result will generally be gamete inviability, but, rarely,
1202 gametes with atypical chromosome numbers (aneuploid and unreduced gametes) may be produced
1203 and viable. The figure shows ways in which viable gametes could be produced in a hypothetical
1204 triploid hybrid (2n = 3x). Unpaired chromosomes during meiosis (in both univalents and
1205 multivalents) migrate to either cell pole at random, resulting in unbalanced gametes (top pathway).
1206 Most of these unbalanced gametes will be inviable, causing a very severe reduction in fertility. A
1207 small fraction of these gametes may by chance end up with the parental cytotype, and are thus
1208 viable. Another small fraction may be viable despite carrying new aneuploid combinations.
1209 Occasionally, gametes may be produced with the entire set of chromosomes present in the hybrid
1210 (unreduced gametes), which may be subsequently involved in polyploid formation.

1211

1212 **Figure 3.** Potential fate of viable hybrids that are able to persist over ecological or evolutionary
1213 timescales after their origin and initial establishment.

Table 1. Examples of the "Significant Eight" alien hybrid complexes of the British Flora recognised by Stace & Crawley (2015). Introduced taxa (neophytes) are indicated with *. Data compiled by Stace & Crawley (2015) and Stace *et al.* (2015).

Hybrid	Parents		Sexual Fertility	Clonal reproduction	Allopolyploid derivative
Fallopia x bohemica **(2n = 66)**	*F. japonica** (2n = 88)	F. sachalinensis* (2n = 44)	Low	Yes	--
Senecio x baxteri **(2n = 30)**	*S. vulgaris* (2n = 40)	*S. squalidus** (2n = 20)	Very low	No	***S. cambrensis*** **(2n = 60)**
Spartina x townsendii **(2n = 62)**	*S. maritima* (2n = 60)	*S. alterniflora** (2n = 62)	Very low	Yes	***S. anglica*** **(2n = 124)**
Mimulus x robertsii **(2n = 44-46)**	*M. guttatus** (2n = 28)	*M. luteus** (2n = 60-62)	Very low	Yes	***M. peregrinus*** **(2n = 92)**
Calystegia x lucana **(2n = 22)**	*C. sepium* (2n = 22)	*C. sylvatica** (2n = 22)	High	Yes	--
Hyacinthoides x massartiana **(2n = 16, 24)**	*H. non-scripta* (2n = 16, 24)	*H. hispanica** (2n = 16, 24)	High	Yes	--
Rhododendron x superponticum **(2n = 26)**	*R. ponticum** (2n = 26)	*R. catawbiense*, R. maximum*, R. macrophyllum** (2n = 26)	High	Yes	--

Centaurea x gerstlaueri **(2n = 44)**	*C. nigra* (2n = 44)	*C. jaceae** (2n = 44)	High?	Yes (but limited lateral spread)	--

Table 2. Reproductive mode and occurrence of 274 alien angiosperm hybrids and 1,590 non-hybrid aliens in the British and Irish flora. Data from Stace and Crawley (2015). Hectad = 10km x 10km square.

Propagation Mode	# Hybrid alien taxa (proportion)	Average # hectads per hybrid taxon (maximum)	# Non-hybrid alien taxa (proportion)	Average # hectads per non-hybrid taxon (maximum)
Seeds only	48 (0.175)	180 (2,242)	559 (0.351)	224 (3,530)
Clonal only	55 (0.200)	157 (1,147)	122 (0.077)	212 (2,723)
Seeds and clonal	71 (0.259)	199 (2,419)	330 (0.207)	218 (2,535)
No reproduction in the British isles	100 (0.365)	32 (444)	579 (0.364)	37 (1,738)
Total	**274**	**126 (2,419)**	**1,590**	**153 (3,530)**

Box 1. The Avon Gorge: A hotspot of hybrid diversity

The genus *Sorbus* (Rosaceae) includes sexual diploid species and apomictic species/taxa with varying ploidy (usually 3x and 4x) that have arisen through hybridisation between sexual species and rare backcrosses with their apomictic allopolyploid derivatives (Rich & Robertson 2015). There are 31 *Sorbus* agamospecies native to the British Isles, 10 of which are reported in *Stace et al.*, (2015). The parentage of these hybrids is often complex but molecular data is helping to resolve their origins (Robertson *et al.*, 2010). 'Hotspots' for *Sorbus* diversity in the British Isles include: the Isle of Arran, Cheddar Gorge, the Wye Valley and the Avon Gorge (Rich & Robertson 2015) – the latter being by far the richest, possibly the richest in the world.

The Avon Gorge contains at least 21 *Sorbus* taxa, six of which are endemic and shown to have evolved within the Gorge, probably within the last 10,000 years since the last ice-age (Robertson *et al.*, 2010; Ludwig *et al.*, 2013). Studies using molecular markers revealed that this *Sorbus* diversification has been driven primarily by a series of interspecific hybridisations and backcrosses among closely related taxa, with each new genotype being fixed and perpetuated via apomixis (Robertson *et al.*, 2010; Ludwig *et al.*, 2013). Once established these new microspecies then occasionally participate in further rare hybridisation events leading to a complex pattern of ongoing reticulate evolution (Robertson et al. 2010; Ludwig *et al.*, 2013). This occurs because of subtle variation ('leakiness') in the apomictic mating system that permits occasional sexual unions, usually involving pollen from the most common species, *S. aria*, which is diploid and sexual (outcrossing) and its close tetraploid relative *S. porrigentiformis*, apomictic. Pollen from these taxa is essential for apomictic seed production by the triploid apomictic hybrid taxa (*e.g.*, *S. bristoliensis* and *S. wilmottiana*) because apomixis is pseudogamous (endosperm formation requires fertilization of the central cell by sperm) and triploids (unlike tetraploids) are self-incompatible (SI) (Ludwig *et al.*, 2013; Ludwig & Hiscock in preparation). This unusual mating system therefore fuels the possibility of rare hybridisations being successful because interspecific pollination is required for apomictic seed production in the triploids, which in all but one microspecies tested, are genetically identical (indicating a single hybrid origin event) and therefore incompatible because they all share the same self-incompatibility (S) genotype (Ludwig *et al.*, 2013). Populations of at least two undescribed microspecies have been identified together with numerous puzzling individuals, which do not fit known taxa (Tim Rich pers. comm.) indicating that these evolutionary processes are ongoing. The 2km long Avon Gorge which cuts through Carboniferous Limestone to a depth of 80m, displays a great diversity of habitats (including woodland, scrub, open rocks and quarries) which has probably facilitated and continues to facilitate the survival of newly divergent (perhaps pre-adapted) *Sorbus* taxa (Rich *et al.*, 2010). Conservation strategies for the rare *Sorbus* taxa endemic to the Avon Gorge have taken these findings on board in revising management regimes such that all *Sorbus* taxa are considered so as to conserve the evolutionary process rather than just the rare ones.

Box 2. Monkeyflower hybrids: The birth of a new species

Mimulus has a long tradition in studies of hybridisation, reproductive isolation and speciation (Vickery 1959, Bradshaw *et al.,* 1995, Fishman & Willis 2001, Brandvain *et al.,* 2014). The spread of some *Mimulus* species beyond their native range thanks to human-assisted dispersal, has created new opportunities for hybridisation between previously isolated *Mimulus* taxa (Vallejo-Marín & Lye 2013). The best studied case is the invasion of the British Isles by two related monkeyflower taxa: The North American diploid *M. guttatus*, and the South American tetraploid *M. luteus*. Both species were introduced into the British Isles in the early 19th century as botanical curiosities, and quickly became naturalised (Stace *et al.,* 2015). Hybridisation between these two taxa produce a highly sterile triploid, which is nevertheless capable of vegetative growth. The hybrid has been established in the wild since at least the 1870's, and it is currently the second most abundant *Mimulus* in the UK after *M. guttatus* being present in approximately 40% of extant populations (Vallejo-Marín & Lye 2013). The triploid hybrid *M. x robertsii*, has produced the new allopolyploid species *M. peregrinus*, which has originated at least twice, independently, in Scotland (Vallejo-Marín 2012, Vallejo-Marín *et al.,* 2015). *M. peregrinus* produces both viable pollen and seeds, as well as retaining its capacity for vegetative reproduction. Multiple origins seem to be the rule rather than the exception for the formation of allopolyploids (Soltis *et al.,* 2014b), and this provides a natural system to investigate hybrid speciation in a replicated fashion.

Although the parentage of *Mimulus* hybrids and the origin of *M. peregrinus* has been recently documented using genome-wide analyses (Vallejo-Marín *et al.,* 2015), a missing piece of the puzzle is to determine which taxon has served as the maternal parent and which as the paternal parent in hybrid formation. Inter-ploidy hybridisation often results in asymmetric reproductive barriers, and it is likely that hybridisation between *M. guttatus* and *M. luteus* does not work equally well in both directions (Roberts 1964). Determining the ancestry of inter-specific hybrids can be done by analysing uniparentally inherited genomes (e.g., chloroplast and mitochondria) (Rieseberg & Brunsfeld 1992, Twyford & Ennos 2012). However, genetic analysis of hybrid ancestry can be complicated by limited availability of species-diagnostic polymorphism in uniparentally-inherited genomes. Recent studies have pointed out how whole genomes of cytoplasmic organelles are recovered in both targeted and whole-genome sequence projects, as by-products of even low-depth sequencing efforts (genome skimming, Dodsworth 2015). This trove of genetic information can be used to identify the taxon that acted as the maternal parent of hybrids, even in the absence of closely related reference genomes (Bakker *et al.,* 2016). Vallejo-Marín *et al.*, (*in press*) applied a genome skimming approach to determine the ancestry of *Mimulus* hybrids in the British Isles. They used data obtained from both whole-genome and targeted sequencing projects, to rescue chloroplast and mitochondrial genomes of *M. x robertsii* and *M. peregrinus* and their parental taxa. They showed that hybrids have been produced unidirectionally, with *M. guttatus* as the maternal and *M. luteus* as the paternal parent. Genome skimming (Straub *et al.,* 2012) holds great potential to investigate the ancestry of neo-hybrids, and we expect similar approaches to be increasingly exploited in the near future.