Tansley review

Hybridization and hybrid speciation under global change

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Summary

An unintended consequence of global change is an increase in opportunities for hybridization 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-geographical isolation and 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, hybridization 'experiments', allowing us to peer into the birth and death of evolutionary lineages.

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 geographical barriers to gene flow between closely related species (Mooney & Cleland, 2001). The loss of ecological and geographical barriers that historically kept closely related species apart is creating unprecedented new opportunities for hybridization (Mable, 2013; Chunco, 2014; Brennan *et al.*, 2015; Taylor *et al.*, 2015), which could potentially have a profound impact on biodiversity and ecosystems world-wide.

Hybridization 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 hybridization. Interspecific hybridization is a regular natural phenomenon and it is estimated that as many as 25% of plant species and 10% of animal species hybridize naturally (Mallet, 2007). Hybridization 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 hybridization 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). Hybridization 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 hybridization at a global scale is changing, and if so at what rate, is still unclear, yet analyses of well-studied floras, such as that of the British Isles, indicate that a significant fraction of hybrid taxa may involve introduced taxa (Stace & Crawley, 2015; Stace *et al.*, 2015). Among the flora of Britain and Ireland, hybridization involving introduced (nonnative) taxa is well documented (Stace *et al.*, 2015; Stace & Crawley, 2015; Table 1), and a recent survey revealed that 33% of hybrid taxa (301 of 909) involve introduced (nonnative) taxa (Preston & Pearman, 2015). Approximately half of these nonnative 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 hybridization under global change are hard to predict. Here we present an overview of the consequences of this new era of increased hybridization 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 pre-zygotic and post-zygotic barriers in maintaining species apart? What is the incidence of human-made hybrids in current floras and is this 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 hybridization, 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 naturalized flora of Britain and Ireland. We speculate that this new scenario is shifting the relative importance of pre-zygotic and post-zygotic 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 post-zygotic than on pre-zygotic barriers. The persistence of newly formed hybrids, and their evolutionary fate, will hinge on mechanisms that stabilize hybrids, including asexual reproduction, selection for increased fertility, polyploidy, and ecological niche diversification. In the next sections, we take a comprehensive approach to understand the processes and mechanisms leading to: hybrid formation, the establishment of hybrids, and the ecological and evolutionary outcomes of hybridization.

Table 1 Examples of the 'Significant Eight' alien hybrid complexes of the British flora recognized by Stace & Crawley (2015)

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

*Introduced taxa (neophytes). Data were compiled by Stace & Crawley (2015) and Stace *et al.* (2015).

II. Hybrid formation

Understanding hybridization 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 hybridization bypasses these barriers. Isolating barriers are traditionally classified as those acting before (pre-zygotic) and after (post-zygotic) zygote formation (reviewed in Coyne & Orr, 2004) (Fig. 1). In plants, pre-zygotic barriers include: (1) 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 (2) 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 geographical 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 geographical locations (Dobzhansky, 1937). However, we include geographical 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 hybridization has long been recognized (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 geographical isolation, paying attention to those barriers that are likely to be affected by global change.

1. Breakdown of geographical isolation

The breakdown of geographical 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 hybridization. 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 globalization mean that the spread of nonnative species is likely to increase (Hulme *et al.*, 2008). The pathways of human-assisted dispersal are varied, and include
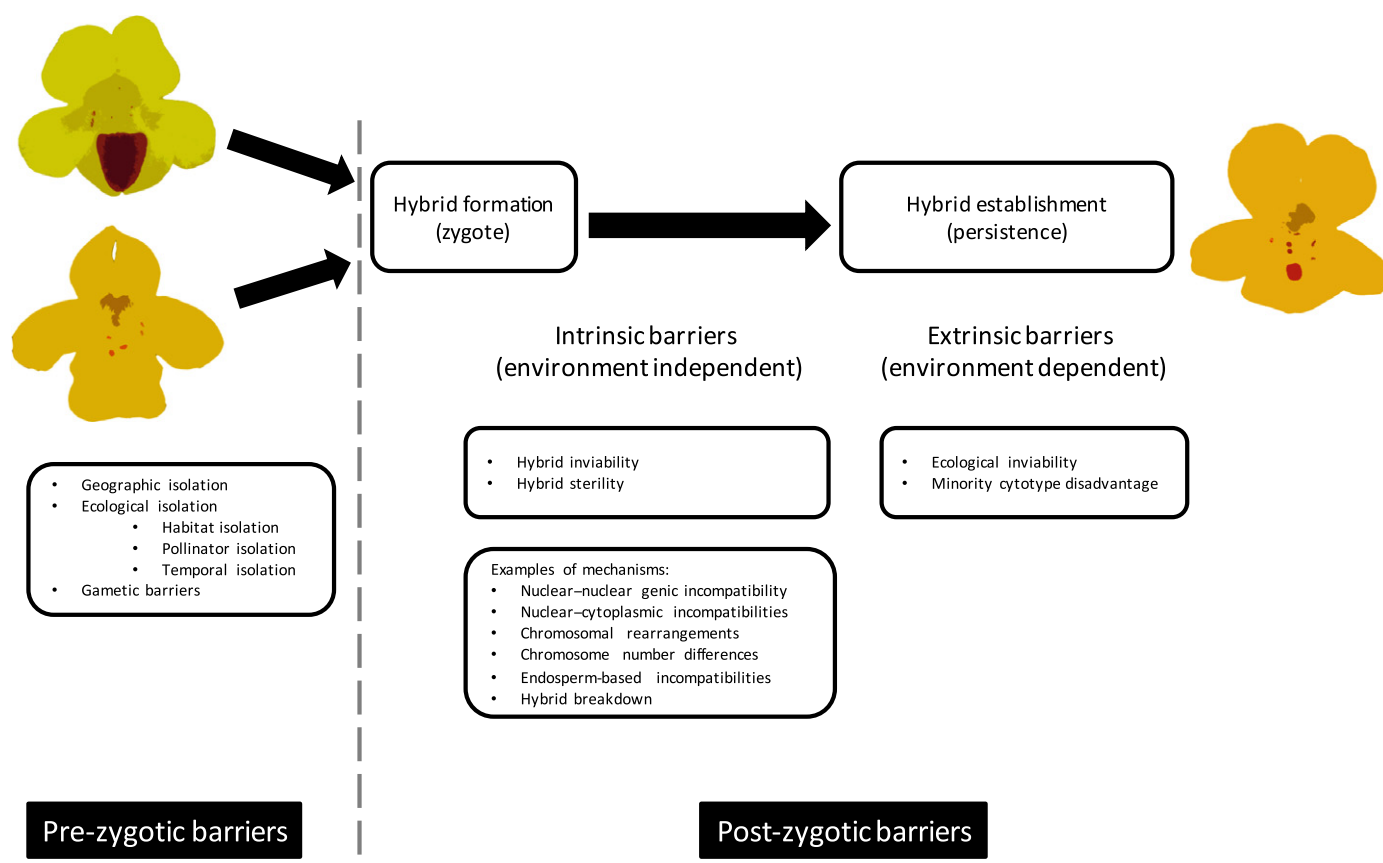

Fig. 1 Reproductive isolation barriers preventing the formation and establishment of hybrids. Reproductive isolation barriers are usually divided into pre-zygotic and post-zygotic. Notice that, in plants, some barriers such as pollen precedence act after mating (pollination) but before zygote formation.

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 on 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 (UK) in the late 18th Century, but it was not until the development of railway lines in the 1800s 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 hybridization events with native *Senecio* species. Crosses between *S. squalidus* and *Senecio vulgaris* have given rise to three new fertile hybrid taxa via a sterile triploid intermediate ('bridge'), *Senecio × baxteri*: the tetraploid introgressant *Senecio vulgaris* var. *hibernicus* (radiate groundsel), the allohexaploid *Senecio cambrensis* (Welsh groundsel), and the tetraploid *Senecio eboracensis* (York radiate groundsel; Abbott & Lowe, 2004). Additionally, hybridization between *S. squalidus* and native *Senecio viscosus* has given rise to the sterile triploid *Senecio 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 geographical 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 × spenneriana* (Nymphaeaceae) is postulated to have arisen during the Late Glacial period *c.* 10 000 yr ago when the ranges of its parental species *Nuphar pumila* (tolerant of cold water) and *Nuphar lutea* (preferring warmer water) overlapped (Preston & Croft, 1998). *Nuphar × spenneriana* then subsequently displaced *N. lutea* at its more northerly locations because of its competitive advantage in tolerating cooler water. A similar story may account

for the current distribution of *Circaea × intermedia* (Onagraceae), a hybrid between *Circaea alpina* and *Circaea 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 hybridization 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 nonnative taxa (Walther *et al.*, 2009). The increases in populations of *Orchis simia* and *Orchis 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 in increasing hybridization rates (Chunco, 2014; Brennan *et al.*, 2015), most evidence in plants remains indirect (e.g. perceived changes in the extent of hybrid zones) or correlative (e.g. comparisons of numbers 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 versus arid habitats and forested versus 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, for example, arising as a consequence of agricultural practices or urbanization, can provide hybrids with new environments where they can establish. Among the British flora, *Silene dioica × Silene latifolia* (=*Silene × hampeana*, Caryophyllaceae) (Marren, 1999) provides a good example of how habitat modification may facilitate hybridization, while *S. 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 hybridization between *Centaurea erythraea* and *Centaurea 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 F_1 hybrids and backcrosses, which appear to differ in fertility (Ubsdell, 1979). Nevertheless, differences in floral morphology and mating system are efficient in reducing hybridization, at least in mixed populations in Belgium, where established hybrids occur at a frequency of *c.* 1% (Brys *et al.*, 2014). Ultimately, the

effect of habitat alteration on hybridization may be dependent on phylogenetic relationships between taxa. For instance, Brennan *et al.* (2015) suggest that habitat alteration may be more important for hybridization 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 synchronization between sympatric species, breaking down temporal isolation barriers and facilitating hybridization. For temperature or precipitation changes to increase hybridization opportunities, it is necessary for one species to change its phenology while the other remains stable or changes more slowly (Chunco, 2014). Experimental data show 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 hybridization 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 hybridization 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 hybridization, 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 specialized on individual plant species are lost, transfer of pollen 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 for hybridization, and these may depend on the particular assemblage of plant and pollinator species. Future studies, akin to that of Bridle *et al.* (2013), should seek to address these questions.

3. Artificial hybridization

Traditionally, artificial hybridization 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, *c.* 17% (152 of 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 nonnative component of many floras, including that of the British Isles (Clement & Foster, 1994; Stace, 2010).

Artificial hybrids may have a disproportionate contribution to hybrid floras, as artificial hybridization can bypass other pre-zygotic barriers such as pollinator isolation, phenology, habitat isolation and geographical 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 hybridization (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 for pre-zygotic, post-pollination barriers will be through increasing the deposition of heterospecific pollen as nonnative 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, such as the global re-shuffling of species through human-mediated dispersal, shifting species distributions and phenology as a consequence of climate change, the erosion of ecological barriers, including the 'hybridization of the habitat', changes in pollinator preference and diversity, the expansion of nonnative species, and the artificial production and spread of hybrids. Although we think that hybrid formation is likely to increase, an alternative view may be that we have reached 'peak' hybridization, and the rate of hybridization is slowing down. For example, it may be argued that both species introductions and invasions reduce local biodiversity, and fewer species should mean fewer hybridization opportunities. Similarly, loss of habitat may reduce contact zones between potentially hybridizing taxa. However, we think that the effect of global change in promoting hybridization through the mechanisms reviewed in this section will by far exceed any hypothetical reduction in hybridization opportunities. As our records of local floras continue to improve, monitoring the temporal patterns of hybridization in floras around the world becomes feasible. Of particular interest will be to monitor floras in developing countries, where expansion of international trade and colossal changes in land use as economies grow may fast-track the upward trend in the formation of hybrids.

III. Hybrid establishment: overcoming intrinsic and extrinsic post-zygotic barriers

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

1. Escaping hybrid inviability and sterility

Hybrids are not uniformly unfit (Arnold & Hodges, 1995; Rieseberg & Carney, 1998), and within a single hybrid taxon (or sometimes a single hybrid cross) it is possible to find individuals with lower, similar or higher fitness relative to their parents (Taylor *et al.*, 2009). Nevertheless, many hybrids have to overcome severe intrinsic post-zygotic barriers before they can become established (Lowry *et al.*, 2008).

Post-zygotic barriers include intrinsic hybrid inviability and sterility (Fig. 1), and may be caused by a variety of mechanisms

(Rieseberg & Blackman, 2010; Baack *et al.*, 2015), including differences in chromosome structure and ploidy level (Stebbins, 1971; Rieseberg, 2001; Levin, 2002), nuclear–nuclear and nuclear–cytoplasmic genic incompatibilities (Lowry *et al.*, 2008), and parental genomic conflict during seed development (Köhler *et al.*, 2010) (Fig. 1). Genic incompatibilities associated with reduced hybrid fertility and viability have been extensively studied at the genetic level in many plant hybrids (Lowry *et al.*, 2008). The most widely accepted model for the accumulation of such hybrid incompatibilities is the Dobzhansky–Muller (DM) model, in which allopatric populations fix different (and mutually incompatible) alleles at one or more loci (Rieseberg & Willis, 2007; Baack *et al.*, 2015). An example of a post-zygotic hybridization barrier that arises through genic incompatibilities is hybrid necrosis, which resembles plant responses to stress including pathogens (Bomblies & Weigel, 2007). Hybrid necrosis can be debilitating or lethal, and generally acts in early (F_1 and sometimes F_2) hybrid generations (Bomblies & Weigel, 2007). Other examples of genic-based, intrinsic post-zygotic barriers in inter-specific crosses include hybrid inviability in *Iris* (Iridaceae) (Martin *et al.*, 2008), and hybrid sterility in *Mimulus* (Phrymaceae) (Fishman & Willis, 2001) and *Solanum* (Solanaceae) (Moyle & Graham, 2005). Postzygotic barriers can thus affect hybrids at different stages (e.g. immediately after zygote formation or in later hybrid generations) and with different consequences (e.g. killing or debilitating hybrids, or rendering them partially or completely sterile).

Among the strongest post-zygotic barriers are those caused by differences in the structure and number of chromosomes of hybridizing species (Levin, 2002; Husband, 2004; Karlsdóttir *et al.*, 2008; Chapman & Abbott, 2010). Hybrid viability can be severely affected by differences in the number of chromosomes between hybridizing species, especially in interploidy crosses (Stebbins, 1958). Hybridization between a diploid and a tetraploid is often associated with endosperm failure, a phenomenon known as triploid block (Bretagnolle & Thompson, 1995; Köhler *et al.*, 2010). However, triploid block may represent a porous hybridization barrier (Scott *et al.*, 2013). For example, hybrid inviability associated with triploid block is often asymmetric, meaning that the viability of the hybrid depends on whether a given taxon is the maternal or paternal parent (Ramsey & Schemske, 1998). In the British Isles, a good example of this asymmetry is *Nasturtium* × *sterile* ($2n = 48$ (45–58), Brassicaceae), where attempts to produce this well-established hybrid through artificial crosses are successful only if *Nasturtium microphyllum* ($2n = 64$) is used as the maternal parent and *Nasturtium officinale* ($2n = 32$) 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 nonnative taxon such as *Anchusa ochroleuca* × *Anchusa officinalis* (Boraginaceae), *Brassica napus* × *Brassica rapa* (Brassicaceae), *Fallopia baldschuanica* × *Fallopia japonica* (Polygonaceae), *Gaultheria mucronata* × *Gaultheria shallon* (Ericaceae), *Mimulus guttatus* × *Mimulus luteus* (Phrymaceae), *Rorippa austriaca* × *Rorippa sylvestris* (Brassicaceae), *Rumex crispus* × *Rumex frutescens/ Rumex obovatus*,

Rumex cristatus × *Rumex palustris* (Polygonaceae), *S. squalidus* × *S. vulgaris* (Asteraceae), *Spartina alterniflora* × *Spartina maritima* (Poaceae), and a number of *Verbascum* (Scrophulariaceae) hybrids (Stace *et al.*, 2015). These taxa provide excellent opportunities to further investigate how interploidy 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 greatly reduced fertility), as a consequence of problems in chromosome pairing during meiosis, leading to unbalanced aneuploid gametes, which are often nonfunctional (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 nonhybrids (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, these possibilities lead to the tantalizing 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.

Even in species with the same number of chromosomes, hybrid fertility can be negatively affected by structural differences between parental species, including chromosomal rearrangements (e.g. fusions, fissions, deletions, insertions and inversions) (Rieseberg, 2001) and differences in the size of homologous chromosomes (Levin, 2002). Reduced fertility among species with structural chromosomal differences is often caused by pairing irregularities during meiosis, which result in unbalanced, and unviable, gametes (Rieseberg, 2001; Levin, 2002). The strength of this type of chromosomal barrier thus depends on the level of differentiation between the hybridizing genomes, and the extent to which these differences cause pairing irregularities (Levin, 2002). Bivalent pairing during meiosis may partly reflect structural similarity of the hybridizing genomes, although recent work in both auto- and allopolyploid systems suggests that it may also be under the control of a few genes (Hollister, 2015). Chromosomal rearrangements have been shown to contribute to hybrid sterility in many plant groups (Rieseberg & Carney, 1998), and they may be particularly important in mediating secondary contact between previously allopatric species (Rieseberg, 2001). However, artificial selection on fertility of initially near-sterile hybrids has shown that increased chromosome pairing and more stable meiosis can evolve very
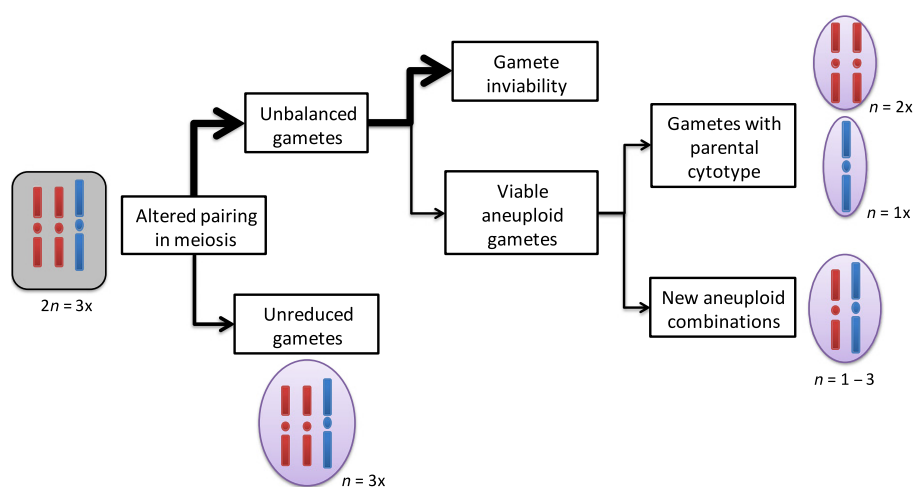

Fig. 2 Meiosis in hybrids is adversely affected by differences in chromosome number and structure between parental species. The result will generally be gamete inviability, but, rarely, gametes with atypical chromosome numbers (aneuploid and unreduced gametes) may be produced and viable. The figure shows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

rapidly and drastically improve hybrid fertility (Grant, 1966). Indeed, some hybrid derivatives between species with divergent chromosome structure have overcome initial reductions in fertility, and formed evolutionarily stable lineages (Rieseberg *et al.*, 1996).

2. Persistence of viable but sexually sterile hybrids

Hybrids may prevail even when the initial F_1 is highly sterile, if they are able to propagate by other means (clonally or apomictically; Fig. 3; Table 1) or by evolving higher sexual fertility (Grant, 1966). In addition, polyploid derivatives produced via unreduced gametes (Fig. 2) or somatic mutation can have increased fertility (Rieseberg, 2001; Stathos & Fishman, 2014); the evolutionary fate of these neo-polyploids is discussed in the 'Allopolyploid speciation' section.

When sexual reproduction is severely impaired, asexual reproduction can allow individuals to persist and spread (Grant, 1971). In the British Isles, perennial hybrids that can propagate through clonal reproduction are more widespread than those that cannot (Preston & Pearman, 2015; Table 2), showing that the capacity for vegetative reproduction is correlated with spatial coverage. Furthermore, analysis of introduced taxa in the recently published alien flora of the British Isles (Stace & Crawley, 2015) indicates that *c.* 20% of introduced hybrid taxa reproduce exclusively via clonal propagation, compared with only 8% of nonhybrid introduced taxa (Table 2). Examples of sterile hybrid lineages that persist

through vegetative propagation include *Circaea × intermedia* (Onagraceae), *Drosera × obovata* (Droseraceae) and *Stachys × ambigua* (Lamiaceae) (Stace *et al.*, 2015). Some of these sterile lineages, for instance the triploid hybrid *Spartina × townsendii*, have not spread widely (Strong & Ayres, 2013). By contrast, other clonal taxa such as the sterile triploid hybrid *Mimulus × robertsii* have spread more extensively (Preston *et al.*, 2002; Vallejo-Marín & Lye, 2013; Box 1). The ability to disperse over larger geographical areas through vegetative propagation alone may depend on the characteristics of the habitat. For instance, hybrids growing along dynamic habitats (e.g. rivers and streams) may disperse clonal propagules more extensively than those where dispersal relies on clonal growth on solid ground. For hybrids exploiting dynamic riparian habitats such as those occupied by introduced *Mimulus* populations in the British Isles, global change may facilitate their spread. For example, if extreme weather events result in more intense or frequent flooding, changes in water flow regimes could help spread clonal propagules further. Thus, clonal propagation provides a (temporary) escape route from sexual sterility in hybrids, and extreme weather events produced by global change may amplify its effects on the spatial spread of some hybrids.

Another way in which asexuality can bypass sexual failure is through the evolution of agamospermy, that is, the production of seeds without sex (Fig. 3). Agamospermy (often referred to as apomixis; Whitton *et al.*, 2008) is frequently associated with polyploidy and to a lesser extent hybridization (Grant, 1971;
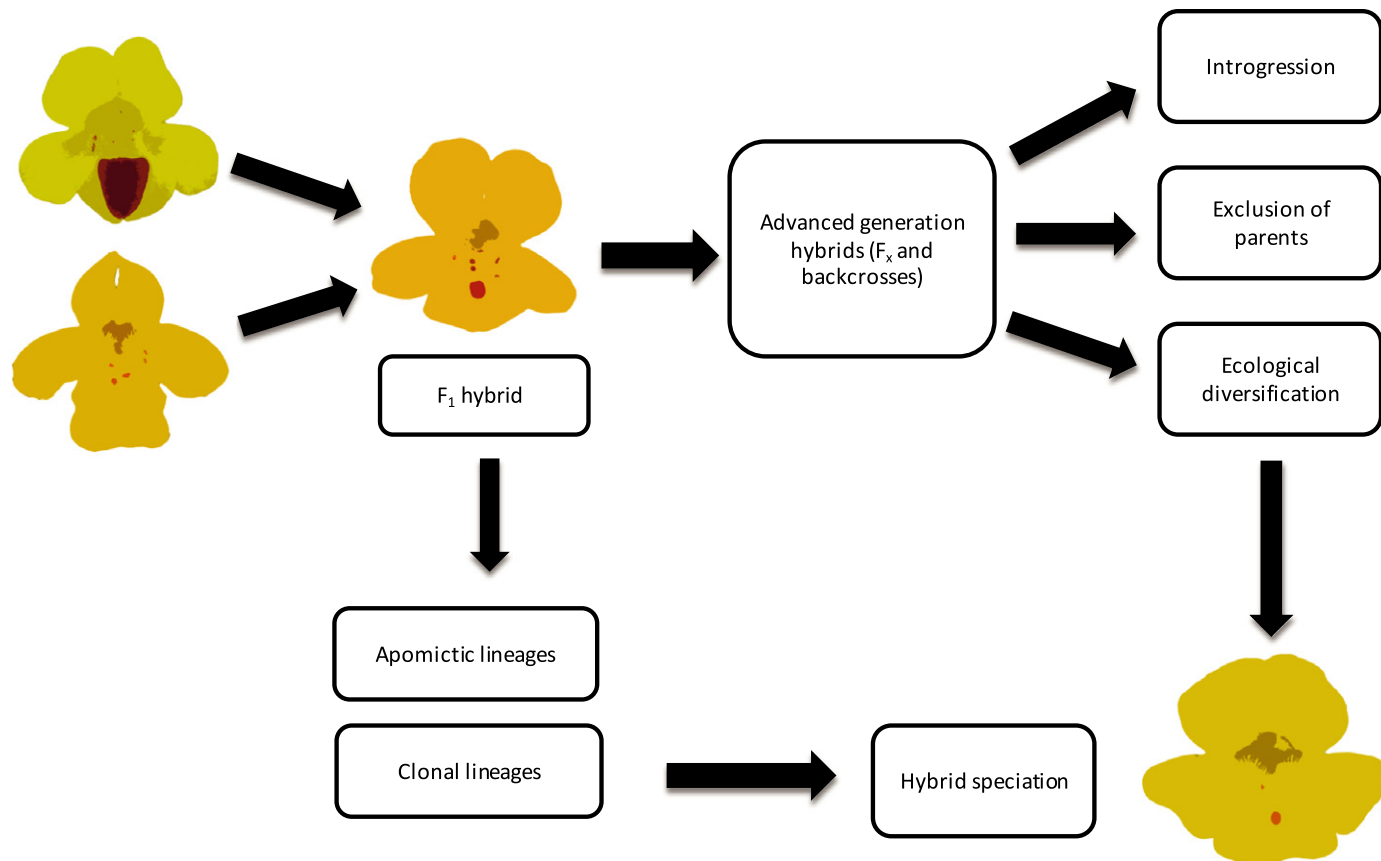

Fig. 3 Potential fate of viable hybrids that are able to persist over ecological or evolutionary timescales after their origin and initial establishment.

Table 2 Reproductive mode and occurrence of 274 alien angiosperm hybrids and 1590 nonhybrid aliens in the British and Irish flora

Propagation mode	No. of hybrid alien taxa (proportion)	Average no. of hectads per hybrid taxon (maximum)	No. of nonhybrid alien taxa (proportion)	Average no. of hectads per nonhybrid taxon (maximum)
Seeds only	48 (0.175)	180 (2242)	559 (0.351)	224 (3530)
Clonal only	55 (0.200)	157 (1147)	122 (0.077)	212 (2723)
Seeds and clonal	71 (0.259)	199 (2419)	330 (0.207)	218 (2535)
No reproduction in the British isles	100 (0.365)	32 (444)	579 (0.364)	37 (1738)
Total	274	126 (2419)	1590	153 (3530)

Data are from Stace & Crawley (2015). Hectad = 10 km × 10 km square.

Box 1 Monkeyflower hybrids: the birth of a new species.

Mimulus has a long tradition in studies of hybridization, 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 hybridization 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 naturalized (Stace *et al.*, 2015). Hybridization 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 1870s, and it is currently the second most abundant *Mimulus* in the UK after *M. guttatus*, being present in *c.* 40% of extant populations (Vallejo-Marín & Lye, 2013). The triploid hybrid *M. × 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). *Mimulus 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 in which to investigate hybrid speciation in a replicated fashion.

Although the parentage of *Mimulus* hybrids and the origin of *M. peregrinus* have been recently elucidated using genome-wide analyses (Vallejo-Marín *et al.*, 2015), a missing piece of the puzzle is to determine which taxon served as the maternal parent and which as the paternal parent in hybrid formation. Interploidy hybridization often results in asymmetric reproductive barriers, and it is likely that hybridization between *M. guttatus* and *M. luteus* does not work equally well in both directions (Roberts, 1964). The ancestry of interspecific hybrids can be determined by analysing uniparentally inherited genomes (e.g. chloroplast and mitochondrial genomes) (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.* (2016) 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. × 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.

Briggs & Walters, 1997; Otto & Whitton, 2000). Seeds produced through apomixis are genetically identical to the parental plant, and because there is no sexual reproduction they are reproductively isolated from progenitor taxa, so act as 'good' biological species. For this reason, collections of similar apomictic lineages are sometimes called microspecies,

agamospecies, agamocomplexes or syngameons (Briggs & Walters, 1997). The flora of the British Isles includes numerous examples of cryptohybrids (ancient hybrids stabilized by apomixis) including syngameons in the genera *Euphrasia* (Orobanchaceae), *Sorbus* (Rosaceae; see Box 2), *Rubus* (Rosaceae), *Hieracium* (Asteraceae), *Taraxacum* (Asteraceae) and *Rosa* (Rosaceae), all of which are relatively understudied. However, apomixis does not necessarily result in the complete loss of sex. Many facultative apomictic species, such as *Sorbus* (Box 2), display sexual 'leakiness', and produce viable pollen and ovules that can contribute to subsequent hybridization events (Ludwig *et al.*, 2013). A further example of variation in reproductive system in apomicts is *Hypericum perforatum* (Hypericaceae). This species is a facultative agamospermous tetraploid ($2n = 32$), where sexual reproduction results in diploid offspring, and agamospermy results in tetraploid and hexaploid plants (Barcaccia *et al.*, 2006). *Hypericum perforatum* hybridizes with other taxa, including diploid and tetraploid *Hypericum maculatum* ($2n = 16, 32$) with which it produces $3x$, $4x$, and $5x$ hybrids, which show variable levels of pollen and seed fertility. Yet, it is not known whether these hybrids reproduce sexually, apomictically, or using a combination of both. An unusual form of reproduction via seeds that has evolved in hybrids with odd-numbered chromosomes occurs in species such as *Rosa canina* ($2n = 5x = 35$). The *R. canina* complex contains a large number of species in which a permanent state of odd-ploidy is maintained by fusion of gametes with complementary genomes (Grant, 1971).

Box 2 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 hybridization 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 are 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 have been shown to have evolved within the Gorge, probably within the last 10 000 yr 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 hybridizations 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 hybridization 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, *Sorbus aria*, which is diploid and sexual (outcrossing), and its close tetraploid relative *Sorbus porrigentiformis*, which is apomictic. Pollen from these taxa is essential for apomictic seed production by the triploid apomictic hybrid taxa (e.g. *Sorbus bristoliensis* and *Sorbus 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; S. Ludwig & S. J. Hiscock, unpublished). This unusual mating system therefore fuels the possibility of rare hybridizations 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 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 (T. Rich, pers. comm.), indicating that these evolutionary processes are ongoing. The 2-km-long Avon Gorge, which cuts through Carboniferous Limestone to a depth of 80 m, 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.

Permanent chromosomal heterozygosity results from fertilization and syngamy between pollen with seven chromosomes and ovules with 28 chromosomes (Grant, 1971). Determining the incidence and genetic consequences of occasional bouts of sexuality and recombination in hybrids with facultative apomixis and other unusual forms of reproduction is of key importance to understand their fate, as lack of sex can have both potential benefits and costs for the maintenance of hybrids at ecological and evolutionary timescales.

One of the potential benefits that arises from bypassing regular sexual reproduction is that the genetic constitution of the hybrids can be preserved ('fixed heterozygosity'), because gene combinations are not broken down by meiosis and recombination. Viable F_1 hybrids have the capacity to show increased vigour (heterosis) relative to their parents (Barton, 2001), and this hybrid vigour can be maintained in the absence of sex and recombination. Therefore, clonality and apomixis may be important not only for the persistence of hybrids, but also as a mechanism to maintain hybrid vigour. In the context of global change, the advantages of asexual reproduction, including fixed heterozygosity, may be balanced by a limited ability to deal with rapidly changing environments because of low genotypic diversity. Yet, in recently formed asexual hybrid populations, genotypic diversity may still occur as remnants of the initial hybridization event (e.g. in hybrids formed from diverse parental stock) or as a consequence of multiple origins of the same hybrid (*Mimulus × robertsii*; Vallejo-Marín & Lye, 2013), which may provide enough raw material for short-term evolutionary change through genotypic selection. Moreover, many highly asexual populations can preserve significant levels of genetic and genotypic diversity (Vallejo-Marín *et al.*, 2010), as even rare bouts of sexual reproduction can significantly increase genetic variation (Bengtsson, 2003). Populations of asexual hybrids may also be able to deal with rapid environmental change through phenotypic plasticity (Nicotra *et al.*, 2010). Additionally, epigenetic variation can also contribute to rapid adaptation to environmental challenges, as suggested by the ecologically differentiated populations of the invasive species *Fallopia japonica* which display abundant epigenetic diversity, despite genetic uniformity (Kilvitis *et al.*, 2014). The variety of mechanisms available to asexual hybrid populations to adapt to different environments may make hybrids more resilient to the rapid modifications brought by global change.

3. Ecological inviability

Hybrids may suffer from low fitness when they are unable to find a suitable ecological niche, even if they are not affected by intrinsic developmental problems (Coyne & Orr, 2004). For instance, hybrids which have intermediate phenotypes might be selected against in parental habitats, resulting in ecological hybrid inviability (Baack *et al.*, 2015). A potential example of such an extrinsic barrier to hybridization in the British Isles flora is the hybrid between *Geum urbanum* and *Geum rivale* (*Geum × intermedium*, Rosaceae). Although the parents of *G. × intermedium* have broadly overlapping distributions they occupy slightly different habitats: *G. urbanum* occurs in well-drained soils, in areas that are partially shaded or sometimes in open disturbed habitats, while *G. rivale* is usually found in wetter soils and more open habitats (Stace *et al.*, 2015). Experimental crosses have shown that F_1 hybrids are viable and fertile, and that seeds produced in zones of contact contain a variety of hybrid genotypes (Ruhsam *et al.*, 2013). Yet, among adult plants only F_1s and backcrosses to *G. rivale* are observed (Ruhsam *et al.*, 2011). Using an experimental garden, Ruhsam *et al.* (2013) showed that hybrids do not have intrinsically lower fitness, raising the possibility that ecological selection may be filtering out certain hybrid classes (Ruhsam *et al.*, 2013). The agent of selection is unknown, but it is possible that the intermediate morphology of hybrids makes them poorly suited for establishing in parental environments, and explain why some advanced generation hybrids are rare despite obvious intrinsic post-zygotic barriers. The role that ecological barriers play in preventing the establishment of recently formed hybrids remains relatively unexplored.

IV. Outcomes of hybridization

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

Global change, through its effects on habitat, climate, and ecological interactions, has the potential to alter the outcomes of hybridization (Campbell & Wendlandt, 2013; Chunco, 2014). Probably the most obvious example of such an effect is the facilitation of hybrid persistence through 'hybridization of the habitat' in which parents occupy different ecological niches and hybrids a third, intermediate, niche (Anderson, 1948; Arnold *et al.*, 2012). Under the bounded hybrid superiority model, in which hybrids enjoy a higher fitness in intermediate habitats but suffer from lower fitness in parental ones (Moore, 1977; Barton & Hewitt, 1985), the creation and distribution of these intermediate habitats should influence not only the formation of hybrids, but also their persistence. Despite the intuitive appeal of the effects of global change on plant hybridization outcomes, there are few good examples from the British Isles flora. Nevertheless, one tantalizing case for the potential of hybridization to result in adaptive introgression comes from hybridization between nonnative species

of *Rhododendron* (Ericaceae). *Rhododendron ponticum* is widespread in the British Isles and displays the signature of hybridization with other species, including the more cold-tolerant *Rhododendron catawbiense* (Milne & Abbott, 2000). Introgression from *R. catawbiense* to *R. ponticum* is more prevalent in colder regions in eastern Scotland than elsewhere in Britain. Given this, Milne & Abbott (2000) raised the possibility that gene flow may confer increased cold tolerance. However, the hypothesis that hybridization results in increased cold tolerance in *R. ponticum*, and that selection (either natural or artificial) is responsible for the geographical distribution of introgression patterns remains to be tested. The success of hybrids under the novel ecological conditions brought about by global change will depend on both the availability and type of new habitats and ecological niches, and on whether hybrids are better equipped to deal with these new environments, either via the ability to thrive in 'intermediate' habitats or through the expression of new adaptive phenotypes, for example, as a result of transgressive segregation in hybrids.

1. Hybrid speciation

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

Allopolyploid hybrid speciation The origin of a new species through hybridization and polyploidization can occur rapidly, as taxa with different chromosome numbers are usually characterized by post-zygotic reproductive barriers (Stebbins, 1971). In principle, a hybrid can give rise to a new species in a single generation via polyploidization (Ramsey & Ramsey, 2014), leading to a 'cataclysmic origin of species' (Dobzhansky, 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 yr (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 yr three new polyploid taxa have arisen in the UK as a consequence of hybridization between native tetraploid *S. 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.

Hybridization between these two species gave rise to three allopolyploid taxa – allohexaploid *S. cambrensis* (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 probably arose following a genome duplication event in the sterile triploid hybrid *S.* × *baxteri*, as hexaploid plants with similar morphology to the wild form of *S. cambrensis* can be produced by treating synthetic triploid *S. vulgaris* × *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) – itself 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 1). 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.* × *robertsii*), which is the product of hybridization between two nonnative 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, naturalized 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 yr) of allopolyploids such as *S. 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 resulting from matings between individuals with different ploidies (minority cytotype exclusion; Levin, 1975; Fig. 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 (M. 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 recent 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 recognized that hybridization 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 the subject of intense scrutiny at the interface 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*, *Dactylorhiza traunsteinerii*, and *Dactylorhiza ebudensis* (Orchidaceae) by Paun *et al.* (2011). Analysis of genome-wide markers (cDNA amplified fragment length polymorphisms (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 colonization of different ecological niches by these three allopolyploid orchids. A similar situation may be responsible for the success of *S. cambrensis*, which also shows altered patterns of gene expression relative to its parents (Hegarty *et al.*, 2006) and also changed patterns of DNA methylation (Hegarty *et al.*, 2011), suggesting the possibility of an epigenetic element to the generation of phenotypic novelty in allopolyploids. Studying the genomic basis and evolution of ecological novelty in polyploids is particularly timely, as we have increasing access to genomic tools for nonmodel organisms, and because understanding ecological adaptation becomes urgent as populations face the challenge to adapt or perish in the new environments produced by global change.

Beyond the earliest stages of allopolyploid speciation, the British Isles flora contains several examples of older allopolyploid taxa, including *Mentha* spp., *Rubus*, *Euphrasia*, *Rorippa*, and *Nasturtium*, to name just a few (Stace *et al.*, 2015). A particularly intriguing case is the rare Scottish primrose, *Primula scotica* ($2n = 6x = 54$, Section *Aleuretia*), endemic to the north of Scotland and Orkney Isles. Early genetic work showed clear evidence that *P. scotica* was formed through an allopolyploidization event (Glover & Abbott, 1995). Furthermore, *P. scotica* is thought to have given rise to another allo-octopolyploid species, *Primula*

scandinavica ($2n = 8x = 72$), through a hybridization event with *Primula farinosa* (Guggisberg *et al.*, 2009), and it may even be involved in the origin of the 14*x*-polyploid *Primula stricta* (Guggisberg *et al.*, 2006). Currently, the distributions of *P. scotica*'s putative parents, *P. farinosa* and *Primula halleri* (Guggisberg *et al.*, 2009), and its potential derivatives *P. scandinavica* and *P. stricta*, do not overlap with that of *P. scotica*, suggesting that they may occupy different ecological niches, a hypothesis that could be tested using ecological niche modelling (e.g., McIntyre, 2012). Recent work on polyploid taxa in *Primula* Sect. *Aleuretia* has shown that polyploids in this section tend to have a smaller distribution and narrower niche breadths than diploids (Theodoridis *et al.*, 2013), which could indicate that genome duplication is associated with habitat specialization. *Primula scotica* and other taxa in Section *Aleuretia* are wonderful examples of how allopolyploid taxa can not only persist over evolutionary time, but also continue to speciate and diversify. The development of genomic tools in *Primula*, including a draft reference genome for *Primula veris* (Nowak *et al.*, 2015), has the potential to elevate this group as a system for the study of evolutionarily established allopolyploids. Notably, the timing of the formation of some of these *Primula* allopolyploids seems to coincide with large-scale environmental changes brought about by historical climate change (e.g. the end of glacial maxima), which spurs further speculation on the incidence and importance of allopolyploid speciation in times of environmental upheaval.

Recently formed hybrids, including those potentially associated with global change, are much more common than the new allopolyploid species they have generated (Stace *et al.*, 2015; Thomas, 2015), posing the question, why? Polyploids are thought to be most commonly formed by fusion of unreduced gametes (Levin, 2013), and the rate of unreduced gamete formation in hybrids can be extremely high in some plant groups (> 25%; Ramsey & Schemske, 1998), indicating ample opportunities for their formation. In the case of sterile hybrids, one key hurdle to overcome in order for an allopolyploidization event to result in a new taxon is the restoration of sexual fertility. In some cases, genome duplication can restore fertility when sterility arises from structural or numeric differences in the parental chromosome sets (Stebbins, 1958; Coyne & Orr, 2004). However, if sterility is rooted in genic incompatibilities between the parents, genome duplication alone will not be sufficient for fertility restoration. Thus, one would expect that those hybrids that have produced allopolyploid species should tend to show few or no genic incompatibilities. This hypothesis can be experimentally tested by inducing polyploidy in sterile hybrids (Hegarty *et al.*, 2013) and assessing their level of fertility (Stathos & Fishman, 2014). If synthetic polyploids are as sterile as their parents, then genic incompatibilities can be inferred (Coyne & Orr, 2004). If polyploidy restores fertility, the absence of allopolyploids in nature could be explained by ecological or perhaps stochastic causes.

Ultimately, determining why allopolyploids are rarer than their hybrid ancestors remains an open question. Their absence is puzzling given the high rate of unreduced gamete production in hybrids (Ramsey & Schemske, 1998). Beyond the barrier of overcoming sexual sterility in allopolyploids, other extrinsic post-

zygotic mechanisms such as minority cytotype disadvantage (Levin, 1975), and ecological competition with their hybrid ancestors, may pose significant barriers to the establishment of recently formed allopolyploids. It is also possible that our records of neo-allopolyploids will continue to accumulate as more recently formed hybrids come of age (Thomas, 2015). Recently formed allopolyploids may be difficult to spot in botanical surveys, particularly in the initial stages when they are quite rare. Large-scale searches for cryptic allopolyploids among recently formed hybrids, using direct or indirect measurements of genome size such as flow cytometry (e.g., Castro *et al.*, 2012), and pollen and stomata size, may provide an effective way to establish if recent allopolyploids are indeed as rare as they appear to be.

Homoploid hybrid speciation In contrast to allopolyploid speciation, homoploid hybrid speciation appears to be less common, although the number of confirmed cases of homoploid hybrid speciation is increasing (Gross & Rieseberg, 2005; Abbott *et al.*, 2013; Schumer *et al.*, 2014). This apparent rarity of homoploid speciation may therefore simply reflect the difficulty in detecting it (Abbott *et al.*, 2013). Homoploid hybrid speciation requires the evolution of a hybrid that is reproductively isolated from its parents in the absence of differences in ploidy level (Gross & Rieseberg, 2005; Yakimowski & Rieseberg, 2014). Reproductive isolation between parental and hybrid taxa could thus be based on differences in chromosome structure, ecological divergences, spatial isolation, or a combination of the above (Rieseberg, 1997). In the British Isles flora, the only confirmed case of recent homoploid hybrid speciation is *S. squalidus* (Oxford ragwort), although the place of origin of the hybrid plants was Sicily (reviewed in Abbott *et al.*, 2013). *Senecio squalidus* is a recent homoploid hybrid species, which evolved in the UK following its introduction from a *Senecio aethnensis* × *Senecio chrysanthemifolius* hybrid zone on Mt Etna *c.* 300 yr ago.

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

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

Taken at face value, homoploid hybrid speciation seems to be rarer than polyploid hybrid speciation (Abbott *et al.*, 2013). The apparent higher facility of allopolyploids to form and establish may be linked, in part, to the reproductive isolation barriers introduced by differences in ploidy level between derivative and parental taxa. But allopolyploid taxa also have the added feature of genome-wide redundancy conferred by polyploidization (Soltis *et al.*, 2014a). It is tempting to speculate that genomic redundancy is causally linked to evolutionary success in allopolyploids, for example by allowing duplicated subgenomes to differentiate and specialize in different functions (subfunctionalization and neofunctionalization; Ohno, 1970; Soltis *et al.*, 2014b). This higher evolutionary potential of allopolyploids may not be immediately realized upon genome duplication (or seen in synthetic allopolyploids; Hegarty *et al.*, 2006), but instead may accumulate as lineages diverge. The higher incidence of allopolyploids versus homoploid hybrid species may thus reflect an evolutionary advantage over the longer term in taxa with highly redundant and malleable genomes. Whether recently formed allopolyploids can keep up with rapid global change remains to be seen.

V. Outlook

Hybridization and hybrid speciation permeate the evolutionary history of plants, and are certainly not novel phenomena. However, the accelerating transformation of the world's biota brought about by global change make the study of hybridization both current and urgent if we are to understand the consequences of eroding reproductive barriers between evolutionarily distinct lineages. For instance, hybridization can threaten the conservation of local biodiversity by altering the genetic integrity of native species through introgression, and genetically swamp rare ones (Vilà *et al.*, 2000; Wolf *et al.*, 2001; Brennan *et al.*, 2015; Chown *et al.*, 2015; Taylor *et al.*, 2015). Changes to ecological communities as a result of hybridization involving nonnative species can also change ecological communities, and hybrids can compete for pollination services and fruit dispersers (Vilà *et al.*, 2000). Moreover, hybrids themselves can become significant invasive pests (Ellstrand & Schierenbeck, 2000) with negative effects for local economies and biodiversity. However, the consequences of hybridization and its effects on biodiversity need not necessarily always be negative, as hybridization can spur accelerated rates of speciation and thus increase biodiversity (Thomas, 2015). More studies are needed to gauge whether the

balance of neo-hybridization is positive or negative. Although the ecological and evolutionary consequences of recently formed hybrids are hard to predict, many hybrids are probably innocuous to local ecosystems as we know them. Regardless of their perceived costs and benefits, recently formed hybrids provide us with the unique opportunity to study, in real time, the breakdown of reproductive barriers and the processes allowing newly formed hybrids to become established, and in some cases speciate (Mallet, 2007; Abbott *et al.*, 2013). The dynamic and rapidly changing nature of our planet's biota has created a global experiment on hybridization. We now have the timely opportunity to use this unplanned experiment to study the basic biological phenomena responsible for the birth and death of species. Capitalizing on this opportunity needs a multidisciplinary approach, combining classic taxonomic studies and catalogues of hybrid floras (Stace *et al.*, 2015) with ecological experiments, phylogenetic analysis, quantitative genetics, and bioinformatics to exploit the new genomic resources available for nonmodel organisms.

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