Review

Plant speciation across environmental gradients and the occurrence and nature of hybrid zones

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Abstract Environmental gradients are very common and many plant species respond to them through adaptive genetic change. This can be a first step along a continuum of change that leads ultimately to the origin of fully reproductively isolated forms, i.e., 'biological species'. Before complete reproductive isolation is achieved, hybrid zones may form between divergent lineages either through primary intergradation or secondary contact. Here, I review the literature on plant hybrid zones between native species and highlight: mode of origin (primary intergradation versus secondary contact); distribution among plant families, genera and life form; type and genotypic composition related to strength and type of reproductive isolation between parental lineages; nature of prezygotic and postzygotic reproductive barriers; level and direction of gene flow; and the stability of hybrid zones in the face of climate change. The total number of plant hybrid zones detected in a literature search was surprisingly small (137). This was the case even for areas of the world with a long history of research into plant evolution, ecology and systematics. Reasons for this are discussed, including the possibility that plant hybrid zones are naturally rare in the wild. Only for a few hybrid zones have attempts been made to distinguish between formation by primary intergradation or secondary contact, and it is assumed that most hybrid zones originate through secondary contact. From the limited information available, it appears that plant hybrid zones may frequently move in response to climate change, but long-term studies are required to confirm this.

Key words: climate change, disturbance, environmental gradients, hybridization, hybrid zones, reproductive isolation, secondary contact, speciation.

1 Introduction

Gradual changes in the natural environment occur commonly across latitudinal, longitudinal and altitudinal gradients, and impose selection on the vegetation type and constituent species that establish across such gradients. On a more local scale, sharp changes in plant environment may occur over short distances reflecting, for example, changes in soil type, moisture, temperature, exposure and light regime, which also select for locally adapted types. Individual species can adapt to changes of environment across both types of gradient through phenotypic plasticity and/or by adaptive genetic divergence. An impediment to adaptive genetic divergence is gene flow, but this may be countered by selection for locally adapted types, which consequently can be isolated from each other by differences in environment.

Theory predicts that local adaptation across an environmental gradient, either with or without gene flow, can be a first step along a continuum of reproductive isolation that leads ultimately to the origin of fully reproductively isolated forms, i.e., biological species in the sense of Mayr (1942). Until complete reproductive isolation is achieved, divergent lineages may form hybrid zones, which can be examined to determine mechanisms that reduce gene flow and genome

merging. A primary focus of this review is to record the occurrence and nature of plant hybrid zones that form across environmental gradients and the information they yield with regard to plant speciation.

2 Local Adaptation across Environmental Gradients

2.1 Heritable phenotypic divergence and adaptation

Turesson (1925) was first to demonstrate that different heritable forms of the same plant species are often associated with different habitats. He showed that morphological differences between plants from different habitats were maintained, at least in part, when grown under the same conditions in a common garden. He called these different forms ecotypes. Clausen et al. (1940) developed Turesson's approach using reciprocal transplant analysis and from studies in California showed that (i) changes in the heritable phenotype of a species could be either continuous across an environmental gradient, i.e., clinal, or discontinuous through formation of local ecotypes isolated by distance (IBD) and environment (IBE) from each other; and (ii) plants had higher fitness in gardens close to their own habitat

relative to those originating from other more distant habitats, i.e., exhibited local adaptation.

Despite some limitations (see Savolainen et al., 2013), the reciprocal transplant approach developed by Clausen et al. (1940) has proved key to determining local adaptation through genetic divergence across environmental gradients (for recent examples, see Gonzalo-Turpin & Hazard, 2009; Fournier-Level et al., 2011; Ågren & Schemske, 2012; Anderson et al., 2015; Samis et al., 2016; Wadgymar et al., 2017). However, local adaptation is not always detected. Thus, a meta-analysis of reciprocal transplant studies involving pairwise site comparisons showed that in less than half of such comparisons (∼45%) were local plants favoured at their respective sites, while in approximately half (51%) one population performed better than the other at both sites (Leimu & Fischer, 2008). The same analysis further indicated that local adaptation more likely evolves in large than small populations, and is independent of plant life history, habitat heterogeneity and geographic distance between sites, though more studies involving a greater number of species are necessary to confirm the generality of these findings.

2.2 Molecular divergence and adaptation

Early studies of changes in gene frequencies within plant species across environmental gradients focused on characters known to be under major gene control, e.g., stem waxiness (Harland, 1947), cyanogenesis (Daday, 1954a, 1954b) and seed coat characters (New, 1958, 1959). In each case, there were strong indications that clinal change was driven by natural selection. Clines across environmental gradients were later reported for alleles at enzyme encoding loci (e.g., Lumaret, 1984), for chloroplast DNA haplotypes (e.g., Tsumura et al., 1994), and a wide range of other molecular markers (RAPDs, AFLPs, SSRs) regarded as neutral to selection, but possibly linked to genes subject to selection. More recently, clinal change in allele (SNP) frequencies at candidate gene loci associated with phenology has been reported across latitudinal gradients in certain tree species (Holliday et al., 2010, 2016; Ma et al., 2010; Chen et al., 2012), strongly implicating its adaptive significance. In addition, evidence of adaptive clinal change in allele frequency associated with soil salinity status has been documented for a sodium transporter gene in the model plant *Arabidopsis thaliana* (Baxter et al., 2010).

Following the development of high throughput sequencing, it has become possible to examine genetic responses to environmental gradients across the genome of a species, though the number of such studies currently remains small and limited to a handful of species (Savolainen et al., 2013). A recent example of this approach has shown that conifers which diverged from each other ∼140 million years ago show convergent local genetic adaptation to spatial variation in temperature or cold hardiness (Yeaman et al., 2016). These studies set the scene for genomic analyses of adaptive divergence and reproductive isolation between species that form hybrid zones across environmental gradients.

2.3 Formation of hybrid zones

Hybrid zones may form across environmental gradients either *in situ* by primary intergradation (Endler, 1977; Caisse & Antonovics, 1978) or following secondary contact between populations that diverged in allopatry (Mayr, 1942). With primary intergradation, selection drives divergence across the environmental gradient in the face of continued and uninterrupted gene flow to produce steep clines of genetic divergence in response to both marked and gradual changes of environment (Haldane, 1948; Endler, 1977). During this process of spatial or geographical differentiation, breeding barriers accumulate between divergent populations located towards the extremes of the cline until they ultimately evolve into reproductively isolated species and the process of parapatric speciation is complete. Before species are fully reproductively isolated from each other a hybrid zone can form, located in the area of contact (Endler, 1977). In hybrid zones formed by secondary contact, breeding barriers between lineages will have evolved to a degree in allopatry, but gene exchange occurs following contact until reproductive isolation is completed, possibly through reinforcement (Hopkins, 2013).

Because primary intergradation and secondary contact produce hybrid zones, which at equilibrium exhibit very similar patterns of genetic and phenotypic variation (Endler, 1977; Barton & Hewitt, 1985; Gompert & Buerkle, 2016), their origins cannot usually be distinguished. Only if the history of a hybrid zone is known or can be reconstructed accurately, might its origin, either by primary intergradation or secondary contact, be determined or indicated.

3 Hybrid Zones: Background

3.1 Definition of hybrid zone

According to Harrison (1993), "*Hybrid zones occur when genetically distinct groups of individuals meet and mate, resulting in at least some offspring of mixed ancestry.*"

Harrison emphasized that, "*This definition is intentionally broad and includes situations ranging from sporadic or occasional hybridization between species that are broadly sympatric (perhaps associated with different habitats or resources) to narrow zones of hybridization between taxa with effectively parapatric distributions*", and furthermore, "*In some cases the outcome is a "hybrid swarm" (a diverse array of recombinant types). In other situations, only F1 offspring (in addition to parental types) are found.*" Also this definition, "*. . .does not depend on either knowledge of the history of the interaction or an understanding of the evolutionary forces acting to maintain it*", and "*. . . it makes no attempt to discriminate on the basis of the geography of hybridization*".

In the review of plant hybrid zones presented here, I follow Harrison's definition of hybrid zones, but exclude studies involving one or more non-native species, i.e., species introduced to a non-native region, either by accident or design, as a result of human activities. These are omitted because a major focus of the review concerns how hybrid zones inform us of natural barriers to hybridization and gene flow between species, which may often be disrupted (particularly prezygotic barriers) following the introduction and establishment of species to non-native areas.

3.2 Types of hybrid zones

Traditionally, three types of hybrid zone have been recognised. These are tension, bounded hybrid superiority, and mosaic hybrid zones. Tension zones occur where there is a balance between the production of hybrids and selection

against them in zones of contact between parental forms. Hybrids exhibit low extrinsic and/or intrinsic fitness relative to their parents and a narrow clinal transition is normally evident between the parents (Barton & Hewitt, 1985). In contrast, in bounded hybrid superiority zones, hybrids exhibit superior fitness to their parents in intermediate habitats, but lower fitness in each parental habitat (Moore, 1977). Bounded hybrid superiority zones tend to be located in ecotones between habitats occupied by parental forms. In mosaic hybrid zones (Harrison & Rand, 1989) a patchwork of environments exists with parental types occupying different habitats. Hybrids are produced where the parental forms meet and may exhibit either lower fitness relative to parents (as in tension zones), superior fitness (as in bounded hybrid superiority zones) or variable fitness as may be the case in hybrid swarms comprising a wide range of early and later generation hybrids. A fourth type of hybrid zone, the evolutionary novelty hybrid zone, has been proposed by Arnold (1997) where the higher fitness of certain hybrids enables them to occupy novel habitats away from the hybrid zone, or replace a parent lineage from its habitat adjacent to a hybrid zone.

Recently, Curry (2015) emphasized that hybrid zones often do not easily fit into any one of these four main types and proposed that such models should be unified across a continuum of selection pressure based on geographic range. Here, direction of selection for or against hybrids and variation in its magnitude over geography, would determine spatial extent (also dependent on dispersal), movement and stability of a hybrid zone. However, this approach has yet to be tested.

3.3 Structure of hybrid zones
Hybrid zones have also been classified according to their multilocus genotypic structure. Harrison & Bogdanowicz (1997) emphasized that whereas some hybrid zones are 'unimodal' consisting largely of F1s, F2s and backcrosses, others are 'bimodal' comprising mainly multilocus genotypes representing parental forms, with intermediates being rare. Jiggins & Mallett (2000) recognised a continuum in genotypic distributions between these two types of hybrid zone with some consisting "*of a more even mixture of parental and hybrid genotypes*". Importantly, Harrison & Bogdanowicz (1997) considered that differences in genotypic composition between hybrid zones reflect differences "*in the effectiveness of pre- and postzygotic barriers to gene exchange*", while Jiggins & Mallet (2000) proposed that they signify different stages in the speciation continuum with a hybrid swarm composition indicating early stages and bimodality when speciation is nearly complete (see also Mallet & Dasmahapatra, 2012).

In addition to these structures, it is now evident that some unimodal hybrid zones may be entirely or largely composed of F1 hybrids, while other hybrid zones are trimodal, containing both parents and mainly F1s. The absence or low frequency of later generation hybrids in these hybrid zones is not surprising when F1s are sterile (e.g., Moccia et al., 2007; Lo, 2010; Twyford et al., 2015), but is unexpected when F1s are fully fertile as documented in several studies (e.g., Milne et al., 2003; Christe et al., 2016). The absence of post-F1 hybrids where F1s are fertile has been attributed to their reduced postzygotic, extrinsic fitness in ecotones relative to F1s, causing them to be outcompeted (Milne et al., 2003), or to a lower intrinsic fitness relative to F1s caused by expression of

Bateson-Dobzhansky-Muller (BDM) incompatibilities and/or breakdown of coadaptive gene complexes following recombination (Christe et al., 2016). The occurrence of unimodal or trimodal F1 dominated hybrid zones (F1-DZs) presents a problem for distinguishing hybrid zones according to type (see section above). Thus, in situations where F1s are better adapted to ecotonal conditions relative to parents and other hybrid classes, the hybrid zone may be considered to fit the bounded hybrid superiority zone model. However, because F1s contribute no offspring to subsequent generations, the hybrid zone can also be interpreted as a tension zone.

4 Occurrence and Nature of Hybrid Zones: A Literature Survey
Hybrid zones are widely recognised as "natural laboratories for evolutionary studies" (Hewitt, 1988) and "windows on evolutionary process" (Harrison, 1990), and their study has contributed much to an understanding of the occurrence and evolution of reproductive isolating mechanisms between species. Recent reviews of plant hybrid zones have been restricted to surveys of those occurring across altitudinal gradients (Abbott & Brennan, 2014) and among trees (De La Torre, 2015). Here, I present a broader survey of the hybrid zone literature that covers trees, herbs and shrubs across a wide range of different environmental conditions. For this survey, hybrid zones were identified using the search term 'hybrid zone' in ISI Web of Knowledge and a range of journals expected to publish articles on the topic. Excluded were hybrid zones not subjected to nuclear gene marker analysis, that involved one or more non-native species (for reasons mentioned earlier), or species of different ploidy.

The literature search identified hybrid zones for 137 different pairs or groups of species (Table 1). Studies of these hybrid zones vary greatly in the quality and quantity of information obtained. Thus, the examination of some hybrid zones entailed an analysis of the genetic structure of a single hybrid population with little or no information provided on isolating barriers and gene flow between parental lineages. In contrast, other studies involved the examination of a range of parent and hybrid populations across well-defined environmental gradients together with relatively detailed investigations of prezygotic and postzygotic isolating barriers. Information on the environmental gradient (where stated), location, and genetic markers used in the analysis of each hybrid zone is listed in Table 1, while information (where available) on type and genetic structure of hybrid zone, hybrid fitness, nature of prezygotic and postzygotic isolating barriers between parental forms, and level and direction of gene flow is presented in Table S1.

The major findings to emerge from a review of this information are summarised below.

4.1 Taxonomic, life form and geographic distribution of hybrid zones
Hybrid zones included in the survey were distributed across 43 plant families (~7% of the total number of plant families) and 72 genera (0.44% of total number of plant genera). In the majority of families and genera containing hybrid zones, hybrid zones were detected for only one pair of lineages

Table 1 Plant hybrid zones detected and analysed using nuclear genetic markers (Full references are listed in Table S2).

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
1	*Abies* (Pinaceae)	*A. alba* × *A. cephalonica* (Trees)	Latitudinal	Southern Balkans	nSSRs, mtDNA NADH length variants	Krajmerova et al., 2016
2		*A. homolepis* × *A. veitchii* (Trees)	Altitudinal	Mount Fuji, Japan	RAPDs, cpDNA, mtDNA markers	Isoda et al., 2000
3	*Aegilops* (Poaceae)	*A. geniculata* × *A. triuncialis* (Herbs)	Altitudinal	Golan Heights, Israel	AFLPs, LTR-RT SSAPs, cpDNA sequence	Senerchia et al., 2016
4	*Aesculus* (Sapindaceae)	*A. flava, A. pavia, A. sylvatica* (Trees)	Latitudinal	Southeast USA	Allozymes, nSSRs and ISSRs, cpDNA	DePamphilis, Wyatt, 1990; Modliszewski et al., 2006; Thomas et al., 2008
5	*Ainsliaea* (Asteraceae)	*A. apiculata* × *A. faurieana* (Herbs)	Forest–riverbank transition	Yakushima Island, Japan	nSSRs	Mitsui et al., 2011
6	*Alnus* (Betulaceae)	*A. crispa* × *A. sinuata* (Trees)	Altitudinal and longitudinal	British Columbia/ Alberta, Canada	Allozymes	Bousqet et al., 1990
7	*Anacamptis* (Orchidaceae)	*A. morio* × *A. papilionacea* (Herbs)	Species sympatric in area of geographical overlap	Southern Italy	ITS and cpDNA length variants, AFLPs	Moccia et al., 2007
8	*Antirrhinum* (Plantaginaceae)	*A. majus. pseudomajus* (magenta flowers) × *A. m. striatum* (yellow) (Herbs)	Not stated	Pyrenees, Spain	Flower colour and non-colour gene sequences	Whibley et al., 2006
9	*Aquilegia* (Ranunculaceae)	*A. formosa* × *A. pubescens* (Herbs)	Altitudinal (soil type, exposure, moisture)	California, USA	nSNPs	Noutsos et al., 2014
10		*A. japonica* × *A. oxysepala* (Herbs)	Altitudinal	Northeast China	nSSRs, cpDNA and nuclear sequence	Li et al., 2014
11	*Arctium* (Asteraceae)	*A. lappa* × *A. minus* (Herbs)	Recently disturbed sites. No gradients evident	Rhine/Main area, Germany	RAPDs	Repplinger et al., 2007
12		*A. lappa* × *A. tomentosum* (Herbs)	Recently disturbed sites. No gradients evident	Rhine/Main area, Germany	RAPDs	Repplinger et al., 2007
13	*Arctostaphylos* (Ericaceae)	*A. patula* × *A. viscida* (Shrubs)	Altitudinal, Aridity (chaparral vs montane forest)	Sierra Nevada, California	Allozymes	Ellstrand et al., 1987; Nason et al., 1992
14	*Argyranthemum* (Asteraceae)	*A. formosa* × *A. pubescens* (Herbs)	Altitudinal	Canary Islands	AFLPs	Fjellheim et al., 2009
15	*Artemisia* (Asteraceae)	*A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana* (Shrubs)	Altitudinal	Wasatch Mts., Utah, USA	Coumarins, flavonoids etc.	Freeman et al., 1991; Miglia et al., 2007; Wang et al., 1997
16	*Asclepias* (Asclepiaceae)	*A. exaltata* × *A. syriaca* (Herbs)	Forest–field transition	Shenandoah National Park, Virginia, USA	Allozymes, cpDNA RFLPs	Broyles, 2002
17	Banksia (Proteaceae)	*B. hookeriana* × *B. prionotes* (Shrubs)	Not stated	Western Australia	AFLPs	Lamont et al., 2003
18		*B. oblongifolia* × *B. robur* (Shrubs)	Swamp-woodland	Southeastern Australia	nSSRs	Usher et al., 2010
19	*Begonia* (Begoniaceae)	*B. heracleifolia* × *B. nelumbiifolia* (Herbs)	Different microhabitats	Mexico	nSSRs, cpSSRs	Twyford et al., 2015
20		*B. heracleifolia* × *B. sericoneura* (Herbs)	Different microhabitats	Mexico	nSSRs, cpSSRs	Twyford et al., 2015
21	*Betula* (Betulaceae)	*B. alleghaniensis* × *B. papyrifera* (Trees)	Sympatric over broad area– microhabitat segregation	Eastern North America	nSSRs	Thomson et al., 2015

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Table 1 Continued

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
22		B. ermanii × B. pubescens (Trees)	Longitudinal	Between Yenisei River and Lake Baikal, Russia	nSSRs	Tsuda et al., 2017
23		B. pendula × B. plathyphylla (Trees)	Longitudinal	Between Yenisei River and Lake Baikal, Russia	nSSRs	Tsuda et al., 2017
24	Borrichia (Asteraceae)	B. arborescens × B. frutescens (Shrubs)	Latitudinal	Florida Keys, Florida, USA	Single copy nuclear gene and cpDNA RFLPs	Cattell, Karl, 2004
25	Callicarpa (Lamiaceae)	C. japonica × C. mollis (Shrubs/Trees)	Light (open vs shaded habitat)	Central Japan	nDNA and cpDNA sequences	Tsukaya et al., 2003
26	Carex (Cyperaceae)	C. curvula curvula × C. c. rosae (Herbs)	Altitude (soil type)	European Alps	AFLPs	Choler et al., 2004
27		C. limosa × C. rariflora (Herbs)	Water depth	Quebec/ Labrador, Canada	Allozymes	McIntire, Waterway, 2002
28	Ceanothus (Rhamnaceae)	C. roderickii × C. cuneatus (Shrubs)	Soil type	Sierra Nevada, California, USA	AFLPs	Burge et al., 2013
29	Cirsium (Asteraceae)	C. californicum × C. occidentale (Herbs)	Altitude, (aridity, chaparral–oak woodland)	Figueroa Mt, California, USA	Allozymes	Wells, 1983
30	Clarkia (Onagraceae)	C. xantiana parviflora × C. x. xantiana (Herbs)	Longitudinal (precipitation, winter temperature)	California, USA	nSSRs and nDNA sequences; cp DNA sequences	Pettengill, Moeller, 2012; Briscoe Runquist et al., 2014
31	Costus (Costaceae)	C. pulverulentus × C. scaber (Herbs)	Latitudinal	Central and South America	nSSRs	Kay, 2006; Surget-Groba & Kay, 2013
32	Dubautia (Asteraceae)	D. arborea D. ciliolata (Shrubs)	Woodland-shrubland transition	Mauna Kea Hawaii	AFLPs	Remington, Robichaux, 2007
33		D. ciliolata × D. scabra (Shrubs)	Different age of lava flow substrate	Hawaii	RAPDs	Caraway et al., 2001
34	Eleocharis (Cyperaceae)	E. cellulosa × E. interstincta (Herbs)	Not stated	Calabash Marsh, Belize	ISSRs, ITS sequence	Košnar et al., 2010
35	Epidendrum (Orchidaceae)	E. calanthum × E. cochlidium (Herbs)	Not stated	Lojar, Ecuador	AFLPS, cpDNA sequence	Vega et al., 2013
36		E. calanthum × E. schistochilum (Herbs)	Not stated	Lojar, Ecuador	AFLPS, cpDNA sequence	Vega et al., 2013
37		E. cochlidium × E. schistochilum (Herbs)	Not stated	Lojar, Ecuador	AFLPS, cpDNA sequence	Vega et al., 2013
38	Eucalyptus (Myrtaceae)	E. acmenoides × E. cloeziana (Trees)	Latitudinal	SE Queensland, Australia	nSSRs, cpDNA sequence	Stokoe et al., 2001
39		E. aggregata × E. rubida (Trees)	Soil drainage	New South Wales, Australia	nSSRs	Field et al., 2011a, 2011b
40		E. brownii × E. populnea (Trees)	Latitudinal	Queensland, Australia	nSSRs, cpDNA sequence	Holman et al., 2003
41		E. cordata × E. globulus (Trees)	Not stated	Tasmania, Australia	AFLPs, cpDNA sequence	McKinnon et al., 2010

Table 1 Continued

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
42	*Fraxinus* (Oleaceae)	*F. angustifolia* × *F. excelsior* (Trees)	Latitudinal (days of frost)	France	nSSRs, EST-SSRs	Gérard et al., 2006, 2013; Fernándes–Manjarrés et al., 2006
43	*Gaillardia* (Asteraceae)	*G. pulchella*, calcicole × calcifuge (Herbs)	Soil type	Texas, USA	Allozymes	Heywood, 1986; Heywood, Levin, 1988
44	*Geum* (Rosaceae)	*G. rivale* (outcrosser) × *G. urbanum* (selfer) -(Herbs)	Shade and drainage	Scotland, UK	AFLPS, cpDNA	Ruhsam et al., 2011, 2013
45	*Gliricidia* (Fabaceae)	*G. maculata* × *G. sepium* (Trees)	Latitudinal	Meso-America (Guatamala, Belize, Mexico)	RAPDs and nuclear RFLPS, mtDNA markers	Dawson et al., 1996
46	*Helianthus* (Asteraceae)	*H. annuus* × *H. petiolaris* (Herbs)	Soil type and moisture content	Nebraska, USA	Allozymes, RAPDs	Rieseberg et al., 1998, 1999; Sambatti et al., 2012
47		*H. annuus* × *H. bolanderi* (Herbs)	Soil moisture and composition	Davis, California	AFLPs	Carney et al., 2000
48	*Impatiens* (Balsaminaceae)	*I. javensis* × *I. radicans* (Herbs)	Altitudinal	Central Java, Indonesia	ITS, cpDNA sequences	Tsukaya, 2004
49	*Ipomopsis* (Polemoniaceae)	*I. aggregata* × *I. tenuituba* (Herbs)	Altitudinal	Rocky Mts, Colorado, USA	Floral morphology, RAPDs, AFLPs, cpDNA sequence	Aldridge, 2005; Aldridge, Campbell, 2009; Campbell & Waser, 2001; Campbell et al., 1997, 2002, 2008; Wu, Campbell, 2005
50		*I. aggregata* subsp. *candida* × subsp. *collina* (Herbs)	Altitudinal	Rocky Mts, Colorado, USA	nSSRs, cpSSRs	Milano et al., 2016
51	*Iris* (Iradaceae)	*I. brevicaulis* × *I. fulva* (Herbs)	Forest–pasture ecotone (difference in water depth and light regime)	Louisiana, USA	RAPDs, cpDNA RFLPs	Cruzan, Arnold, 1993, 1994; Johnston et al., 2001; Tang et al., 2010; Hamlin, Arnold, 2014
52		*I. fulva* × *I. hexagona* (Herbs)	Forest–cypress marsh ecotone (difference in water depth and light regime)	Louisiana, USA	rDNA RFLPs, allozymes	Arnold et al., 1990a,1990b; Hodges et al., 1996; Carney et al., 1994, 1996
53	*Leucosceptrum* (Lamiaceae)	*L. japonicum* × *L. stellipilum* (Shrubs/Small trees)	Latitudinal	Central Japan	ITS sequence, cpDNA, nSSRs	Li, Maki, 2015; Li et al., 2015
54	*Liparis* (Orchidaceae)	*L. kumokiri* (self-compatible) × *L. makinoana* (self-incompatible) (Herbs)	Possibly latitudinal, species overlap over broad area	South Korea	Allozymes	Chung et al., 2005
55	*Lomatia* (Proteaceae)	*L. myricoides* × *L. silaifolia* (Shrubs)	Latitudinal	New South Wales, Australia	nSSRs	McIntosh et al., 2014
56	*Magnolia* (Magnoliaceae)	*M. salicifolia* × *M. stellata* (Trees)	River/marsh–dry site transition	Aichi Prefecture, Japan	nSSRs, cpSSRs	Muranishi et al., 2013
57	*Metrosideros* (Myrtaceae)	*M. polymorpha* high × low altitude populations (Trees)	Altitudinal	Hawaii	nSNPs	Izuno et al., 2017

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Table 1 Continued

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
58	*Mimulus* (Phrymaceae)	*M. guttatus* (outcrosser) × *M. nasutus* (selfer) - (Herbs)	Seasonal aquatic–terrestrial transition	Washington, USA	nSNPs	Kenney, Sweigart, 2016
59		*M. aurantiacus* ssp. *australis* (yellow flowered) × ssp. *puniceus* (red flowered) (Herbs)	Longitudinal	California, USA	nSNPs, AFLPs, cpDNA RFLPs,	Streisfeld, Kohn, 2005, 2007; Streisfeld et al., 2013; Stankowski, Streisfeld, 2015; Stankowski et al., 2015, 2017; Sobel, Streisfeld, 2015
60	*Ophrys* (Orchidaceae)	*O. fusca* × *O. lutea* (Herbs)	Not obvious	Portugal	nSSRs, cpSSRs	Cotrim et al., 2016
61	*Orchis* (Orchidaceae)	*O. mascula* × *O. pauciflora* (Herbs)	No obvious habitat difference or environmental gradient	Southern Italy	rDNA and cpDNA RFLPs, AFLPs	Pellegrino et al., 2000; Cozzolino et al., 2006; Scopece et al., 2013
62		*O. militaris* × *O. purpurea* (Herbs)	Forest–grassland transition	Belgium	AFLPs	Jacquemyn et al., 2012
63	*Pericallis* (Asteraceae)	*P. cruenta* × *P. echinata* (Herbs)	Altitudinal	Tenerife, Canary Islands	AFLPs	Van Hengstum et al., 2012
64		*P. cruenta* × *P. tussilaginus* (Herbs)	Altitudinal	Tenerife, Canary Islands	AFLPs	Van Hengstum et al., 2012
65	*Phlomis* (Lamiaceae)	*P. crinita* × *P. lychnitis* (Herbs)	*P. crin.* restricted to limestone areas	Southern and Eastern Spain	Allozymes	Albaladejo et al., 2004; Albaladejo, Aparicio, 2007
66	*Phlox* (Polemoniaceae)	*P. cuspidata* (pink flower) × *P. drummondii* (red flower) (Herbs)	Aridity	Texas, USA	Allozymes	Levin, 1975; Hopkins, Rauser, 2012
67	*Phyllodoce* (Ericaceae)	*P. aleutica* × *P. caerulea* (Shrubby herbs)	Early–late snowmelt transition	Hokkaido, Northern Japan	nSSRs, AFLPs, cpDNA sequence	Kameyama, Kudo, 2011; Kameyama et al., 2008
68	*Picea* (Pinaceae)	*P. abies* × *P. obovata* (Trees)	Longitudinal	Urals, Russia	nSSRs and nDNA sequence, mtDNA	Tsuda et al., 2016
69		*P. engelmanii* × *P. glauca* (Trees)	Latitudinal and altitudinal	British Columbia, Canada	nSSRs and SNPs	De La Torre et al., 2014a, 2014b, 2015
70		*P. glauca* × *P. sitchensis* (Trees)	Maritime–continental climate	British Columbia, Canada	nSSRs and SNPs, cp and mt DNA	Hamilton, Aitken, 2013; Hamilton et al., 2013a, 2013b
71		*P. mariana* × *P. rubens* (Trees)	Latitudinal	Northeastern North America, Canada & USA	nSNPs	De Lafontaine et al., 2015; De Lafontaine, Bousquet, 2017
72	*Pinus* (Pinaceae)	*P. banksiana* × *P. contorta* (Trees)	Longitudinal	Alberta and NW Territories, Canada	nSSRs and SNPs	Cullingham et al., 2012, 2013
73		*P. echinata* × *P. taeda* (Trees)	Latitudinal	Georgia, USA	Allozymes, cpDNA RFLPs	Edwards-Burke, 1997
74		*P. hwangshanensis* × *P. massoniana* (Trees)	Altitudinal	Anhui Province, China.	EST-SSRs	Zhang et al., 2014
75		*P. mugo* × *P. sylvestris* (complex) (Trees)	Longitudinal, but complex	Southern and Central Europe	nSNPs, cpDNA RFLPs	Kormutak et al., 2008; Wachowiak, 2016

Table 1 Continued

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
76		P. parviflora × P. pumila (Trees)	Altitudinal	Honshu, Central Japan	SSCPs	Watano et al., 1995, 2004
77	Piriqueta (Turneraceae)	P. caroliniana caroliana × P. c. viridis (Herbs)	Latitudinal	Florida, USA	Allozymes, RAPDs	Martin, Cruzan, 1999; Cruzan, 2005
78	Pitcairnia (Bromeliaceae)	P. albiflos × P. staminea (Herbs)	Not clear	Rio de Janeiro, Brazil	nSSRs, cpSSRs	Palma-Silva et al., 2011
79	Platanthera (Orchidaceae)	P. aquilonis × P. dilatata (Herbs)	Not evident	Maine, USA	RAPDs, cpDNA RFLPs	Wallace, 2006
80	Polystichum (Dryopteridaceae)	P. imbricans × P. munitum (Herbs–ferns)	Soil moisture and light level	Trinity County, California, USA	cpDNA RFLPs, allozymes	Kentner, Mesler, 2000
81	Populus (Salicaceae)	P. alba × P. tremula (Trees)	Flooding	Central Europe, and Xinjiang, China	nSSRs and SNPs, cpDNA sequence	Lindtke et al., 2012, 2014; Christe et al., 2016, 2017; Zeng et al., 2016
82		P. angustifolia × P. deltoides (Trees)	Altitudinal	San Miguel River, Colorado, USA	nSSRs, cpSSRs, cpLPs	Hersch-Green et al., 2014
83		P. angustifolia × P. fremontii (Trees)	Altitudinal	Utah, USA	nDNA and mtDNA RFLPs	Whitham, 1989; Martinsen et al., 2001; Schweitzer et al., 2002
84		P. balsamifera × P. deltoides (Trees)	Not clear	Alberta and Quebec, Canada	nSNPs, cpSNPs	Hamzeh et al., 2007; Roe et al., 2014
85		P. laurifolia × P. nigra (Trees)	Soil moisture content	Xinjiang, China	nSSRs, nSNPs, cpDNA FLPs	Jiang et al., 2016
86	Primula (Primulaceae)	P. beesiana × P. bulleyana (Herbs)	Light regime (shade vs open)	Yunnan, China	AFLPs, cpDNA	Ma et al., 2014
87	Quercus (Fagaceae)	Q. affinis × Q. laurina (Trees)	Latitudinal, longitudinal and altitudinal	Trans-Mexican Volcanic Belt and Northern Oaxaca, Mexico	RAPDs	González-Rodríguez et al., 2004; Ramos-Ortiz et al., 2016
88		Q. austrocochinchinensis × Q. kerrii (Trees)	Closed moist forest–open habitat transition	Xishuangbanna nature reserve, Yunnan, China	AFLPs, nSSRs	An et al., 2017
89		Q. berberidifolia × Q. durata (Trees)	Serpentine–Non-serpentine soils	California, USA	nSSRs	Ortego et al., 2017
90		Q. coccifera × Q. ilex (Trees)	Not clear	Spain	nSSRs	Ortego, Bonal, 2009
91		Q. crassifolia × Q. crassipes (Trees)	Not clear	Eje Neovolcanico, Mexico	RAPDs	Tovar-Sánchez, Oyama, 2004
92		Q. crispula × Q. dentata (Trees)	Coastal-inland transition	Hokkaido, Japan	AFLPs	Ishida et al., 2003
93		Q. douglasii × Q. lobata (Trees)	Not evident. Parental species are broadly sympatric	Santa Lucia Mountains, California, USA	nSSRs	Craft et al., 2002
94		Q. gambelii × Q. grisea (Trees)	Mosaic of dry-mesic sites across altitudinal gradient	Mt Withington, New Mexico, USA	RAPDs	Howard et al., 1997; Williams et al., 2001

Table 1 Continued

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
95		*Q. geminata* × *Q. virginiana* (Trees)	Soil type and moisture content	Southeastern USA	nSSRs	Cavender-Bares, Pahlich, 2009
96		*Q. ilex* × *Q. suber* (Trees)	Not evident	Mediterranean, Europe	nSSRs	Burgarella et al., 2009
97		*Q. kelloggii* × *Q. wislizeni* (Trees)	Altitudinal. Dry chapparal–mesic forest transition	San Jacinto Mountains, California, USA	Allozymes	Nason et al., 1992
98		*Q. liaotungensis* × *Q. mongolica* (Trees)	Latitudinal/ longitudinal	North China	nSSRs. AFLPs, cpSSRs, cpDNA sequences	Zeng et al., 2011
99		Q. *magnoliifolia* × Q. *resinosa* (Trees)	Altitudinal	Tequila volcano, Jalisco, Mexico	nSSRs	Albarrán-Lara et al., 2010
100		*Q. petraea* × *Q. pubescens* (Trees)	No gradient–single sympatric population examined	Berignone-Tatti, Central Italy	nSSRs	Salvini et al., 2009
101		*Q. petraea* × *Q. pyrenaica* (Trees)	Latitudinal. Seasonal dry-mesic transition	Montejo, Central Spain	nSSRs	Valbuena-Carabaña et al., 2005
102		*Q. petraea* × *Q. robur* (Trees)	Not evident. Species widely sympatric in Europe	Europe	Allozymes, nSSRs	Bacilieri et al., 1996; Streiff et al., 1999; Gugerli et al., 2007; Lepais, Gerber, 2011; Abadie et al., 2012; Gailing, Curtu, 2014
103		Mixed stand of *Q. frainetto*, *Q. petraea*, *Q. pubescens*, *Q. robur* (Trees)	Heterogeneous for soil type and moisture content	West-central Romania	Allozymes, nSSRs, cpDNA sequence	Curtu et al., 2007
104		Hybridization between *Q. coccinea*, *Q. falcata*, *Q. rubra*, *Q. velutina* (Trees)	Not evident	North Carolina, USA	nSSRs	Moran et al., 2012
105		Hybridization between *Q. ellipsoidalis*, *Q. velutina*, *Q. coccinea*, *Q. rubra* (Trees)	Partly latitudinal (complex)	Indiana and Michigan, USA	nSSRs, EST-SSRs, AFLPs	Sullivan et al., 2016
106		Hybridization of *Q. wislizeni* with *Q. agrifolia*, *Q. kelloggii* and *Q. parvula* (Trees)	Environmental gradients between mosaic of different habitats	California, USA	AFLPs	Dodd, Afzal-Rafii, 2004
107	*Rhinanthus* (Orobanchaceae)	*R. angustifolia* × *R. minor* (Herbs)	Possible dry-moist microsite transitions in disturbed areas	Belgium	RAPDs, ISSRs, cpDNA RFLPs	Ducarme et al., 2010; Natalis, Wesselingh, 2012
108	*Rhizophora* (Rhizophoraceae)	*R. apiculata* × *R. mucronata* (Trees)	Not evident	Sri Lanka	ISSRs, cpDNA and nuclear ITS sequences	Lo, 2010
109		*R. apiculata* × *R. stylosa* (Trees)	Not evident	Australia, Micronesia and Guam	ISSRs, cpDNA and nuclear ITS sequences	Lo, 2010

Table 1 Continued

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
110		R. mangle × R. racemosa (Trees)	Coastal zone (salinity) transition	Central American Isthmus, and South America	nSSRs	Cerón-Souza et al., 2010
111		R. samoensis × R. stylosa (Trees)	Not evident	Fiji	ISSRs, cpDNA and nuclear ITS sequences	Lo, 2010
112	Rhododendron (Ericaceae)	R. aganniphum × R. phaeochrysum (Shrubs)	Altitudinal	Yunnan, China	AFLPs	Marczewski et al., 2015
113		R. caucasicum × R. ponticum (Shrubs)	Altitudinal	Tiryal Dag, Turkey	RAPDs, ISSRs	Milne et al., 2003
114		R. decorum × R. delavayi (Shrubs)	Not clear	Yunnan, China	AFLPs, ITS and cpSNPs	Zha et al., 2008
115		R. delavayi × R. irroratum (Shrubs)	Altitudinal	Yunnan, China	AFLPs, ITS and cpSNPs	Zha et al., 2010
116		R. eriocarpum ×. R. indicum (Shrubs)	Coastal-Inland transition (saline, temperature, soil moisture gradient)	Yakushima Island, Japan	AFLPs	Tagane et al., 2008
117		R. ferrugineum × R. hirsutum (Shrubs)	Soil type (acid-basic transition)	European Alps, Austria	RAPDs	Milne, Abbott, 2008
118		R. spiciferum × R. spinuliferum (Shrubs)	Not stated	Yunnan, China	nSSRs, cpDNA sequence	Yan et al., 2017
119	Rorippa (Brassicaceae)	R. amphibia (self-incompatible) × R. palustris (self-compatible) - (Herbs)	Reed bank–open river site transition	North Germany	Allozymes, cpDNA sequence	Bleeker, Hurka, 2001
120		R. amphibia × R. sylvestris (Herbs)	Reed bank–flooded grassland/gravel bank transition	River Elbe, North Germany	Allozymes, cp DNA sequence	Bleeker, Hurka, 2001
121	Sabatia (Gentianaceae)	S. arenicola × S. formosa (Herbs)	Soil type (clay–sand transition)	La Marque, Texas	Allozymes	Bell, Lester, 1978
122	Salix (Salicaceae)	S. alba × S. fragilis (Trees)	Not clear	Danube, SE Germany	AFLPs, nSNPs	Oberprieler et al., 2013
123		S. eriocephala × S. sericea (Small trees)	Not clear (soil moisture implicated)	New York state, USA	RAPD, ITS and cp DNA markers	Hardig et al., 2000; Fritz et al., 2006
124		S. helvetica × S. purpurea (Shrubs/dwarf trees)	Altitudinal and soil type	Glacier forefield, Switzerland	nSSRs	Gramlich, Hörandl, 2016; Gramlich et al., 2016
125		Mixed stand of S. dasyclados, S. schwerinii and S. viminalis (Trees)	Not clear	Lake Baikal, South Siberia, Russia	nSNPs, cpDNA SSRs	Fogelqvist et al., 2015
126	Sarracenia (Sarraceniaceae)	Mixed stand of S. leucophylla, S. alata, and S. rubra (Herbs)	No evident gradients in recently, naturally disturbed site	Alabama, USA	nSSRs	Furches et al., 2013
127	Schiedea (Caryophyllaceae)	S. menziesii × S. salicaria (Shrubs)	Longitudinal	Halepohaku, West Maui, Hawaii	nSSRs, cpDNA sequence	Wallace et al., 2011
128	Senecio (Asteraceae)	S. aethnensis × S. chrysanthemifolius (Herbs)	Altitudinal	Mount Etna, Sicily, Italy	Allozymes, RAPDs, nSSRs, EST-SSRs	James, Abbott, 2005; Brennan et al., 2009, 2014, 2016; Chapman et al., 2005, 2013,

Table 1 Continued

	Genus	Taxa	Environmental gradient	Location	Genetic markers	References
						2015; Filatov et al., 2016
129		S. hercynicus × S. ovatus (Herbs)	Altitudinal	Harz Mts, and Bavarian National Park, Germany	RAPDs, AFLPs	Raudnitschka et al., 2007; Bog et al., 2017
130	Silene (Caryophilaceae)	S. dioica × S. latifolia (Herbs)	Altitudinal	European Alps, Switzerland and Italy	AFLPs	Minder et al., 2007; Minde, Widmer, 2008; Karrenberg, Favre, 2008; Rahmé et al., 2009; Favre et al., 2017
131	Sphagnum (Sphagnaceae)	S. capillifolium × S. quinquefarium (Herbs, mosses)	Dry pine forest–moist spruce forest transition	Sweden	ISSRs, cpDNA RFLPs	Natcheva, Cronberg, 2007
132	Tithonia (Asteraceae)	T. rotundifolia × T. tubaeformis (Herbs)	Altitudinal	Mexico	RAPDs	Tovar-Sanchez et al., 2012
133	Vincetoxicum (Apocynaceae)	V. atratum × V. japonicum (Herbs)	Latitudinal/ Longitudinal	Japan	nSSRs	Li et al., 2016
134	Viola (Violaceae)	V. bissetii × V. rossii (Herbs)	Sunny, dry southern aspect–shaded moist northern aspect transition	Mt Ougi, central Japan	AFLPs	Nagano et al., 2015
135		V. chaerophylloides × V. eizanensis (Herbs)	Open grassland - shaded forest transition	Tochigi Prefecture, Japan	AFLPs, cpDNA sequence	Toyama et al., 2015
136	Yucca (Asparagaceae)	Y. brevifolia × Y. jaegeriana (Trees)	Longitudinal. Due to east-west parapatric distribution of different species-specific pollinators	Tikaboo Valley, Mojave Desert, Nevada	nSNPs	Royer et al., 2016
137	Zaluzianskya (Scrophulariaceae)	Z. microsiphon × Z. natalensis (Herbs)	Not stated	Mt. Gilboa, Kwazulu-Natal, South Africa	ISSRs	Archibald et al., 2004

Genetic markers: AFLPs, amplified fragment length polymorphisms; cpDNA, chloroplast DNA; cpSNPs, chloroplast single nucleotide polymorphisms; cpSSRs, chloroplast simple single repeats; EST-SSRs, expressed sequence tag simple sequence repeats; ISSRs, inter simple sequence repeats; ITS, nuclear ribosomal internal transcribed spacer sequence; LTR-RT SSAPs, long terminal repeat transposon sequence specific amplified polymorphisms; mtDNA, mitochondrial DNA; nDNA, nuclear DNA; nSSRs, nuclear simple sequence repeats; nSNPs, nuclear single nucleotide polymorphisms; RAPDs, random amplified polymorphic DNAs; SSCPs, single strand conformation polymorphisms; rDNA, ribosomal DNA; RFLPs, restriction fragment length polymorphisms.

(Figs. 1a, 1b; Table S3). Greater numbers of hybrid zones per family were recorded for Fagaceae and Asteraceae with intermediate numbers recorded for Ericaceae, Orchidaceae, Pinaceae and Salicaceae. The Asteraceae and Orchidaceae are two of the largest plant families, each comprising more than 20 000 species, so it is not surprising that more hybrid zones have been studied in these families than in most others. With regard to genera, *Quercus* (oaks) contained most studied hybrid zones (20), while *Eucalyptus, Picea* (spruce), *Pinus, Populus, Rhizophora* (mangrove), *Rhododendron* and *Salix* (willow) each contained four to seven studied hybrid zones

representing different pairs or groups of species. These eight plant genera are well known for containing many interfertile species, and it is perhaps surprising that relatively few hybrid zones (with the exception of *Quercus*) have been recognised and studied in each of them.

Studies of hybrid zones on herbs and trees were approximately equally represented in the survey, and more common than those recorded for shrub species (Fig. 1c; Table S3). Almost all studies were conducted on flowering plants or conifers, with only one hybrid zone study conducted in each of ferns and mosses. With regard to geographical
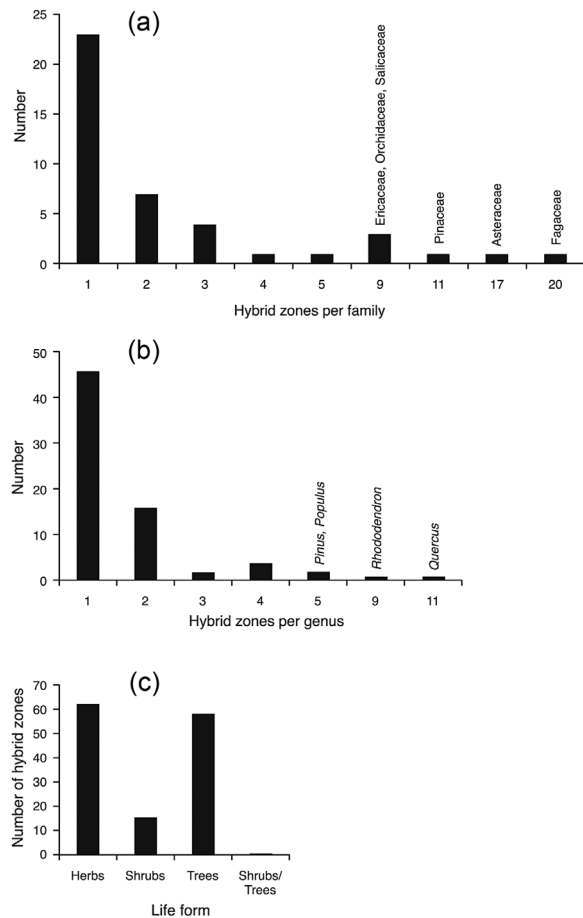
Fig. 1. Frequency of hybrid zones per **a,** family, **b,** genus and **c,** life form, for hybrid zones detected and analysed using nuclear genetic markers.

distribution, most hybrid zones studied are located in North and Central America, Asia and Europe (54, 32 and 30, respectively, Table 1), eight were located in Australia, six in South America, six in Hawaii and additional Pacific islands, three in the Canary Islands, and one in Africa. Note that hybrid zones studied between *Populus alba* and *P. tremula,* *Rhizophora apiculata* and *R. stylosa,* and *Rhizophora mangle* and *R. racemosa,* were located in Europe and Asia, Australia and several Pacific islands, and Central and South America, respectively. The uneven geographical distribution across the continents almost certainly reflects the human, scientific and financial resources available for studying plant hybrid zones in different parts of the world, rather than the relative frequency of hybrid zones in these different regions.

It is not possible to draw firm conclusions on the taxonomic, life form and geographic distributions of all plant hybrid zones (studied and not studied) from a survey of only those that have been studied genetically. However, given the known ability of many species to hybridize (Whitney et al., 2010; Guo, 2014; Stace et al., 2015), it is surprising that so few plant hybrid zones have been studied genetically, particularly in parts of the world where there is a long history of plant evolutionary research. For one such region—botanically rich California—only 12 hybrid zones involving different pairs or groups of native plant species

were recorded and four of these were in the 'outlier' genus *Quercus.* The low occurrence in this region possibly suggests that plant hybrid zones are relatively rare in California and, by extension, may also be rare elsewhere in the world. Alternatively, it may reflect that they have been grossly under-recognised and understudied by evolutionary biologists.

4.2 Hybrid zone type, multilocus genotypic structure and hybrid fitness

In many hybrid zone reports, no statement was made of the type of hybrid zone that best fitted the data obtained, i.e., tension, bounded hybrid superiority, mosaic or evolutionary novelty hybrid zone. Sometimes hybrid zone type could be inferred or the pattern of variation described simply as clinal, but for many an entry of 'not stated' remains (Table S1). The distribution of hybrid zones according to type (Fig. 2A; Table S4) shows the mosaic form is the most common type reported or inferred, followed in turn by the tension and bounded hybrid superiority types. The least frequent type was the evolutionary novelty zone, for which only three possible examples could be inferred. In certain cases, where more than one hybrid zone was examined for a pair of lineages, more than one type of zone was distinguished. For example, with the species pair *Senecio hercynicus* and *S. ovatus,* a hybrid zone located in the Harz Mountains of Germany was described as mosaic (Raudnitschka et al., 2007), whereas in the Bavarian National Park (Bog et al., 2017) the hybrid zone seemed a better fit to the evolutionary novelty type. In addition, a particular hybrid zone type could be apparent for certain nuclear genetic markers, but not for others. Thus, for *Antirrhinum majus pseudomajus* (magenta flowers) and *A. m. striatum* (yellow flowered) and for *Mimulus aurantiacus* ssp. *australis* (yellow
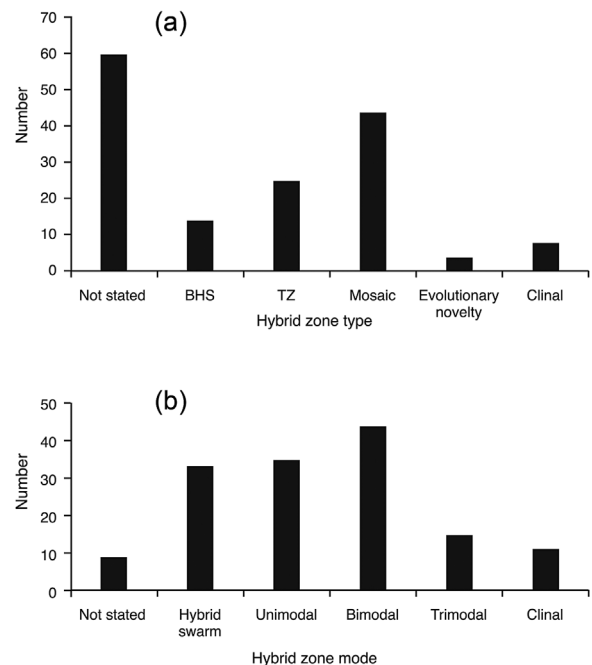

Fig. 2. Frequency of **a,** hybrid zone type (BHS = Bounded hybrid superiority; TZ = Tension zone), and **b,** hybrid zone mode among hybrid zones detected and analysed using nuclear genetic markers.

flowered) and ssp. *puniceus* (red flowered), narrow tension zones were evident for genes controlling flower color, whereas no apparent clines or weak clines existed for other molecular markers (Whibley et al., 2006; Sobel & Streisfeld, 2015; Stankowski et al., 2017). This indicates that the genomes of these taxa are porous to gene flow except at key loci distinguishing the phenotypes of parental lineages.

Figure 2b (Table S4) shows that in terms of modal structure, bimodal hybrid zones were most common followed by unimodal and trimodal (comprising only or mainly F1s and both parent forms) types. However, unimodal hybrid zones varied in structure and included those containing only or mainly F1s, those comprising mainly F1s and F2s, and those comprising one parent form and backcrosses to it (Table S4). Similarly, bimodal hybrid zones varied in composition from those comprising both parental forms and backcrosses to them (and sometimes a few early generation hybrids), to those comprising one parent type and backcrosses to the other parent, and those containing F1s and one parent form and/or backcrosses to it (Table S4). Clearly, classifying hybrid zones neatly into unimodal and bimodal types obscures a range of structural heterogeneity, and undermines such use to infer the strength of reproductive isolation between parental lineages as proposed by Harrison & Bogdanowicz (1997) and Jiggins & Mallett (2000). As already pointed out, an F1 dominated unimodal hybrid zone reflects strong reproductive isolation between parental lineages, rather than weak isolation as Jiggins & Mallett (2000) proposed. Similarly, a bimodal hybrid zone comprising one parent type and backcrosses to the other parent indicates unidirectional gene flow, rather than strong reproductive isolation between parental lineages. In addition to these problems, many hybrid zones (~36% of the total) could not be classified as unimodal, bimodal or trimodal based on information provided. Approximately 22% were best described as hybrid swarms containing a wide range of hybrid types along with parental classes. For others (~8%) a cline was apparent, while in the remainder none of the foregoing types were stated or could be inferred. Occasionally, unimodal and bimodal hybrid zones were reported for the same species pair. This was the case for *Phlomis crinita* and *P. lychnitis*, with unimodal hybrid zones present in Southern Spain and bimodal zones in eastern Spain (Albaladejo & Aparicio, 2007), and was also evident for the species pair *Ipomopsis aggregita* and *I. tenuituba* (Aldridge & Campbell, 2009).

For most hybrid zones, no direct study of hybrid fitness in terms of survivorship or fecundity was conducted, and in approximately one third of cases no information on F1 fertility was presented or could be inferred. Often, hybrids were stated as fertile or sterile based on personal observation, or was inferred from the presence or absence of later generation hybrids in a hybrid zone. Figure 3 (Table S5) indicates that for most hybrid zones where information on F1 fertility was available, F1s were fertile or partially fertile and only in a handful of cases (~7%) were they sterile. For a few hybrid zones (in *Artemisia*, *Ipomopsis*, *Picea*) reciprocal transplant analyses were conducted and indicated that hybrids had a higher fitness than parent forms in ecotones between parental habitats. In three further cases (*Antirrhimum*, *Costus* and *Yucca*) it was shown or inferred that pollinator visitation was lower to hybrids than to parental forms.
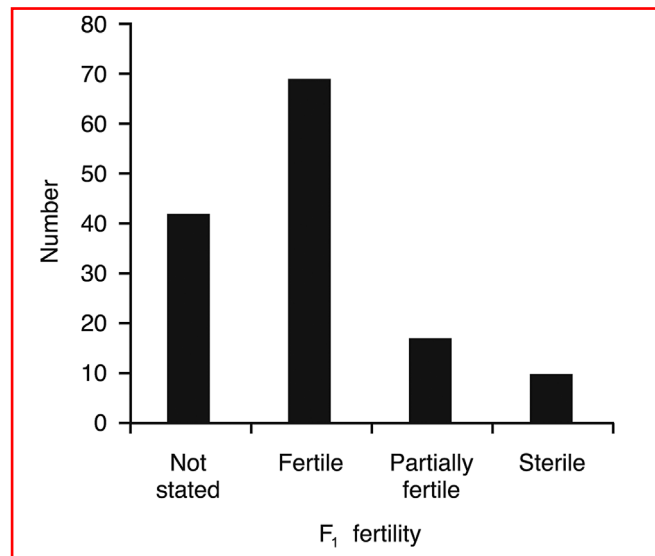

Fig. 3. F1 fertility for taxa that form hybrid zones detected and analysed using nuclear genetic markers.

4.3 Prezygotic and postzygotic reproductive barriers

For most hybrid zones, no investigations have been conducted on the nature of prezygotic and postzygotic reproductive barriers between parental lineages. However, comments were often made on whether parental lineages exhibited divergent phenology and/or habitat preference. From these comments, and occasionally some quantitative analyses, parental lineages could be inferred to exhibit divergent habitat preferences in 84 cases, show divergent phenologies in 38 cases, and in 24 cases exhibit both divergent phenology and habitat preference (Fig. 4a; Table S6). In addition, it was reported that divergent pollinator preference in 18 cases, selfing of one or both parental lineages in 12 cases, spatial clustering of individuals in seven cases and conspecific pollen precedence in six cases, could be inferred or were demonstrated to act as prezygotic barriers between certain lineages that form hybrid zones.

A lack of information on postzygotic barriers is apparent by the fact that in 52 cases no information on such barriers was provided (Fig. 4b; Table S6). Where information was available, it was inferred that postzygotic barriers were absent or weak in 27 cases, strong in 18 cases, and of intermediate strength (due to partial F1 sterility) in 16 cases. A chromosomal or genic incompatibility basis to reproductive isolation was demonstrated or inferred in 4 and 46 cases, respectively, and post-F1 hybrid breakdown (possibly due to genic incompatibility) was apparent in 9 cases. The number of cases of genic incompatibility may be inflated by the fact that often it was inferred from reduced hybrid fitness, which in some instances could have resulted from an extrinsic rather than intrinsic postzygotic effect (Tables S1 and S6). Because it is often difficult to distinguish between these effects, all such cases were grouped under genic incompatibility. In some instances where genic incompatibility was implied or demonstrated, hybrids were fertile in one direction of a cross but not in the other direction, indicating cytonuclear incompatibility. In a handful
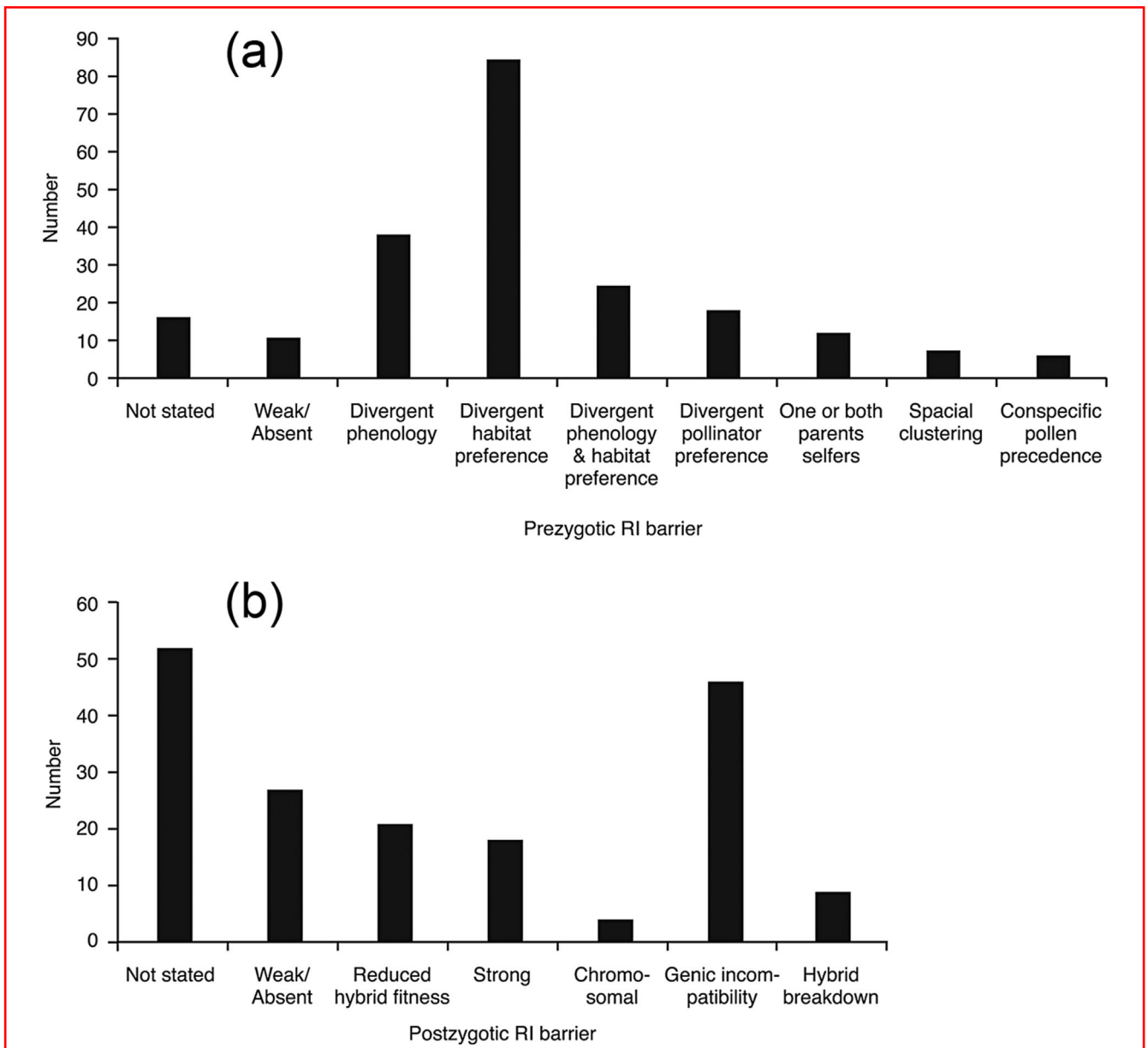
Fig. 4. Frequency of **a,** prezygotic and **b,** postzygotic reproductive isolating (RI) barriers between taxa that form hybrid zones detected and analysed using nuclear genetic markers.

of cases, genic incompatibility due to BDM incompatibilities and/or cytonuclear incompatibility was demonstrated from an analysis of genetic mapping families produced from reciprocal crosses (e.g., in *Helianthus, Iris, Mimulus* and *Senecio*).

Only for a few taxa that form hybrid zones have detailed analyses been conducted of prezygotic and postzygotic reproductive isolating barriers across the life cycle. This has been done for *Clarkia xantiana parviflora* and *C. x. xantiana* (Briscoe Runquist et al., 2014), *Costus pulverulentus* and *C. scaber* (Kay, 2006), *Helianthus annuus* and *H. petiolaris* (Sambatti et al., 2012), *Mimulus guttatus* and *M. nasutus* (see Kenney & Sweigart, 2016) and *Orchis mascula* and *O. pauciflora* (Scopece et al., 2013). In each case it was shown that a range of prezygotic and postzygotic isolating mecha-nisms contribute positively to reproductive isolation, though

in combination do not completely impede gene flow. More studies of this kind to supplement investigations of the genetic structure of hybrid zones are required.

4.4 Level and direction of gene flow
Levels and directions of gene flow across hybrid zones were indicated from the frequency and types of advance generation hybrids present in a hybrid zone, and occasionally from estimations based on population genetic data and simulation. Gene flow appeared to be high across a relatively large number of hybrid zones (54), but low/very low/absent in a greater number (76) (Fig. 5; Table S7). In some instances, gene flow could be high in certain hybrid populations of a species pair, but low in others (e.g., in *Ipomopsis, Lomatia* and *Phlomis*). In a relatively high number of cases (45) asymmetric gene flow was detected or inferred, while bidirectional gene flow was less
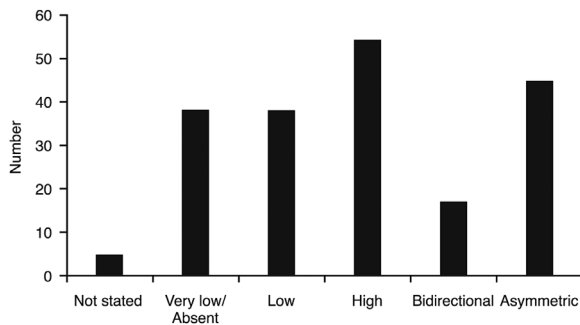
Fig. 5. Frequency of level and direction of gene flow for taxa in hybrid zones detected and analysed using nuclear genetic markers.

commonly reported (17 cases). In hybrid populations between *Rhododendron spiciferum* and *R. spinuliferum*, bidirectional gene flow was most common, although asymmetric introgression was evident in some populations. Clearly, levels and directions of gene flow vary considerably across plant hybrid zones, and likely reflect different stages in the evolution of reproductive isolation between parental lineages across the speciation continuum. The relatively frequent occurrence of asymmetrical gene flow across hybrid zones indicates a range of factors that might act as causes of this phenomenon, e.g., differential abundance of parental lineages, differential gamete production and fertilization, and differential embryo development and offspring survival (Tiffin et al., 2001; Turelli & Moyle, 2007; Lowry et al., 2008). However, only in a few cases have these been investigated in any detail.

There is now mounting evidence that gene flow between hybridizing plant lineages is not evenly distributed across the genome (Payseur & Rieseberg, 2016). At one extreme, genes may flow freely across the genomes of divergent lineages except at a relatively low proportion of loci that distinguish these lineages. This is the case for the different flower colour subspecies of *Mimulus guttatus* (Sobel & Streisfeld, 2015; Stankowski et al., 2017), whose genomes are mainly undifferentiated. At the other extreme, when speciation is at a more advanced stage, the genomes of hybridizing lineages may be far more differentiated with gene flow restricted to much fewer regions of the genome as is the case for *Populus alba* and *P. tremula* (Christe et al., 2017). Future studies of the comparative genomics of divergent lineages that form hybrid zones will enable the extent of genomic porosity to gene flow to be established between lineages across the divergence continuum. Furthermore, such studies will pinpoint genomic regions and candidate genes involved in adaptive introgression between lineages (Suarez-Gonzalez et al., 2016) across environmental gradients.

4.5 Formation of hybrid zones
Information on the possible origins of the hybrid zones studied also varied greatly in both quality and quantity. It was frequently assumed that secondary contact, often following environmental disturbance (see below), precipitated the formation of a hybrid zone. Usually, this was based on evidence or an assumption that parental lineages were primarily isolated by prezygotic barriers that failed, or were

significantly reduced in effect, when the environment was disturbed naturally or through human activities. Alternatively or in addition, phylogeographic evidence was presented to indicate that parental lineages had recently come into contact, possibly as a result of climate or geological change, following a period of divergence in allopatry. However, for very few hybrid zones were analyses conducted to distinguish between the possibility of an origin by primary intergradation or secondary contact. In these cases, coalescent-based simulations were conducted to determine which of the two models provided the best fit to population genetic data. An origin following secondary contact after allopatric divergence provided the best fit for the hybrid zone between *Clarkia xantiana parviflora* and *C. x. xantiana* (Pettengill & Moeller, 2012) and for hybrid zones that exist between the four white oak species, *Quercus petraea, Q. pubescens, Q. pyrenaica and Q. robur* (Leroy et al., 2017), whereas primary intergradation proved a better fit for the origin of the hybrid zone between *Senecio aethnensis* and *S. chrysanthemifolius* (Filatov et al., 2016). Acceptance of the primary intergradation model for the origin of a hybrid zone relies on rejecting the possibility of an allopatric phase having occurred at some stage during the divergence of parental forms. However, even complex models of the type used by Filatov et al. (2016) are likely to be much simpler than reality and therefore possibly miss brief periods of allopatry. Such periods could be key to the development of prezygotic and postzygotic isolating barriers between parental types that reduce gene flow following secondary contact.

Although the importance of environmental disturbance in promoting hybridization between species has been recognized since the landmark papers of Anderson (1948) and Anderson & Stebbins (1954) (see also Guo, 2014), and was often implicated as a trigger to hybrid zone formation in the studies reviewed here (see below and Lamont et al., 2003, in particular), only one study attempted to distinguish the relative importance of different types of environmental disturbance in promoting hybridization between a particular species pair. This was conducted on two Californian oak species, *Quercus berberidifolia* and *Q. durata* (Ortego et al., 2017), and showed that genetic admixture increased with wildfire frequency, but surprisingly not with urbanization, land clearance for agriculture. Clearly, the type as well as degree of environmental disturbance may be important in promoting hybrid zone formation.

4.6 Hybrid zone stability and movement across environmental gradients
Hybrid zones may have a transient or long-term existence. Those that establish as a result of anthropogenic disturbance may quickly disappear when such disturbance ends. Other hybrid zones that form more naturally might be maintained over longer periods, though move across environmental gradients in response to environmental change. Buggs (2007) reviewed the literature on hybrid zone movement, pointing out that for plants of equivalent ploidy, only one hybrid zone had been monitored over a sufficient period to detect movement directly. This was a hybrid zone between *Helianthus annuus* and *H. bolanderi* (Tables 1 and S1) formed most likely as a result of human disturbance, and in which an advance of *H. annuus* at the expense of *H. bolanderi* was detected over a period of 55 years (Carney et al., 2000).

However, hybrid zone movement is also indicated indirectly by asymmetrical introgression between parental lineages across a hybrid zone. It has been shown that when a species invades an area occupied by another and hybridizes with that species, it is normal for unidirectional introgression to proceed towards the invading species (Currat et al., 2008). Thus, as an introgressed invader advances, the centre of the hybrid zone which it forms with another species also advances, and a signature of where hybrid zones were previously located is indicated by a trail of historically introgressed neutral genes that extends back from the hybrid zone to areas where only the invading species is now present.

Based on this type of genetic signature, it appears that hybrid zone movement across altitudinal gradients may have occurred for hybrid zones formed between *Pinus massoniana* and *P. hwangshanensis* in Anhui, China (Zhang et al., 2014), *Populus angustifolia* and *P. fremontii* in Utah, USA (Martinsen et al., 2001), *Senecio aethnensis* and *S. chrysanthemifolius* on Mount Etna, Sicily (James & Abbott, 2005; Chapman et al., 2013), and *Senecio hercynicus* and *S. ovatus* in Bavaria, Germany (Bog et al., 2017). In the case of *Senecio*, the genetic signatures of asymmetric introgression indicate that the introgressed lowland species, *S. chrysanthemifolius* and *S. ovatus*, are advancing to higher altitudes, possibly in response to recent climate warming, and displacing their higher altitude counterparts from these areas. In contrast, for *Pinus* and *Populus*, asymmetric introgression towards the higher altitude species, *Pinus hwangshanensis* and *Populus angustifolia*, respectively, suggests that these species may have advanced to lower altitudes during an earlier stage in their recent history. Martinsen et al. (2001) proposed that for *P. angustifolia* this could have occurred during the Holocene when temperature was higher and lowland *P. fremontii,* and the hybrid zone it forms with *P. angustifolia,* occurred at higher altitude. Whether this difference in direction of hybrid zone movement between these two plant groups (*Senecio* versus *Pinus* and *Populus* species), possibly in response to different periods of climate change, might be explained by differences in generation time has yet to be tested. However, due to their longer generation times, it is feasible that lowland trees, such as *Pinus massoniana* and *P. fremontii,* have not yet begun to ascend in any noticeable way to higher elevations in response to very recent anthropogenic climate warming, whereas short-lived herbaceous plants, such as the two lowland *Senecio* species, have.

A more complex genetic signature of historical introgression is evident between the two forms of *Piriqueta caroliniana* that form a hybrid zone in Florida (Table 1), indicating that the more introgressed *P. c. viridis* has advanced northwards displacing *P. c. caroliniana* in southern Florida, pushing the hybrid zone northwards, possibly as a result of climate warming (Martin & Cruzan, 1999; Cruzan, 2005). Patterns of asymmetric introgression also indicate hybrid zone movement for some *Picea* species, e.g., for the northward movement of a hybrid zone between *P. engelmannii* and *P. glauca*, possibly as a result of climate warming since the Last Glacial Maximum (De La Torre et al., 2015), and a postglacial westward movement of the hybrid zone between *Picea abies* and *P. obovata* (Tsuda et al., 2016). However some hybrid zones have remained remarkably stable in the face of climate change as appears to be the case for that between two North American firs, *Abies balsamea* and

A. lasiocarpa. A genetic analysis of this hybrid zone indicates that it has not moved since it originated at the end of the last glacial period, approximately 11 kyr ago (Cinget et al., 2015).

In addition to moving, hybrid zones may disappear in response to climate change. This can happen if climate change causes the geographical ranges of parental species to pull apart such that they no longer hybridize. A consequence is that such species may frequently bear genomic signatures of past hybridization and introgression events. Alternatively or in addition, allopolyploid and homoploid hybrid taxa may occur in areas where a hybrid zone formerly existed, but where one or both parental species are no longer present. Liu et al. (2014) proposed such a scenario to account for the occurrence of a homoploid hybrid species of *Ostryopsis* (*O. intermedia*) close to one of its parents in China (*O. nobilis*), but hundreds of kilometers south of the geographical distribution of its other parent (*O. davidiana*). Subsequently, Kadereit (2015) showed that homoploid and allopolyploid species formed during the Quaternary are frequently ecogeographically displaced from their parental taxa and proposed that this was often due to them occupying areas where their parental taxa were formerly in contact and hybridized during glacial periods (see also Klein & Kadereit, 2016). Kadereit (2015) argued that because of the evolutionary novelty generated by hybridization (Abbott et al., 2013), certain hybrids were more likely to be adapted to the changed environmental conditions within such areas, allowing them to maintain a presence and evolve into hybrid species after their parents retreated from such areas in response to climate change.

4.7 Genetic basis of local adaptation and reproductive isolation

The ability to conduct genomic scans and construct genomic maps to search for and locate parts of the genome that are highly differentiated between species which form hybrid zones has led in recent years to investigations of the genetic basis of differences in local adaptation between such species and the traits involved in reproductive isolation. Genomic mapping also provides information on whether genomic (chromosomal) rearrangements distinguish species, which, in turn, may reduce the fitness of hybrids and prevent the breakup (through recombination) of blocks of adaptive genes contained within such rearrangements. A review of this literature is beyond the scope of this paper; however, it is worth mentioning briefly some key findings to emerge from the literature review. For some species pairs, large-scale chromosomal rearrangements appear to be an important cause of reduced hybrid fitness and preservation of adaptive differences, e.g., for *Helianthus annuus and H. petiolaris* (Burke et al., 2004), whereas in some other species they appear not to be, e.g., for *Mimulus guttatus* and *M. nasutus* (see Fishman et al., 2013), and *Senecio aethnensis* and *S. chrysanthemifolius* (Brennan et al., 2014, 2016), where BDM and cytonuclear incompatibilities are important. Also evident is that highly diverged genomic regions detected by genomic scans represent a small component of the total genome and are often, though not always, spread across the genome rather than strongly clustered (Strasburg et al., 2012; Chapman et al., 2013; Brennan et al., 2016). Candidate genomic regions/genes affecting particular traits, possibly involved in adaptive divergence/reproductive isolation between species that form hybrid zones, have been identified by

genomic scans (e.g., Christe et al., 2017), though have yet to be subjected to functional analysis.

5 General Conclusions and Future Directions

From the review of the plant hybrid zone literature presented here, it is evident that with the exception of a few comprehensive investigations, most hybrid zone studies provide only preliminary information on the nature of the hybrid zone investigated and the mechanisms that maintain parental forms in the face of gene flow. Nonetheless, these studies are important in providing information on the occurrence of hybrid zones. What emerges is that surprisingly few hybrid zones have been recognised and studied genetically. Taxonomists are good at recording naturally occurring hybrids based on morphology (Guo, 2014; Stace et al., 2015) and frequently assign names to hybrids, indicating that they are distinct and recognisable entities. Although the name of a hybrid should apply to all hybrid progeny of the parents, no matter how much they vary, only early generation hybrids are likely to be recognised as such, with later generation backcrosses resembling one or both parents missed. Consequently, many bimodal hybrid zones comprising mainly backcrosses and parental types will not be recognised as hybrid zones in the wild based on morphological analysis alone. Thus, population genetic analysis is required to confirm the existence and structure of these and other hybrid zones, and this is likely to have imposed a constraint on the number of hybrid zones detected, due to the scientific and financial resources required for such analysis. It is to be expected that a combined population morphological and genetic approach should lead in future to the discovery of many more plant hybrid zones.

Despite this, there are reasons to suggest that plant hybrid zones may occur more rarely in the wild than anticipated from the known ability of many plant species to hybridize (Whitney et al., 2010; Guo, 2014; Stace et al., 2015). In both North America and Europe, relatively few plant hybrid zones have been recognised and analysed, despite a long history of research into plant evolution, ecology and systematics. In California, only twelve hybrid zones involving different pairs or groups of native plant species have been reported and studied genetically since initial studies were conducted in the 1980s (Wells, 1983; Ellstrand et al., 1987).

Why might hybrid zones be relatively rare, if in fact this is the case? Hybridization is generally thought to be limited to closely related species, which are genetically similar. This has been demonstrated for some plant genera (Moyle et al., 2004; Scopece et al., 2008) and was recently confirmed for animal species from analyses of genomic data (Roux et al., 2016). Moreover, Levin (2012) has shown that postzygotic isolation (hybrid sterility) of herbaceous plant lineages is achieved, on average, approximately 4–5 million years after divergence. Thus, hybrid zones containing fertile hybrids are expected to form only between closely related, genetically similar taxa. However, many of such taxa are reproductively isolated from each other by very effective prezygotic isolating mechanisms such as geographic barriers, divergent phenology, divergent

pollinators, and mating system differences, as well as postzygotic extrinsic mechanisms involving immigrant and hybrid inviability (Lowry et al., 2008; Baack et al., 2015). These barriers are likely to prevent such species from hybridizing and forming hybrid zones in sympatric and parapatric situations unless they are disrupted by natural or anthropogenic disturbance. The literature surveyed indicates that almost one third of hybrid zones occur in environmentally disturbed areas (Table S8); however, this is likely to be an underestimate as often no statement is made with regard to disturbance, though sampling was conducted close to roads and pathways which would indicate local habitat disturbance. The possibility that hybrid zones might in fact be rare needs, of course, to be fully tested. More examples of hybrid zones will no doubt accumulate in the literature over future years and improve our understanding of the frequency and taxonomic range of hybrid zones throughout the world. In the meantime, it would be useful to target genera already known to contain a relatively high proportion of interfertile species. In these genera, it would be expected that hybrid zones should be frequent, as in oaks. If, however, this is normally not found to be the case, particularly in areas not subject to anthropogenic disturbance, then the rarity hypothesis would be supported and genera such as oaks would be confirmed as outliers.

For a number of hybrid zones, considerable information has been obtained on hybrid fitness, isolating barriers between parental forms, local adaptation and gene flow, e.g., in *Helianthus*, *Iris*, *Mimulus*, *Picea*, *Populus*, *Quercus* and *Senecio*. Nonetheless, our understanding of these matters remains far from complete even for these hybrid zones. For example, in the case of local adaptation, which is considered a key mechanism in the origin and maintenance of hybrid zones, advances are being made from genomic analyses in understanding the genetic basis of adaptive differences between species that form hybrid zones, but in most cases in the absence of testing for local adaptation using reciprocal transplants. Continuing and detailed research on these hybrid zones, and the parental taxa, should be encouraged, in order to understand further the mechanisms involved in processes of plant speciation.

At the outset of this review, emphasis was placed on plant adaptation across environmental gradients and its potential role in plant speciation. There is now abundant evidence to suggest that local adaptation can occur in the face of gene flow (see for example, Abbott & Comes, 2007) and increasing evidence that this can lead to speciation (Nosil, 2008; Papadopulos et al., 2013; but see Yang et al., 2017). Endler (1977) pointed out that an intermediate step in the process of speciation with gene flow, moving from local adaptation to fully isolated biological species, is the formation of hybrid zones by primary intergradation. Alternatively, hybrid zones across environmental gradients may originate as a result of secondary contact between partially reproductively isolated species, following their divergence in allopatry. For many of the hybrid zones covered in this review, it was inferred or assumed that an origin by secondary contact had occurred. Only for one was an origin by primary intergradation advanced (Filatov et al., 2016), and this was based on a modelling approach that could miss brief, but important allopatric phases, during which divergence causing reproductive isolation may have occurred. Based on current methodology, it is

almost impossible to show that a hybrid zone originated by primary intergradation rather than secondary contact. Nonetheless, from the available evidence, most hybrid zones across environmental gradients seem to have originated by secondary contact rather than primary intergradation, indicating that ecological speciation with gene flow across environmental gradients might be a rare phenomenon.

Another feature to emerge from the current literature is that plant hybrid zones may often move, possibly in response to climate change, although this is based on genetic signatures of responses to historic climate change and, therefore, is open to interpretation (Taylor et al., 2015). Long-term studies of existing hybrid zones are now required to determine how plant hybrid zones are responding to current climate change from both a demographic and evolutionary perspective. In general, hybrid zones offer great potential for understanding the mechanisms involved in plant adaptation and speciation. However, it remains the case that for most hybrid zones studied to date only preliminary information is available on these aspects. Greater attention should be focused on plant hybrid zones in the future if their potential to serve as windows on plant adaptation and speciation is to be fully realised.

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Supplementary Materials

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12267/suppinfo:

Table S1. Hybrid zone type, hybrid zone mode (genotypic composition), hybrid fitness, isolating barriers and interspecific gene flow for 137 different species combinations listed in Table 1. (HZ = Hybrid Zone; TZ = Tension Zone; BHS = Bounded Hybrid Superiority zone; F1-DZ = F1 dominated hybrid zone; Pre-Z = Prezygotic; Post-Z = Postzygotic; TRD = Transmission ratio distortion).

Table S2. References for citations listed in Table 1.

Table S3. Number of hybrid zones (HZs) per family, per genus, per life form and geographical region based on hybrid zones listed in Table 1.

Table S4. Hybrid zone type and mode for each taxon combination listed in Table 1. (BHS = Bounded hybrid superiority; TZ = Tension zone).

Table S5. F1 fertility for each taxon combination listed in Table 1.

Table S6. Prezygotic and postzygotic reproductive isolating (RI) barriers between taxon combinations that form hybrid zones listed in Table 1.

Table S7. Level and direction of gene flow between taxa in hybrid zones listed in Table 1.

Table S8. Occurrence of hybrid zones in anthropogenically or naturally disturbed sites for taxon combinations listed in Table 1.