

# Asymmetrical crossing barriers in angiosperms

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Patterns of reproductive isolation between species may provide insight into the mechanisms and evolution of barriers to interspecific gene exchange. We used data from published interspecific hybridization experiments from 14 genera of angiosperms in order to test for the presence of asymmetrical barriers to gene exchange. Reproductive isolation was examined at three life-history stages: the ability of interspecific crosses to produce seeds, the viability of F<sub>1</sub> hybrids, and the fertility of F<sub>1</sub> hybrids. Statistically significant asymmetries in the strength of reproductive isolation between species were detected in all genera and at each of the three life-history stages. Asymmetries in seed production may be caused by a variety of mechanisms including differences in stigma/style lengths, self compatibility and differential fruit abortion. Asymmetries in post-zygotic isolation are probably caused by nuclear–cytoplasmic interactions. Asymmetrical reproductive isolation between plant taxa may have important implications for the dynamics of hybrid zones, the direction of genetic introgression and the probability of reinforcement.

**Keywords:** nuclear–cytoplasmic interactions; gene flow; artificial hybridizations; speciation; reproductive isolation

## 1. INTRODUCTION

Barriers to gene flow between species are often categorized according to whether they reduce the likelihood that gametes will combine to form a viable zygote (pre-zygotic) or reduce the viability or reproductive potential of interspecies hybrids (post-zygotic). In plants, barriers to gene exchange are often divided into pre- and post-pollination mechanisms. Pre-pollination barriers, which are exclusively pre-zygotic, include ecological factors that prevent individuals from different lineages from growing close enough to exchange gametes and reproductive factors that result from genetic differences in flowering times and divergence of floral characters (Levin 1978). Post-pollination isolation may result from pre-zygotic or post-zygotic mechanisms (Snow 1994). Pre-zygotic mechanisms include pollen–pistil or pollen–ovule interactions that manifest themselves as low pollen germination rates, slow pollen tube growth and failure of pollen tubes to penetrate ovule walls; post-zygotic mechanisms include hybrid inviability and hybrid sterility.

Dobzhansky (1936) and Muller (1939) developed what has become the predominant model explaining the evolution of post-zygotic barriers to gene exchange between phylogenetic lineages. This model is conceptually simple. Briefly, assume that a single ancestral diploid population with genotype *aabb* is divided into two daughter populations by an external (pre-pollination) barrier to gene flow. Within one daughter population, a mutation *A* goes to fixation resulting in a uniform population of *AAbb* genotypes. In the second daughter population, a *B* allele goes to fixation resulting in *aaBB* genotypes. The derived alleles are compatible with the ancestral allele at the same locus and with the ancestral alleles at the second locus in both populations. Incompatibilities between the two daughter populations result when the two derived alleles are incompatible (i.e. *A–B* genotypes produce

inviable or sterile phenotypes). In these cases, hybrids between populations will be inviable or sterile thus causing partial or complete reproductive isolation between the populations.

According to the Dobzhansky–Muller model, alleles causing post-zygotic isolation act asymmetrically (Coyne & Orr 1998) since the derived *A* allele is compatible with the ancestral *b* allele but not the derived *B* allele and, conversely, the derived *B* allele is compatible with the ancestral *a* allele but not the derived *A* allele. However, asymmetries in allele action do not imply asymmetries in reproductive isolation (Levin 1978). In fact, if the genes causing reproductive incompatibilities are nuclear and show Mendelian inheritance, then the strength of reproductive isolation between species pairs should be independent of the gender of the species being crossed. In other words, reproductive isolation will be symmetrical in the sense that reciprocal crosses will not differ in their fitness. This is simply because, for species without heterogametic sex determination, like the vast majority of plant species, the nuclear genes that each of the parental species contribute to the F<sub>1</sub> are independent of the gender of the individuals crossed. If nuclear incompatibilities fully explain the evolution of post-zygotic isolation, we would expect no post-zygotic asymmetries between reciprocal crosses.

Chromosomal rearrangements are also recognized as a potentially important mechanism of post-zygotic reproductive isolation in plants (Stebbins 1950, 1958; White 1978; Rieseberg *et al.* 1999). Hybrids formed from crosses involving parents with different chromosome structure may have low fitness because chromosomal deletions, duplications, inversions and rearrangements cause abnormal segregation or recombination during meiosis. Abnormal meiosis may in turn result in gametes with genetic duplications and deficiencies that reduce hybrid fertility. Chromosomal rearrangements share two similarities with Dobzhansky–Muller interactions between nuclear loci. They are expected to evolve through fixation

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Table 1. *The genera (family), number of species, number of pollinations, measures of reproductive isolation and sources of data* (SS, seed or fruit set; VS, viable seeds; VP, F<sub>1</sub> pollen viability. All taxa are species with the exception of *Guizota*, *Heuchera*, *Phlox*, *Potentilla* and *Solanum*, which include 2, 3, 17, 3 and 2 subspecies or varieties, respectively.)

genus (family)	number of taxa	mean number of pollinations	measures of reproductive isolation	source of data
<i>Aphelandra</i> (Acanthaceae)	9	50 <sup>a</sup>	SS <sup>f</sup>	McDade & Lundberg (1982)
<i>Carduus</i> (Compositae)	9	50 <sup>a</sup>	SS, VS and VP	Gremaud (1981)
<i>Cucumis</i> (Cucurbitaceae)	7	15	SS and VP	Singh & Yadava (1984)
<i>Guizota</i> (Compositae)	4	115	SS <sup>b</sup>	Dagne (1994)
<i>Heuchera</i> (Saxifragaceae)	9	27	SS and VP	Wells (1979)
<i>Ipomoea</i> (Convolvulaceae)	9	70	SS <sup>c</sup> and VP	Diaz <i>et al.</i> (1996)
<i>Leucaena</i> 2N (Leguminosae)	12	172	SS and VS	Sorensson & Brewbaker (1994)
<i>Leucaena</i> 4N	4	373	SS and VS	Sorensson & Brewbaker (1994)
<i>Paspalum</i> (Poaceae)	5	5277	VS <sup>d</sup>	Quarin & Norrman (1990)
<i>Phlox</i> (Polemoniaceae)	26	22	SS <sup>e</sup>	Levin (1966)
<i>Potentilla</i> (Rosaceae)	7	12	SS <sup>b,c</sup> and VS <sup>e</sup>	Davidson & Lenz (1989)
<i>Salix</i> (Salicaceae)	6	9	VS	Mosseler (1990)
<i>Silene</i> (Caryophyllaceae)	7	10	SS <sup>b</sup>	Prentice (1978)
<i>Solanum</i> (Solanaceae)	9	30	SS	Grun (1961)
<i>Ulmas</i> (Ulmaceae)	11	900 <sup>a</sup>	VS	Mittempergher & La Porta (1981)

<sup>a</sup> Minimum number of crosses.

<sup>b</sup> Includes only well-developed seeds.

<sup>c</sup> Includes only capsules with seeds.

<sup>d</sup> Includes only hybrid plants that survived until flowering.

<sup>e</sup> Divided by the mean of the outcrossed intraspecific cross of parents.

<sup>f</sup> Divided by the crossing success of the seed parent.

<sup>g</sup> Number of seeds produced.

of different rearrangements in geographically isolated populations (Hedrick 1981; Lande 1985) and, because the two parents contribute equally to the chromosomal composition of hybrids, reproductive isolation is expected to be symmetrical.

Reproductive isolation resulting from either Dobzhansky–Muller interactions or chromosomal rearrangements is expected to be symmetrical. However, some evidence has suggested that, at least for pre-zygotic isolation, asymmetries may be common, having been reported in *Drosophila* (Kaneshiro 1980), salamanders (Arnold *et al.* 1996), leaf beetles (Funk 1998) and several plant species (e.g. Grant 1954; Lewis & Crowe 1958; Rick 1963; Kiang & Hamrick 1978; Prentice 1978). If asymmetries between lineages occur commonly, then reproductive isolation may be caused by mechanisms other than fixation of incompatible nuclear alleles or chromosomal rearrangements. The primary objective of this investigation was to assess the prevalence of asymmetrical post-pollination isolation barriers between plant species. We analysed data from previously reported crossing studies involving species from 14 genera of plants. By analysing data from many genera we hoped to identify general patterns that typify the nature of reproductive isolation in plants.

## 2. METHODS

### (a) Data

Data sets were located by searching (i) the Biological Abstracts database for the reciprocal crosses of keywords, experimental taxonomy and interspecific hybridization, (ii) the indexes for the past 30 years of the *American Journal of Botany*, *Botanical Journal of the Linnean Society*, *Rhodora* and *Systematic*

*Botany*, and (iii) the references of these papers and texts by Stebbins (1950) and Grant (1981). We only included data sets if they reported reciprocal crosses from a minimum of four species and reported quantitative measures of compatibility. Our search for data, although somewhat haphazard, was not biased with regard to findings—all data sets located and meeting the above criteria were included in our analyses. Our objective was to gather sufficient data from a range of plant families to enable identification of broad patterns of isolation. These data do not represent an exhaustive search of the available data. The data we analysed can be found in electronic Appendix A available on The Royal Society's Web site.

The data came from studies that all used similar methods. In general, parental plants were grown in a common environment, either a greenhouse or outdoor garden and were hand pollinated by applying pollen from one species to the stigma of a second species. All pollinations were conducted without competition, meaning that pollen from only a single species was placed on each stigma. Measures of crossing success included fruit set, seed set, the proportion of seeds that were viable (F<sub>1</sub> seed viability) and F<sub>1</sub> pollen viability (table 1). Seed viability was generally assayed by germination tests in common environmental conditions and F<sub>1</sub> pollen viability was assayed by pollen staining. The number of species in each data set ranged from 4 to 26. Between 9 and 1000 pollinations were performed for each interspecific cross. We excluded crosses between species with different levels of ploidy when data on the ploidy of the species were available. Thus, the genus *Leucaena* was split into diploids and tetraploids for analysis. Polyploid speciation, which is a common form of speciation in plants (Lewis 1980; Ramsey & Schemske 1998), may be due to mechanisms distinctly different from speciation that does not involve changes in ploidy (Levin 1978). Although asymmetry in crossing barriers may be important during polyploid speciation, we did not

Table 2. Number of species pairs that exhibited significant asymmetries in reproductive isolation

(The numbers of reciprocal crosses analysed are followed by the numbers of species crossed in parentheses. The number of crosses exhibiting significant asymmetries are presented for  $p < 0.05$  and  $p < 0.001$ . The dashes indicate that data on the success of reciprocal crosses were not available. A complete listing of species names and crosses are available in electronic Appendix A.)

genus	seed or fruit set			viable seeds			F <sub>1</sub> pollen viability		
	crosses	$p < 0.05$	$p < 0.001$	crosses	$p < 0.05$	$p < 0.001$	crosses	$p < 0.05$	$p < 0.001$
<i>Aphelandra</i>	32 (9)	6	0	13 (7)	6	3	—	—	—
<i>Carduus</i>	8 (8)	3	2	8 (8)	4	0	8 (8)	1	0
<i>Cucumis</i>	15 (7)	5	0	—	—	—	2 (3)	1	1
<i>Guizotia</i>	6 (4)	5	3	—	—	—	—	—	—
<i>Heuchera</i>	29 (9)	9	8	—	—	—	8 (6)	3	3
<i>Ipomoea</i>	9 (7)	2	1	—	—	—	5 (7)	3	3
<i>Leucaena</i> (2N)	63 (11)	33	16	63 (11)	21	17	—	—	—
<i>Leucaena</i> (4N)	6 (4)	5	3	6 (4)	5	4	—	—	—
<i>Paspalum</i>	—	—	—	8 (5)	3	2	—	—	—
<i>Phlox</i>	29 (20)	9	0	—	—	—	—	—	—
<i>Potentilla</i>	21 (7)	14	11	21 (7)	13	8	—	—	—
<i>Salix</i>	6 (4)	2	0	—	—	—	—	—	—
<i>Silene</i>	11 (6)	4	0	—	—	—	—	—	—
<i>Solanum</i>	35 (9)	12	3	—	—	—	—	—	—
<i>Ulmus</i>	23 (11)	22	19	—	—	—	—	—	—
total	293 (116)	132	37	132	60	38	23	8	7

include crossing studies conducted on species that differed in chromosome numbers in this review.

### (b) Definitions of reproductive isolation and statistical analysis

Reproductive isolation was defined separately for each of three life-history stages: seed/fruit set (hereafter referred to as seed set), F<sub>1</sub> seed viability and F<sub>1</sub> pollen viability. Seed set may be affected by both pre-zygotic and post-zygotic interactions, whereas F<sub>1</sub> seed and pollen viability will be affected solely by post-zygotic interactions. Reproductive isolation was calculated as one minus the proportion of successful crosses and was calculated for each stage independently. Reproductive isolation at seed set was defined as one minus the proportion of pollinations that produced seeds or fruits, reproductive isolation due to seed inviability was defined as one minus the proportion of viable seeds produced, and reproductive isolation due to F<sub>1</sub> pollen inviability was defined as one minus the proportion of viable pollen grains produced on F<sub>1</sub> plants. Likelihood ratio  $\chi^2$ -tests were used to test whether the success of a cross was significantly affected by which species was the pollen parent and which species was the seed parent. Separate tests were conducted for each of the stages at which isolation was measured.

We had few data on the phylogenetic independence of crosses within each genus. Lack of phylogenetic independence may be a problem because species related through evolutionary history are not statistically independent (Felsenstein 1985). Studies examining the relationship between reproductive isolation and genetic distance (Coyne & Orr 1989, 1998; Sasa *et al.* 1998) have corrected for phylogenetic dependence by averaging data across bifurcations of a phylogenetic tree, thereby producing a set of evolutionarily and statistically independent data points (Felsenstein 1985). We did not use this approach for the primary reason that developing phylogenetically independent data points requires well-resolved, species-level phylogenies, which were generally not available for the genera we examined.

### 3. RESULTS

Significant asymmetries in the strength of reproductive isolation between species pairs were found within all genera and at all three stages of isolation (table 2). The success of reciprocal crosses was significantly affected by which species was the seed parent in 45% of 293 species pairs for the seed or fruit set, 45% of 132 species pairs for seed viability and 35% of 23 species pairs for pollen viability. The prevalence of asymmetries ranged from 22 out of 23 crosses for viable seed production among *Ulmus* species to two out of nine crosses for seed production among *Ipomoea* species. Moreover, approximately half of the asymmetries significant at  $p < 0.05$  were also significant at  $p < 0.001$  (67 out of 132). Because we did not correct the data for phylogenetic dependencies multiple asymmetries in some genera may have resulted from crosses involving a single species or lineage. However, regardless of the phylogenetic relationship among species within genera, the occurrence of significant asymmetries indicates that at least some asymmetrical reproductive isolation is present in all 14 genera.

With the exception of *Aphelandra* and *Potentilla*, the above data were not corrected for differences in the receptivity or fecundity of the parental taxa. However, parental taxa may differ in their potential to set seed or in the proportion of viable seeds they produce under experimental conditions. In such cases, asymmetry in reproductive isolation may be caused by the genetics of the parental species or interactions between parental species and the experimental environment rather than interactions between the genomes of the two species (McDade & Lundberg 1982). In order to determine whether differences in the reproductive success of parental taxa was a common cause of asymmetry we reanalysed the data from the four studies that included data on the

success of intraspecific crosses (*Heuchera*, *Leuceana*, *Phlox* and *Salix*) after adjusting for differences in the parental taxa that produced seed. For these analyses we calculated compatibility as the seed set of the interspecific cross divided by the average seed set from intraspecific crosses (McDade & Lundberg 1982). The results from these analyses were consistent with the results from the original analyses; 50 significant asymmetries were detected out of 133 species pairs using the compatibility index whereas 58 significant asymmetries were detected in the original analyses. Thus, although differences in the fecundity of parental taxa may be responsible for some of the specific asymmetries we detected, they do not appear to be primarily responsible for the overall pattern of asymmetrical reproductive isolation observed.

#### 4. DISCUSSION

Asymmetries in reproductive isolation among plant species appear to be common and taxonomically widespread. The reproductive isolation between species pairs in the data we analysed depended upon which of the parental species was the pollen parent and which was the seed parent for at least some species pairs in all genera and at all stages of isolation. These stages included seed and fruit set, which are probably affected by both pre- and post-zygotic mechanisms and F<sub>1</sub> seed and pollen viabilities, which are only affected by post-zygotic mechanisms. Our results suggest that mechanisms other than the fixation of incompatible nuclear alleles (the Dobzhansky–Muller model) or chromosomal rearrangements are commonly responsible for reproductive isolation between angiosperm species.

Various pre-zygotic mechanisms that may account for asymmetries in the seed and fruit set have been proposed, including differences in style length (Kiang & Hamrick 1978; Sorensson & Brewbaker 1994), mating system, i.e. self-compatible versus self-incompatible (e.g. Lewis & Crowe 1958) and differential fruit abortion (Levin 1978; Howard *et al.* 1998). Although our data do not allow a rigorous evaluation of the relative importance of these mechanisms, the patterns of the asymmetries in some genera are consistent with these mechanisms. For example, asymmetrical incompatibilities between diploid species of *Leuceana* were attributed in part to difference in style length (Sorensson & Brewbaker 1994). In addition, four of the studies (*Aphelandra*, *Heuchera*, *Leucaena* and *Ulmus*) reported data on the seed set of crosses between self-compatible and self-incompatible species (see electronic Appendix A). Twenty-three out of the 39 crosses between self-compatible and self-incompatible species exhibited significant asymmetries in seed set; the self-compatible seed parent had greater seed set than the self-incompatible seed parent in 18 (78%) of these crosses, which is consistent with self-incompatible species being less receptive to foreign pollen than self-compatible species.

Asymmetries in pre-mating isolation among animal taxa are most often attributed to differences in mate choice behaviours that evolve in response to sexual selection (Arnold *et al.* 1996). The evolutionary forces acting on plant gametes during reproduction may be similar to the evolutionary forces acting on traits that experience

sexual selection in animals, i.e. variation in reproductive success may occur because of pollen competition for access to ovules or because seed parents differentially exclude pollen phenotypes (Willson 1979, 1990; Lyons *et al.* 1989; Arnold 1994). If sexual selection does act on plant gametes during reproduction it is plausible that the evolutionary dynamics of pre-zygotic isolation may be similar in plants and animals. Some of the theories that have been developed for explaining the evolution of pre-zygotic isolation in animal systems may be fairly easy to test in plants. For example, the Kaneshiro (1980) hypothesis of asymmetrical mate choice predicts that males from an ancestral taxon will mate with females from a derived taxon, but not vice versa. This prediction could be tested by performing crosses between species with established phylogenetic relationships. The expectation would be that pollen from ancestral lineages would be able to fertilize ovules from derived populations but that pollen from derived lineages would be unable to fertilize ovules from the ancestral lineage.

In contrast to relatively frequent reports of asymmetry in pre-zygotic isolation among both plant and animal taxa (reviewed in Levin 1978; Coyne & Orr 1998), few previous investigations have reported significant asymmetry in post-zygotic isolation. A notable exception is the cytoplasmically inherited bacteria *Wolbachia* that affect the viability of interspecific hybrids in several insect genera (reviewed in Werren 1997). Asymmetry in post-zygotic asymmetrical incompatibility between plant species may result from one of several types of nuclear–cytoplasmic interactions (Grun 1976; Levin 1978).

One of the most thoroughly investigated nuclear–cytoplasmic interactions in plants involves cytoplasmic male sterility elements and nuclear genes that restore male fertility (Grun 1976; Saumitou-Laprade *et al.* 1994). Cytoplasmic male sterility elements may have been responsible for the asymmetries that we found in F<sub>1</sub> pollen viability if male sterility in one maternal lineage was not restored in the hybrid nuclear background. Asymmetry may also result from divergent evolution of nuclear and cytoplasmic genes coding for proteins that interact in photosynthesis or respiration (Michaelis 1954; Levin 1978; Wu *et al.* 1999). Genetic analyses have shown that this is the basis of hybrid chlorosis and inviability in some *Oenothera* hybrids (Van der Meer 1974). A third cause of nuclear–cytoplasmic asymmetries may be transposable elements, which are abundant in many plant genomes. The activity of at least some transposable elements can be suppressed by maternally inherited factors (Engels 1989) and, thus, hybrids with a seed parent from a population that has not evolved with a transposable element may experience greater transposon activity, which may in turn cause genetic disruptions that reduce hybrid fitness. Transposable elements have been implicated as the cause of hybrid dysgenesis in *Drosophila* and have recently been shown to exhibit increased activity in a newly formed rice hybrid (Liu & Wendel 2000). Finally, it is possible that some plant lineages contain cytoplasmic parasites that are detrimental to undefended hosts, similar to the action of *Wolbachia* in insect genera, although we know of no reports of this in plants.

Nuclear–cytoplasmic incompatibilities that cause asymmetry in reproductive isolation may evolve in a fashion

similar to the nuclear incompatibilities predicted by the Dobzhansky–Muller model. Assume that a single evolutionary lineage is divided into two daughter lineages by an external barrier to gene flow. One of the daughter lineages is then invaded by a cytoplasmic parasite (e.g. a cytoplasmic male sterility-like element) or selfish nuclear element (e.g. a transposable element). The host then evolves defences that mitigate the parasite's deleterious effects but do not eliminate the parasite. Crosses between individuals from different populations may then produce hybrids with reduced defence that are exposed to the negative effects of the parasite. For example, seed parents from a population with 'cytoplasmic parasites' and 'nuclear defence' will produce hybrids more vulnerable to the parasite (because the hybrids only inherit half the nuclear defence elements). In contrast, seed parents from a population with 'nuclear parasites' and cytoplasmically inherited defence will produce hybrids that are not susceptible to the parasite. It is, of course, also possible that the changes in the nuclear and cytoplasmic genes occur within a single lineage. This model is conceptually similar to the Dobzhansky–Muller model, but differs in two ways. First, this model explicitly involves both nuclear and cytoplasmic elements and, second, reproductive isolation between divergent populations may be asymmetrical.

No significant asymmetries were detected in over half the crosses that we analysed. This lack of asymmetry, although not unequivocal evidence for Dobzhansky–Muller interactions between nuclear genes or chromosomal rearrangements, is consistent with the expectations of these mechanisms. Moreover, even in those crosses that exhibit strong asymmetries it is possible (or perhaps even probable) that these types of nuclear interactions contribute to isolation. Nevertheless, the presence of significant asymmetrical incompatibility suggests that mechanisms other than epistatic interactions between nuclear loci or chromosomal rearrangements contribute to genetic barriers to interspecific gene exchange. In these cases the forces responsible for the evolution of asymmetrical incompatibilities may play an important role in the evolution of reproductive isolation.

Regardless of the specific underlying genetic mechanisms, asymmetrical reproductive isolation may affect the evolutionary dynamics of partially isolated lineages upon secondary contact. Theoretical models of reinforcement generally assume that reciprocal crosses between lineages will be equally compatible, i.e. the success of reciprocal crosses between members of different lineages is symmetrical (Felsenstein 1980; Liou & Price 1994; Kelly & Noor 1996). However, Servedio & Kirkpatrick (1997) showed that asymmetries in gene flow due to asymmetrical migration between partially isolated populations may greatly reduce the probability that reinforcement evolves. Assuming that asymmetrical migration and asymmetrical crossability have similar effects on gene flow then, upon secondary contact, lineages that exhibit asymmetries in reproductive isolation may be more likely to introgress than evolve reinforcement. If this is true, then the probability of particular modes of speciation may depend upon the nature of the genetic interactions underlying reproductive isolation; reinforcement will be less important for taxa in which nuclear–

cytoplasmic interactions are a key component in reproductive isolation.

Asymmetries may also alter the dynamics of introgression (Ferguson *et al.* 1999). Upon secondary contact, populations with asymmetries in reproductive isolation may produce dynamics similar to those expected from populations with symmetrical barriers to gene exchange but different population sizes (Rieseberg 1995). In these situations, introgression is likely to be directional with genes moving predominantly from a more discriminating species into a less discriminating species. Unidirectional introgression may in turn affect the probability of hybridization contributing to phenotypic and genotypic variation in natural populations (e.g. Stebbins 1959), the proportion of parental genomes that are found in hybrid species and differential cytoplasmic versus nuclear introgression in hybrid zones (Rieseberg 1995).

An important caveat to our findings is that the data we analysed do not include several potentially important stages of isolation. In particular, pre-pollination mechanisms, including differences in flowering time and floral morphology that result in differential pollinator specificity, have often been thought to be among the most important barriers to gene exchange between plants (Levin 1978; Grant 1981; Schemske & Bradshaw 1999) and these were not included in this study. In addition, the pollinations from which these data came were conducted without pollen competition, although in natural conditions pollen competition may be important in determining the probability of hybrid formation (Emms *et al.* 1996; Arnold 1997). Finally, these data did not include the fitness of F<sub>1</sub> hybrids grown in natural environments. Even if hybrids are completely viable and fertile in common garden experiments, hybrids may have low fitness in natural conditions because they are poorly adapted to the physical habitats of the parent species (Schluter 1998), have low mating success due to pollinator discrimination (Schemske & Bradshaw 1999) or suffer from hybrid breakdown upon backcrossing (e.g. Breeuwer & Werren 1995; Edmands 1999). However, these limitations do not detract from our finding that the strength of post-pollination barriers to gene exchange between plant species often depends on which of the species served as the pollen parent and which served as the seed parent. It would be of interest to know whether asymmetry in reproductive isolation in animals is as common as it appears to be in plants or if there is something particular about the barriers to gene exchange among plant taxa that results in a higher incidence of asymmetry in reproductive isolation.

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