

## THE ROLE OF HOMOPLOID HYBRIDIZATION IN EVOLUTION: A CENTURY OF STUDIES SYNTHESIZING GENETICS AND ECOLOGY<sup>1</sup>

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While homoploid hybridization was viewed as maladaptive by zoologists, the possibility that it might play a creative role in evolution was explored and debated by botanists during the evolutionary synthesis. Owing to his synthetic work on the ecological and genetic factors influencing the occurrence and effects of hybridization, G. Ledyard Stebbins' contributions to this debate were particularly influential. We revisit Stebbins' views on the frequency of hybridization, the evolution of hybrid sterility, and the evolutionary importance of transgressive segregation, introgression, and homoploid hybrid speciation in the context of contemporary evidence. Floristic surveys indicate that ~10% of plant species hybridize, suggesting that natural hybridization is not as ubiquitous as Stebbins argued. There is stronger support for his contention that chromosomal sterility is of greater importance in plants than in animals and that selection drives the evolution of hybrid sterility. Stebbins' assertions concerning the frequent occurrence of transgressive segregation and introgressive hybridization have been confirmed by contemporary work, but few studies directly link these phenomena to adaptive evolution or speciation. Stebbins proposed a mechanism by which chromosomal rearrangements partially isolate hybrid lineages and parental species, which spurred the development of the recombinational model of homoploid speciation. While this model has been confirmed empirically, the establishment of reproductively independent hybrid lineages is typically associated with the development of both intrinsic and extrinsic reproductive barriers. We conclude by reflecting on outcomes of hybridization not considered by Stebbins and on possible future research that may extend our understanding of the evolutionary role of hybridization beyond Stebbins' legacy.

**Key words:** disturbance; hybrid; homoploid speciation; introgression; invasion; selection; Stebbins; transgressive segregation.

In the early years of the modern evolutionary synthesis (1924–1950), interspecific hybridization was generally considered to be rare and of little evolutionary significance, a view shaped by researchers focusing on animal systems with strong interspecific reproductive barriers. However, ever since Linnaeus, botanists have been describing natural hybrids (Roberts, 1929). By the time of the synthesis, botanists, especially G. Ledyard Stebbins and Edgar Anderson, had established analytical methods for identifying hybrids and were putting them to use. Interspecific hybridization was found to be common in plants and apparently more common than in animals. As a consequence of these observations, Stebbins developed and promoted the view that hybridization created variation relevant to evolutionary change, a hypothesis that represents one of his most important contributions to the evolutionary synthesis.

In this review, we discuss Stebbins' work and views on the role of hybridization in evolution. He considered hybridization's role in the context of both polyploid and homoploid hybridization,

but here we focus on the latter (see the centennial review by Soltis et al. [2014] for a treatment of polyploid hybridization). We first review what is known about the frequency of hybridization in plants and the origin and evolution of hybrid sterility. We then examine studies of how hybridization augments genetic variation within populations, the role of introgressive hybridization as a means of gene exchange among species, and the process of homoploid hybrid speciation. We summarize the current state of these areas of hybridization research and assess how Stebbins' views hold up in the light of contemporary data and theory. We conclude by considering the frequency and evolutionary importance of different outcomes of hybridization, including several not considered by Stebbins, and discuss promising research directions that may extend our understanding of the role of hybridization in evolution.

### (1) FREQUENCY OF HYBRIDIZATION

The opinions of early evolutionary biologists on the prevalence of hybridization differed substantially between zoologists, such as Mayr (1942) and Dobzhansky (1953), who rarely observed hybrid formation, and botanists such as Stebbins (1950) who considered it ubiquitous: "Occasional hybridization between recognizable species ... is the rule in flowering plants" (Stebbins, 1959, p. 234). He did, however, suspect that certain groups of plants were more susceptible to hybridization than

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others (Stebbins, 1959). Of course, these workers were influenced by the organisms and regional floras and faunas familiar to them. Do modern surveys support the view that hybridization is much more common in plants than in animals? And, is hybridization nearly ubiquitous among plants as Stebbins declared?

Although the ubiquity of hybridization across plants was accepted into the 1990s (Raven, 1976; Whitham et al., 1991), surveys of floras suggest that this is not the case, with estimates of the proportion of plant species that hybridize ranging from ~3% in the Concord Township flora in Massachusetts (Mayr, 1992; Mallet, 2005) to ~25% for the flora of the British Isles (Stace, 1975, 1997; Mallet, 2005), with an overall frequency of 0.09 hybrid combinations per nonhybrid species (Whitney et al., 2010a). However, these may be underestimates because floristic treatments are limited in time and space. Hybridization appears to be especially common between crop plants and their progenitors (Ellstrand, 2003) and in invasive species (Ellstrand and Schierenbeck, 2000). Natural hybridization has been reported in 22 of the world's 25 most important crops (Ellstrand, 2003). And although overall proportions are not known, Schierenbeck and Ellstrand (2009) list 35 examples of hybridization preceding plant invasions. Newly developed evolutionary genomic methods make it possible to detect both contemporary and ancient hybridization events (Durand et al., 2011; Lai et al., 2012) and their implementation should allow more accurate estimates of the frequency of hybridization both currently and in the past.

The other important observation from floristic surveys is that hybridization is unevenly distributed taxonomically (Ellstrand et al., 1996), with hybrids reported in approximately 40% of families and 16% of genera in the most comprehensive analysis (Whitney et al., 2010a). There is a strong phylogenetic signal ( $\lambda$ ) in the propensity of plant genera to hybridize:  $\lambda = 0.93$  based on an ordinal level phylogeny, where 0 = no phylogenetic signal and 1 = complete phylogenetic dependence (Whitney et al., 2010a).

Current estimates of the proportion of animal species that hybridize range from 1 to 10%, and in contrast to plants, no taxonomic bias in hybridization has been detected (Schwenk et al., 2008). Thus, hybridization is still considered more common in plants than animals, and Stebbins was correct that some plant groups are associated with a higher propensity for hybridization. However, he may have overstated the ubiquity of hybridization in plants.

## (2) HYBRID STERILITY

Hybrid sterility is a common form of postzygotic reproductive isolation in plants. Like other reproductive barriers, hybrid sterility reduces gene flow between divergent populations and may thereby contribute to the formation of species and to their coexistence in sympatry. Stebbins' views on the genetic basis and evolution of hybrid sterility (Stebbins, 1958) have largely been confirmed by current work (reviewed by Rieseberg and Blackman [2010]), although many new details about the molecular changes underlying hybrid sterility are now known.

**Sources of hybrid sterility**—Both gene incompatibilities and chromosomal rearrangements can cause hybrid sterility. The relative importance of these two factors remains controversial because of practical difficulties in distinguishing between genic and chromosomal sterility and also because the establishment

of rearrangements that strongly reduce fitness in heterozygotes (i.e., underdominance) is considered unlikely, except in small, inbred populations (Hedrick, 1981). One widely used approach to discriminate between genic and chromosomal sterility involves duplication of the hybrid genome. Genome doubling provides an exact copy of each chromosome in hybrids and thus is expected to restore pairing and fertility in chromosomally divergent hybrids, but to have no effect on incompatibilities caused by genes (Dobzhansky, 1933). Stebbins (1958, p. 234) noted that fertility is typically restored by genome doubling in plants, although not in animals, leading him to assert that "chromosome structure has been far more important in plants than in animals as a source of hybrid sterility," a conclusion that has been supported by modern genetic and genomic analyses (Coyne and Orr, 2004). Unfortunately, a convincing explanation for this difference remains elusive.

Despite the emphasis of the early botanical literature on chromosomal sterility, Stebbins (1958) recognized that gene incompatibilities played an equally important role, noting that while gametic sterility was typically caused by chromosomal rearrangements, sterility affecting diploid tissue is typically genic. This generalization may not be entirely correct because, to our knowledge, all hybrid sterility genes cloned to date in plants contribute to haploid sterility (Rieseberg and Blackman, 2010). An exception is cytoplasmic male sterility, which can affect both haploid and diploid tissues. We expect that most examples of diploid sterility will be genic as well, but as far as we are aware, the genetic factors underlying such sterility have not yet been characterized using molecular genetic approaches.

**The evolution of hybrid sterility**—Another important issue concerns the evolutionary forces underlying the origin of hybrid sterility. Stebbins (1958, p. 193) argued that "the available data on species hybrids leads us inevitably to the hypothesis that selection plays an important role in the origin of the inviability and sterility barriers which separate species." While we agree with this assertion on theoretical grounds, there is surprisingly little direct evidence for the action of divergent selection on sterility genes that have been cloned to date (Rieseberg and Blackman, 2010), although a recent study showed that selection on a copper tolerance locus in *Mimulus* has indirectly caused a hybrid incompatibility allele to occur at high frequency due to genetic hitchhiking (Wright et al., 2013). Likewise, there is evidence from theoretical (Kirkpatrick and Barton, 2006; Yeaman, 2013) and empirical (Lowry and Willis, 2010; Fishman et al., 2013) studies that chromosomal rearrangements minimizing recombination can be favored by adaptation in heterogeneous environments. However, this process seems unlikely to result in fixed differences between species, especially for strongly underdominant rearrangements. Possibly, female-meiotic drive accounts for the latter (de Villena and Sapienza, 2001), although see Fishman and Saunders (2008).

**Rates of hybrid sterility evolution**—Stebbins observed that chromosomal sterility appears to evolve more rapidly in annual than perennial herbs. He suggested that annual populations are more likely to experience greater fluctuations in population size than perennial ones. In his view, this would facilitate the establishment of sterility factors through "random fixation" or via stronger ecological selection on "linked genes with a particularly high adaptive value" (Stebbins, 1958, p. 198).

Stebbins' observations about the tempo of hybrid sterility evolution have recently been assessed with modern comparative

methods in three groups within the family Asteraceae. The first such study examined two clades in the genus *Coreopsis* and showed that, as suggested by Stebbins, the transition to an annual life history greatly accelerates the evolution of hybrid sterility (Archibald et al., 2005). In a second study (Owens and Rieseberg, 2014), annual–annual crosses were shown to exhibit a much higher mean sterility than perennial–perennial crosses in both *Helianthus* sunflowers (90% vs. 41%) and the subtribe Madiinae (93% vs. 55%). In all three groups, cytogenetic studies indicate that chromosomal rearrangements are more common in annual than perennial species, suggesting that the evolution of chromosomal-based sterility is driving this pattern. However, Stebbins' hypothesis about potential demographic differences between annual and perennial populations is unlikely to explain this pattern, as *Helianthus* annual sunflowers exhibit very high effective population sizes making extreme bottlenecks unlikely (Strasburg et al., 2011). An alternative mechanism proposed for this difference is that there are more meiotic events per generation in annuals, which likely accelerates chromosomal mutation rates.

Interestingly, the most rapid rate of hybrid sterility evolution in plants was recently reported within perennial circumpolar species of the genus *Draba* (Grundt et al., 2006). However, genetic studies indicate that the sterility in these species is mainly caused by gene incompatibilities. Thus, Stebbins' (1958) conclusion about the more rapid evolution of chromosomal sterility in annuals still holds, although his explanation for this pattern is likely incorrect.

### (3) HYBRIDIZATION AS A SOURCE OF PHENOTYPIC NOVELTY

“In organic evolution, as in many other affairs, both natural and human, the decisive influence is wielded not by the orthodox majority, but by a significant, progressive minority” (Stebbins, 1959, p. 236).

Stebbins (1959, p. 231) defined hybridization as “crossing between individuals belonging to separate populations which have different adaptive norms.” Individuals from the  $F_1$  generation of an interspecific hybrid cross tend to have low fertility and mostly display intermediate trait values. However, transgressive trait variation, defined as phenotypic trait values that extend beyond the range of traits observed in parental populations, is common in both first and later generation hybrids. Stebbins was aware of cases of transgressive variation in plants (e.g., increased flower size *Nicotiana* (Smith, 1953). Building on these observations, Stebbins noted that if this type of extreme variation was exposed to a new environment, natural selection would have the opportunity to form new races or subspecies. He further notes that “by possessing some degree of reproductive isolation from both of their parental species, may form the beginning of an entirely new species” (p. 246), a process that we discuss later. Thus, transgressive trait variation appears to have been viewed by Stebbins as a critical step in the establishment of new hybrid lineages.

We now have a more complete understanding of the genetic basis of transgressive traits and the rate at which they occur (deVicente and Tanksley, 1993; Rieseberg et al., 1999; Stelkens and Seehausen, 2009). Although rare recessive alleles, chromosome number variation, epistasis, and overdominance may account for a small proportion of transgressive phenotypes, quantitative trait loci (QTL) studies have shown that “complementary gene

action” provides a more general explanation for the genetic basis and observed rate of transgressive segregation. The idea is that if parental lines are composed of sets of fixed differences that have opposing and additive effects, in the  $F_2$  generation recombination can increase the number of QTL with the same trait direction within an individual, resulting in hybrids with trait values exceeding either parental value (see Table 2 in Rieseberg et al., 2003).

Overall, transgressive traits are quite common in plants. In a survey (Rieseberg et al., 1999) of 579 plant traits (domesticated and wild), 58% were reported to be transgressive. Most were morphological traits, but others were traits associated with fecundity, biochemistry, physiology, life history, and tolerance to biotic/abiotic factors. However, among crosses between wild populations, only 38% of traits were transgressive (and all studies yielded at least one transgressive trait), whereas 92% of crosses between inbred domesticated lines yielded transgressive traits. This difference makes sense given that complementary gene action requires fixed differences between lines, which are most likely to accumulate in inbred lines. In a more recent study on transgressive variation in hybrids of wild plant and animal species, ~36% of plant hybrids were reported as transgressive, and a significant positive correlation was found between transgression frequency and genetic distance (Stelkens and Seehausen, 2009). More distantly related species are expected to accumulate a larger number of fixed differences, resulting in greater transgression. Thus, transgressive traits are a relatively common outcome of hybridization, especially in crosses between inbred lines or genetically diverged species. Later, we will discuss Stebbins' proposed link between transgressive variation, novel ecological habitat and selection.

### (4) INTROGRESSIVE HYBRIDIZATION

Hybridization is most commonly observed in the context of hybrid zones or hybrid swarms, where a gradient or mixture of parental and hybrid individuals are observed in sympatry. Stebbins wrote repeatedly that the formation of these populations was likely promoted by disturbance (see below). This observation was first made by botanist Edgar Anderson (1949), whose work on “introgressive hybridization” appears to have strongly influenced Stebbins. They envisioned the process beginning with the formation of  $F_1$  hybrids between well-established species. The following generation would be dominated by backcrossing to parental genotypes due to the high frequency of parentals relative to  $F_1$ 's, rather than due to  $F_1 \times F_1$  mating. They also viewed backcrosses as more likely to survive and reproduce than true  $F_2$ 's due to optimal combinations of characters already having been shaped by selection in the parental species. Continued mating of the most-fit backcross genotypes (i.e., those with the highest survivorship and fecundity) with parental genotypes was recognized as a potentially important means for the exchange of genes between species. Oddly, Stebbins did not view this process as “gene flow” and generally ignored the literature on this topic (Ellstrand, 2014). Stebbins, and in a more conservative manner, Anderson, envisioned hybrid genetic variants becoming a permanent feature of the population, altering the genetic structure of the population, and potentially fostering new adaptations due to the occurrence of novel gene combinations. “By introgressive hybridization elements of an entirely foreign genetic adaptive system can be carried

over into a previously stabilized one, permitting the rapid reshuffling of varying adaptations and complex modifier systems. Natural selection is presented...with segregating blocks of genic material belonging to entirely different adaptive systems” (Anderson and Stebbins, 1954, pp. 378–379).

**In search of adaptation**—The detection of genetic introgression between species using molecular markers is now routine (Rieseberg et al., 1990; Sweigart and Willis, 2003). However, detecting evidence of hybrid variants being directly involved in important ecological adaptations is considerably more challenging. Two of the most complete examples are briefly described below.

One such example comes from the Louisiana irises, which have been an important study system since Anderson’s 1949 monograph *Introgressive Hybridization*. Arnold and colleagues, following in the tradition of Anderson’s classic work, have used a combination of molecular genetic and ecological studies to link hybrid variation to increased fitness in a hybrid habitat (Arnold, 2004; Martin et al., 2005, 2006). Their most relevant study focused on hybrids of *Iris fulva* and *Iris brevicaulis*, the former being more flood-tolerant and occurring in bayous and swamps, the latter occurring in drier hardwood forest. Hybrid and parental genotypes were planted in two plots along a gradient from dry forest to associated swamp, representative of the habitat where hybrid swarms are found. Field results showed that *I. fulva* and backcrosses to *I. fulva* are the most flood-tolerant as expected. Most importantly, several introgressions from *I. fulva* were shown to increase the survivorship of *I. brevicaulis* backcross plants in flood conditions. This scenario reflects the type of adaptive gene-exchange Anderson and Stebbins hypothesized was possible via introgressive hybridization.

Another example, in which the genes underlying adaptive trait introgression were identified, comes from studies of two ragwort species in the United Kingdom (Kim et al., 2008). Here, two linked *CYCLOIDEA*-like genes, which underlie the development of ray flowers in the sunflower family, were derived via natural introgression from a diploid outcrossing species (*Senecio squalidus*) into a tetraploid selfing species (*S. vulgaris*) that lacked ray flowers. Experimental studies indicate that the ray-flowered form of *S. vulgaris* is more attractive to pollinators and has a higher outcrossing rate, which may contribute to the ongoing spread of the introgressed locus (Abbott and Irwin, 1988), although outcrossing is associated with the cost of passing only half the genes to offspring relative to selfed offspring (Abbott et al., 1998).

While there are several other well-documented examples of adaptive trait introgression in plants (e.g., Whitney et al., 2006, 2010b), the kinds of detailed ecological-genetic studies required to provide convincing documentation remain rare.

**Fluctuation not fixation**—Another approach that can provide insight into patterns of selection and stability of hybrid populations is long-term monitoring of the distribution of phenotypes and genotypes. Stebbins recognized the potential value of studying the temporal dynamics of hybrid zones, and in collaboration with K. Daly, he collected an 8-yr morphological data set from a sunflower population near Davis, California. The population occurs along an ecological gradient from wetter to drier conditions and was likely created by disturbance due to road construction. The population contains individuals exhibiting traits associated with *Helianthus annuus*, known for occupying

wet, disturbed sites, with *H. bolanderi*, found on drier, less-disturbed sites, and with intermediate phenotypes. Intermediate phenotypes were found to persist throughout the 8-yr study and comprised the majority of the eastern half of the population. Stebbins and Daly also found that the eastern and western halves exhibited different patterns of change over the 8 years: the eastern half fluctuated, with the hybrid index declining toward more *H. bolanderi*-like phenotypes until the final year of study when the hybrid index was estimated as more *H. annuus*-like than in the first year of study. The western half of the population was more stable and exhibited a bimodal distribution of *H. annuus*-like and *H. bolanderi*-like individuals (Stebbins and Daly, 1961).

This hybrid population was revisited 38 yrs later (Carney et al., 2000). Both parental and intermediate types were found to remain in the population, although genetically pure parentals were rare. In the eastern half of the population, morphological variation was reduced and appeared to have stabilized around an *H. annuus*-like phenotype. However, genotypic data showed that these eastern individuals possess a highly introgressed genome. Similar discord between morphological and molecular patterns of hybridization has been reported in *Senecio*, where hybrid *S. squalidus* exhibits mostly *S. chrysanthemifolius*-like phenotypic characteristics rather than *S. aethnensis*-like despite a stronger molecular pattern of hybrid intermediacy (Brennan et al., 2012), implying strong ecological selection on hybrids for parental-like trait values.

The western half of the *Helianthus* hybrid population still showed a bimodal distribution of phenotypes, but shifted from a bias toward *H. bolanderi* individuals to one favoring *H. annuus*. Although molecular marker estimates of hybridity also show a bimodal distribution of genotypes, this distribution is considerably more centralized and the “pure” parental phenotypes are genetically introgressed by 25–30%. This half of the population exhibits a pattern consistent with a “tension zone” in which intermediate hybrid phenotypes are continually negatively selected, but are replaced each generation by offspring from crosses between plants with parental-like phenotypes. In the region surrounding this hybrid population, *H. bolanderi* appears to be declining in abundance, whereas populations of *H. annuus* are increasing. It would be useful to perform a landscape genomic study of the region to test whether any introgressed genotypes have been successful at colonizing new populations, invading or co-occurring with other *H. annuus*. Although there has been an overall shift toward *H. annuus*, this hybrid zone population has maintained parental and intermediate types over a 50 yr period, supporting Stebbins’ view that such populations may be reservoirs of variation.

**Genetic variation in hybrid populations**—Stebbins predicted that introgressive hybridization should increase the “variation pattern” of hybrid populations. Although this seems intuitively obvious, such a pattern has not been observed when comparing genetic variation of homoploid hybrid species relative to their parental species (*Helianthus*, *Iris*, *Pinus*, and *Stephanomeria*; Rieseberg, 1997). However, in hybrid lineages that have become reproductively isolated from parental species, perhaps genetic variation has been eroded by bottlenecks during the origin of new hybrid lineages, as well as by the processes of colonization of novel habitat and selection. Here we update this survey and expand it to include comparisons of parental and hybrid populations, in which hybridization is still

ongoing (Table 1). Indeed, populations associated with contemporary hybridization are more consistently associated with higher estimates of genetic diversity, relative to parental populations, than in taxa associated with homoploid hybrid speciation. Note that the only taxon not exhibiting this pattern (*Liparis*) exhibits no genetic variability in one parental species. It is also worth highlighting that a recent comparison of various molecular marker types (allozymes, indels, EST-derived SSRs, and random SSRs) detected differences in diversity estimates among the different kinds of markers, but the pattern of low to equal genetic diversity in the hybrid species was consistent across marker type (Brennan et al., 2012). Finally, a similar pattern has been noted in some plant invaders; hybrid populations of *Raphanus*, *Secale*, and *Viola* exhibited higher genetic variation than populations of the parental species (Ellstrand and Schierenbeck, 2000), supporting the hypothesis that hybridization increases genetic variation.

*Plant invasions*—Hybridization is hypothesized to play a role in the success of invading species (Stebbins, 1985; Abbott, 1992; Ellstrand and Schierenbeck, 2000; Hovick and Whitney, in press). The diversity of segregants in a hybrid population is expected to increase the probability of extreme or novel traits, providing the raw material for adaptation, and potentially enabling the colonization of novel habitats far beyond the range of origin (Stebbins, 1985). Fixed heterosis and the purging of genetic load in bottlenecked colonizing populations are also proposed to increase the fitness and invasiveness of hybrid populations (Ellstrand and Schierenbeck, 2000).

Stebbins (1985) considered the role of hybridization and invasion in the context of polyploidy and recognized that polyploidization due to both hybridization between “previously isolated and adaptively differentiated populations” (p. 830) within a species (autopolyploidy) and between species (allopolyploidy) could result in an invasive lineage. There is indeed a strong association between polyploidy and invasiveness, with a recent meta-analysis reporting that circa 67% of invasive plant hybrids reported in the literature are polyploid hybrids (Hovick and Whitney, in press). Here we are interested in the 37% of hybrid plant invaders that do not have a polyploid ancestry.

Given the prominent role of disturbance and the possibility of multiple introductions in invasion, it may not be surprising to find invasion associated with hybridization. Is hybridization coincident to invasion or does hybridization supply critical genetic variation to fuel invasion? Meta-analysis showed that naturally occurring hybrids were more fecund and larger than their most invasive parental species; however, no difference was detected in early generation synthetic hybrids, suggesting that selection likely plays a role in increasing the invasive characteristics of hybrids (Hovick and Whitney, in press). On the other hand, no increase in invasive species was found in plant families that are more prone to hybridization (Whitney et al., 2009). Thus, hybridization itself is not a good predictor of which plant taxa are likely to become problematic invaders.

Most of these published reports of invasive plant hybrids involved interspecific hybridization (Abbott, 1992; Ellstrand and Schierenbeck, 2000). However, there is increasing interest in the role of intraspecific hybridization in invasiveness, in which admixture between genetically differentiated populations of a single species appears to have contributed to successful invasions (e.g., Lavergne and Molofsky, 2007; Rius and Darling, 2014).

TABLE 1. Survey of indices of genetic diversity for parental (P) and hybrid groups in five taxonomic groups associated with homoploid hybrid (HH) speciation and four taxonomic groups in which hybrid populations or swarms (H) form. Marker type is indicated in parentheses following genus name.  $H_e$  = expected heterozygosity,  $A$  = mean number of alleles per locus,  $\pi_t$  = total nucleotide diversity,  $\theta_w$  = nucleotide polymorphism

Taxon		Indices of diversity	
<i>Helianthus</i> (allozymes)		$H_e$	$A$
P	<i>annuus</i>	0.065	1.3
P	<i>petiolaris</i>	0.123	1.5
HH	<i>anomalous</i>	0.069	1.2
HH	<i>deserticola</i>	0.022	1.1
HH	<i>paradoxus</i>	0.027	1.1
<i>Iris</i> (allozymes)		$H_e$	$A$
P	<i>brevicaulis</i>	0.167	1.7
P	<i>fulva</i>	0.122	1.4
P	<i>hexagona</i>	0.152	1.6
HH	<i>nelsonii</i>	0.134	1.5
<i>Pinus</i> (nuclear sequence)		$\pi_t$	$\theta_w$
P	<i>tabuliformis</i>	0.0070	0.0092
P	<i>yunnanensis</i>	0.0046	0.0060
HH	<i>densata</i>	0.0065	0.0098
<i>Stephanomeria</i> (allozymes)		$H_e$	$A$
P	<i>exigua</i>	0.098	2.6
P	<i>virgata</i>	0.109	2.6
HH	<i>diegensis</i>	0.082	2.3
<i>Senecio</i> (SSRs, indels and allozymes)		$H_e$	$A$
P	<i>aethnensis</i>	0.41	3.53
P	<i>chrysanthemifolius</i>	0.41	3.39
H	Sicilian hybrid	0.49	4.12
HH	<i>squalidus</i>	0.39	2.23
<i>Carpobrotus</i> (allozymes)		$H_e$	
P	<i>acinaciformis</i>	0.406	
P	<i>edulis</i>	0.328	
H	hybrid swarm	0.420	
<i>Epidendrum</i> (chloroplast sequence)		$\pi_t$	
P	<i>calanthum</i>	0.0008	
P	<i>cochlidium</i>	0.0005	
P	<i>schistochilum</i>	0.0002	
H	hybrids	0.009	
<i>Eucalyptus</i> (SSRs)		$H_e$	$A$
P	<i>aggregata</i>	0.715	6.33
P	<i>rubida</i>	0.794	9.66
H	hybrid populations	0.858	9.84
<i>Liparis</i> (allozymes)		$H_e$	$R_s$
P	<i>makinoana</i>	0.319	2.20
P	<i>kumokiri</i>	0	1.00
H	hybrids	0.084	1.5

<sup>1</sup> Rieseberg et al., 1991; <sup>2</sup> Arnold et al., 1990; <sup>3</sup> Gao et al., 2012; <sup>4</sup> Gallez and Gottlieb, 1982; <sup>5</sup> Brennan et al., 2012; <sup>6</sup> Suehs et al., 2004; <sup>7</sup> Vega et al., 2013; <sup>8</sup> Field et al., 2011; <sup>9</sup> Chung et al., 2005.

In this context, it is worth noting that the majority of successful invasions appear to involve multiple origins (Dlugosch and Parker, 2008), although it is unclear whether this association is due to propagule pressure or intraspecific admixture or both.

One of the best-documented examples of the successful colonization of a hybrid plant species involves the Oxford ragwort, *Senecio squalidus*, which was originally derived from a hybrid zone between *S. aethnensis* and *S. chrysanthemifolius* on Mount Etna, Sicily, Italy (James and Abbott, 2005). Herbarium and literature records indicate that the hybrid *Senecio* germplasm was introduced to the Oxford Botanical Garden in the early part of the 18th century. In 1794 it was reported as a garden escape in Oxford and over the next two centuries it spread across most of the UK, aided initially by the railway system (Harris, 2002; James and Abbott, 2005). Oxford ragwort is distinctive from its parental species and Sicilian hybrids in terms of quantitative traits and allelic frequencies (Brennan et al., 2012), implying that selection on hybrid variation likely contributed to its successful colonization of the United Kingdom.

**Ecological predictions**—Throughout his writing on introgressive hybridization, Stebbins repeatedly referenced the potential effects of two ecological factors:

(1) *Habitat diversity provides niches for establishment of introgressed individuals*—Stebbins and his contemporaries recognized that variation in the ecological conditions in which hybrids occur would affect their survival and capacity to reproduce (i.e., fitness). As a consequence, there is considerable interest in how the fitness of hybrids compares to that of parental individuals in parental, intermediate, and novel environments. Results from experiments carried out in the field or greenhouse indicate that hybrid fitness is highly variable, ranging from reduced to equivalent to greater fitness than parental genotypes (Arnold and Hodges, 1995). However, hybrids are rarely uniformly more or less fit than their parental genotypes across all habitats (Lexer et al., 2003b). Rather, in most instances, hybrid fitness is contingent on the genotype of the hybrids (i.e.,  $F_1$ 's,  $F_2$ 's, backcrosses) and the environment in which fitness was tested (genotype  $\times$  environment interactions; Johnston et al., 2001; Miglia et al., 2005; Campbell et al., 2008; Arnold et al., 2012; Ross et al., 2012). The relative fitness of hybrids also has been shown to vary temporally due to environmental fluctuations (Arnold and Martin, 2010), leading to correlated changes in the frequency of hybrids over the same time period (e.g., Heiser, 1979). These results confirm and reinforce Stebbins' prediction that hybrid fitness should vary according to habitat.

More recently, progress has been made in several systems toward identifying QTL or candidate genes underlying fitness differences in natural hybrid zones. In some instances, QTL analyses have been performed on segregating populations that were transplanted into the field (e.g., Lexer et al., 2003a; Martin et al., 2006), whereas in other instances, mapping has exploited naturally occurring hybrids (e.g., Gardner et al., 2000; Lindtke et al., 2013). The results from the field-based QTL studies are similar to those obtained from laboratory or greenhouse experiments—traits associated with habitat adaptation or adaptive phenotypic differentiation appear to be mainly controlled by QTL with additive, dominant, or overdominant effects, whereas epistatic QTL are more likely to influence survivorship and fertility.

Another exciting development has been the identification and analyses of candidate genes putatively underlying fitness variation in hybrid zones. In snapdragon, for example, candidate

genes underlying natural variation in flower color were functionally validated and shown to exhibit exceptionally steep geographic clines in natural hybrid zones—a pattern suggestive of strong divergent natural selection (Whibley et al., 2006). In a number of other systems, a genome scan approach has been taken, in which genes that show the sharpest geographic and/or genomic cline are viewed as likely targets of divergent natural selection (Gompert and Buerkle, 2011; Hamilton et al., 2013). However, as far as we know, the candidate genes identified via these approaches have yet to be functionally validated.

(2) *Disturbed areas are more likely to experience high levels of introgression*—Stebbins argued that disturbance will often be an important promoter of hybridization. Disturbance can profoundly alter fitness relationships in plant communities, potentially causing parental species to be maladapted, degrading ecologically based reproductive barriers, and opening niche space for hybrids. While many contemporary hybrid swarms appear to have formed as a result of anthropogenic disturbances, Anderson and Stebbins (1954) suggested that similar forms of disturbance were likely common in the past as well and might even be responsible for bursts of speciation observed in the paleobotanical record. Although the latter claims are too speculative for our taste, the Anderson and Stebbins hypothesis that disturbance facilitates hybrid establishment is often-cited and influential; for example, restoration ecologists have considered the potential benefit of using a hybrid mixture, putatively containing greater variation, to re-establish unpredictable disturbed sites (Lesica and Allendorf, 1999). While studies that directly assess and quantify the role of disturbance remain relatively rare, recent work has begun to reveal some of the biological mechanisms underlying the positive association between disturbance and hybridization. For example, Lamont et al. (2003) surveyed 262 populations of *Banksia hookeriana* across its geographic range in western Australia, identifying putative hybrids with *B. prionotes* based on intermediate morphology (confirmed to have intermediate molecular hybrid indices). They found no putative hybrids in undisturbed sites, whereas putative hybrids were detected in 11% of disturbed sites (defined as roadways, abandoned mine pits, railway lines, firebreaks). Furthermore, a detailed analysis of flowering across a disturbance gradient revealed that disturbance increases and lengthens the period of flowering for both species, whose flowering phenologies rarely overlap in undisturbed sites, increasing the overlap in flowering between the two species by 10–54 $\times$  (across season).

##### (5) HOMOPLOID HYBRID SPECIATION

Stebbins' interest in speciation was, in part, motivated by the insight that by evolving reproductive isolation, species are able to coexist in the same habitat, thereby facilitating the accumulation of biodiversity. In plants, hybridization with an increase in ploidy (allopolyploidy) is associated with speciation much more commonly than homoploid hybridization, in part due to reproductive isolation between hybrids and parents of different ploidy (Soltis and Soltis, 2009; Soltis et al., 2014). It is less obvious how hybrid lineages that do not experience a change in ploidy might achieve reproductive isolation (homoploid hybrid speciation). At the time of the publication of Stebbins' seminal monograph *The Variation and Evolution of Plants* (1950), his views on introgression were well developed, whereas his work on the evolution of reproductively isolated homoploid hybrid species was just beginning.

In his book, he noted that hybridization can result in “types that are actually new” and provided examples of putative hybrid species (e.g., *Delphinium*), but at the time offered only vague possibilities of the reduction of mutation suppressors and increase in structural changes of hybrids as possible factors in establishing new homoploid hybrid species.

**Recombinational model of homoploid hybrid speciation**—By the end of the 1950s, Stebbins’ contributions to this area had increased substantially, largely inspired by empirical work on hybridization involving two genera of grasses, *Elymus* and *Sitanion* (Snyder, 1951; Stebbins, 1957b). Briefly, Stebbins managed to generate two F<sub>1</sub> hybrids between *E. glaucus* × *S. jubatum*. While the F<sub>1</sub> plants were greater than 99.99% sterile, a single viable seed was produced, apparently through backcrosses with *E. glaucus*. The resulting backcrossed (BC<sub>1</sub>) plant had high seed fertility and exhibited almost complete reproductive isolation from the original parents. To account for the rapid evolution of reproductive isolation between the homoploid hybrids and their parental lineages, Stebbins developed what is now termed the recombinational model of homoploid hybrid speciation based on the sorting of chromosomal rearrangements that differentiated the parental species. In the simplest model, a partially sterile hybrid is generated between parental species that differ by two independent chromosomal rearrangements (Stebbins, 1957a). This hybrid produces new homozygous recombinant types of the rearrangements via segregation and recombination. The recombinants are fertile within the hybrid line but at least partially sterile with both parents. Stebbins (1959) later recognized that genic incompatibilities can cause similar patterns of segregation. If these recombinant hybrid lines can reproduce and become numerous enough to form a stable population, they have the potential to become a new hybrid species. This basic model was developed more formally and named by Verne Grant (1958) and continues to provide a basis for theoretical and empirical treatments of the topic (Grant, 1958, 1981; Templeton, 1981; Rieseberg, 1997; Buerkle et al., 2000).

Is it possible to corroborate the recombinational model of homoploid hybrid speciation (Rieseberg, 1997; Gross and Rieseberg, 2005)? Comparative genetic mapping can reveal chromosomal rearrangements between the parental species and extant hybrid species, an observation consistent with their role in hybrid speciation. Theoretically, the greater the number of independent chromosomal or genic incompatibilities, the greater the likelihood that a newly established hybrid lineage will be at least partially reproductively isolated from its parental species and from other hybrid lineages derived from the same two parents. While increased numbers of incompatibilities does not enhance the likelihood or speed of hybrid establishment (McCarthy et al., 1995), it does increase their evolutionary independence (Buerkle et al., 2000). Simulating the early stages of hybrid speciation through careful crossing experiments, such as those performed by Stebbins in *Elymus*, can further demonstrate the potential role of such rearrangements in the establishment and isolation of a new hybrid species. Lastly, comparing the genomes of artificially synthesized hybrids to established hybrid species can provide insight on whether novel structural variants in the hybrid species were likely to have arisen via de novo mutations in early-generation hybrids or whether they have arisen after hybrid speciation.

The best empirical support for the recombinational model comes from *Helianthus*, where two widespread sunflowers, *Helianthus annuus* and *H. petiolaris* are known to have given rise

to at least three diploid hybrid species: *H. anomalus*, *H. deserticola*, and *H. paradoxus* (Rieseberg, 1991). Comparative genetic mapping indicates that the hybrid sunflowers differ by 7–12 chromosomal rearrangements from their parental species, and that two-thirds of these appear to have arisen de novo in the hybrid lineages (Lai et al., 2005). Is there any evidence that these rearrangements contribute to sterility between parental and hybrid species? In support of this, the majority (9 of 11) pollen sterility QTL were found to map to chromosomal break-points (Lai et al., 2005), although two sterility QTL were detected on collinear chromosomes, suggesting that genic incompatibilities also contribute to sterility. Lastly, crossing studies revealed that the hybrid species are strongly isolated from each other and from their parental species by hybrid sterility barriers, providing evidence of their evolutionary independence.

A caveat is that these conclusions were based on low-resolution maps (300–1000 markers per species), so ongoing work is aimed at improving estimates of the number and position of chromosomal rearrangements and pollen sterility QTL using ultra-high density sequence-based maps. In addition, by comparing the extent of karyotypic divergence in early-generation synthetic hybrids relative to the established hybrid species, we hope to better estimate the importance of karyotypic evolution in the early stages of homoploid hybrid speciation.

**Mating system and homoploid hybrid speciation**—Stebbins also considered the potential role of mating system on the outcome of early generations of hybrid mating. Considering simple scenarios of complementary gametic lethals, he showed how selfing of F<sub>1</sub> hybrids could greatly increase the probability of yielding fertile hybrid lines that are (semi) sterile with both parental lines relative to backcrossing between F<sub>1</sub> and parental lines, the most likely crosses to occur in an outbreeding population. This general idea was further championed by Verne Grant in several papers and books (Grant, 1958, 1966, 1981) and is most often attributed to him. A theoretical (simulation) investigation of the role of selfing on hybrid speciation has confirmed Stebbins’ earlier conjectures (McCarthy et al., 1995). Interestingly, selfing species are also known to produce higher levels of transgressive traits, likely due to the high levels of fixed differences required for complementary gene action (see above), further predisposing selfing lineages to possible hybrid speciation. Yet, we are aware of only one well-supported example of homoploid hybrid speciation in a selfing plant species (*Senecio eboracensis*; Lowe and Abbott, 2004). One possible explanation for this mismatch between theory and data are that there may be lower rates of natural hybridization among selfing lineages in the first place (Rieseberg, 1997).

**Role of extrinsic isolation in homoploid hybrid speciation**—Although Stebbins’ most influential contribution to the study of homoploid hybrid speciation may have been the recombinational model, which focused on the evolution of intrinsic postzygotic isolation, he continued to emphasize the importance of unoccupied ecological niches or disturbance/rapid environmental change for the persistence and spread of a new hybrid species: “If two or more related species exist in a stable unoccupied habitat to which all are well adapted, and if no unoccupied ecological niches are available, hybridization will be kept down to a minimum” and “If...the same species meet in an environment that is marginal for them, and particularly if the environment is changing in such a way that new ecological niches are being opened up...the selective action of

the new environment will tend to increase certain hybrid derivatives" (Stebbins, 1959, p. 248). Furthermore, he predicted that the combination of hybridization and selection could result in hybrid lineages that could spread into novel habitats "selection on hybrid derivatives can in some instances continue for many generations... and can be accompanied by their spread to regions far removed from the original site of hybridization."

However, interest in the role of ecological factors waned in the latter half of the 20th century and the recombinational model of homoploid hybrid speciation dominated the literature until the early 2000s when there was a resurgence in the interest of the role of ecology in hybrid speciation (Gross and Rieseberg, 2005; Abbott et al., 2010). Although there are few examples of homoploid hybrid speciation for which the role of ecology has been rigorously tested, a well-developed framework now exists to formally test whether ecology plays the role envisioned by Stebbins. This framework includes testing whether (1) ecological divergence contributes to reproductive isolation, (2) new combinations of genes/traits that allow the hybrid to survive in an ecologically divergent habitat are under selection in the new habitat, (3) these traits can be recreated by experimental hybridization, and (4) selection for these traits is strong enough to allow divergence in the face of gene flow from parental populations, which is likely during the early stages of hybrid speciation (Gross and Rieseberg, 2005).

In 79% of the proposed cases of homoploid hybrid speciation (Table 2), the habitat of the hybrid species is reported to be divergent from the habitat of parental species, likely contributing to reproductive isolation. For instance, *Pinus densata* is distributed along a different range of latitude and altitude than both of its progenitors (Wang et al., 2001). In *Helianthus*, each of the three diploid hybrid species discussed above are ecologically divergent from the parental species, occurring in harsher ecological conditions and more restricted geographic ranges in the

southwestern United States: *H. anomalus* occurs on sand dunes, *H. deserticola* occurs in deserts, and *H. paradoxus* is restricted to a handful of brackish salt marshes. A series of transplant experiments involving parentals and hybrids in hybrid habitat tested the role of extrinsic isolation in homoploid hybrid speciation. Results indicate that ecological conditions in the hybrid habitat appear to contribute to isolation from the parental species: Parentals exhibit zero survival upon exposure to the saline *H. paradoxus* habitat. In *H. anomalus* habitat an initial experiment using transplanted juveniles suggested fitness of parentals and hybrids are similar (Ludwig et al., 2004); however, more recent experiments tracking seedling emergence in the habitat of *H. anomalus* showed lower fitness of parentals (zero to low seed emergence) relative to hybrids (Donovan et al., 2010). In contrast, experiments in the habitat of *H. deserticola* have shown that parentals have equal or greater fitness than hybrids (Gross et al., 2004; Donovan et al., 2010). Therefore, there is evidence for home-site advantage of hybrids in *H. paradoxus* and *H. anomalus*, suggesting that adaptation to their novel habitat is likely to have played a role in the formation of these hybrid species. The lack of home-site advantaged *H. deserticola* to date could be an artifact of the year or site in which experiments were conducted; such experiments are inherently limited by our ignorance of the ecological conditions under which a hybrid species originally evolved.

To examine the potential role of transgressive traits in the ecological divergence of the hybrid species, Rosenthal et al. (2002) compared phenotypes of individuals from parental populations and each of the three hybrid species to a large hybrid backcrossed population (BC<sub>2</sub>) of *H. annuus* × *H. petiolaris*. Of 40 phenotypic traits examined, 27–37% of traits were found to be transgressive in the established hybrid species and 62–67% traits were transgressive in the synthetic hybrids, relative to the parental species. Moreover, 67% (*H. deserticola*), 85% (*H. anomalus*), and 100%

TABLE 2. Putative examples of homoploid hybrid speciation in flowering plants. Any hybrid species that is known to be associated with ecological divergence (differ in habitat type, timing of flowering, or pollinators) is indicated. If available, any evidence of genetic incompatibility is indicated using the following codes: A = crossing experiments indicate reduced viability between hybrid and parental populations, B = chromosome rearrangements identified through cytological methods, C = chromosome rearrangements identified through comparative mapping, D = genic incompatibility supported through QTL mapping.

Taxon	Ecological divergence	Genetic incompatibility	References
<i>Argyranthemum sundingii</i>	habitat	A	Brochmann et al., 2000
<i>Castilleja christii</i>	habitat and pollinator	unknown	Clay et al., 2012
<i>Collinsia tinctoria</i>	habitat	B	Baldwin et al., 2011
<i>Helianthus anomalus</i>	habitat	A, C, D	Rieseberg, 1991; Lai et al., 2005
<i>Helianthus deserticola</i>	habitat	A, C, D	Rieseberg, 1991; Lai et al., 2005
<i>Helianthus paradoxus</i>	habitat	A, C, D	Rieseberg, 1991; Lai et al., 2005
<i>Iris nelsonii</i>	habitat and pollinator	no rearrangements found	Arnold, 1993; Taylor et al., 2013
<i>Nicotiana</i> spp.	unknown	unknown	Clarkson et al., 2010
<i>Ostryopsis intermedia</i>	habitat	unknown	Liu et al., 2014
<i>Peaonia</i> spp.	habitat	unknown	Ferguson and Sang, 2001; Pan et al., 2007
<i>Penstemon clevelandii</i>	pollinator	unknown	Wolfe et al., 1998
<i>Picea purpurpea</i>	habitat	unknown	Sun et al., 2014
<i>Pinus densata</i>	habitat	unknown	Wang et al., 2001
<i>Pinus funebris</i>	habitat	unknown	Ren et al., 2012
<i>Pinus takahasii</i>	habitat	unknown	Ren et al., 2012
<i>Senecio eboracensis</i>	temporal and pollinator	A	Lowe and Abbott, 2004
<i>Senecio squalidus</i>	habitat	unknown	Abbott et al., 2009; Brennan et al., 2012
<i>Stephanomeria diagenensis</i>	habitat	A	Gallez and Gottlieb, 1982; Sherman and Burke, 2009
<i>Yucca gloriosa</i>	none (sympatric with parentals in disturbed habitat)	unknown	Rentsch and Leebens-Mack, 2012



(*H. paradoxus*) of the traits were within the phenotypic trait range observed in the synthetic hybrid line, showing that these extreme hybrid traits could have been generated by early-hybrid generations (Rieseberg et al., 2003). Importantly, investigation of the genetic architecture of mineral uptake and survivorship traits in a *H. annuus* × *H. petiolaris* BC<sub>2</sub> population grown in the *H. paradoxus* habitat detected QTL with effects in opposing directions for survivorship and for all mineral ion uptake traits with more than one detected QTL. This finding supports the role of complementary gene action in the evolution of traits critical to survival in harsh saline environment.

Is there evidence that the combinations of genes/traits that allow the hybrid to survive in a novel habitat are under selection in the new habitat? Selection gradients or differentials for ecologically important traits in artificial, early-generation hybrid populations between the parental species, grown in the habitats of *H. paradoxus* and *H. deserticola* were mostly in the predicted direction for generating phenotypes of the hybrid species (Lexer et al., 2003b; Gross et al., 2004). However, in the habitat of *H. anomalus*, selection gradients differed between artificial hybrid lines, and selection toward the hybrid species' phenotype was only partly supported (Ludwig et al., 2004).

Finally, we are left to disentangle the relative roles that genetic incompatibilities and ecological divergence may have played in the evolution of homoploid hybrid species. Although Stebbins did not test the relative strength of genetic and ecological factors, his view was that the combination of both isolating mechanisms was important for hybrid speciation. This seems to be the case in *Helianthus*, as models of fertility selection (genetic incompatibility) and phenotypic selection (for ecological divergence) showed that both types of selection jointly best predict marker parentage in the genomes of the three homoploid hybrid species (Karrenberg et al., 2007). Phenotypic selection did correctly predict marker parentage for significantly more cases and was associated with higher multiple logistic regression coefficients than fertility selection, suggesting phenotypic selection may have been stronger during speciation (or is currently stronger). Overall, these results suggest that both types of selection were likely involved in the formation of three homoploid hybrid sunflower species. Data generated for 19 cases of confirmed homoploid hybrid speciation based on molecular marker data appear to agree with this view (Table 2): Ecological divergence of the hybrid species from parental species has been observed in 16 cases (uninvestigated in one case, not found in one case), and evidence of chromosomal or genic incompatibility was detected in six of seven cases where it was investigated.

## (6) CONCLUSION: THE ROLE OF HYBRIDIZATION IN EVOLUTION—BEYOND STEBBINS

After mutation and selection, Stebbins viewed hybridization as (one of) the next most important evolutionary forces (Stebbins, 1950). However, most contemporary evolutionary biologists consider hybridization to be a kind of gene flow, rather than an independent force. While gene flow (including both intra- and interspecific genetic exchange) is widely recognized as an important evolutionary mechanism known to influence the effects of mutation, drift, and selection (see Ellstrand, 2014). Stebbins said surprisingly little about the role of gene flow within species. Nonetheless, many of his assertions about the role of hybridization in evolution also apply broadly to our understanding of how gene flow might impede or accelerate adaptation and speciation.

Although Stebbins was among the first to recognize that hybridization could have a range of outcomes, including the merger of species, the development and transfer of adaptations through introgressive hybridization, and the origin of new homoploid hybrid species, he failed to discuss other potential outcomes such as the formation of stable hybrid zones and the reinforcement of premating reproductive barriers. Like many other botanists of his day, his comments about the role of hybridization in evolution emphasized creative outcomes involving introgressive hybridization and hybrid speciation. As we have discussed throughout this article, there is now strong evidence for each of the outcomes Stebbins proposed (as well as for those he did not mention). On the other hand, far less progress has been made toward ordering their importance.

Theoretical studies suggest that, in the absence of an open habitat for hybrids, the formation of stable hybrid zones is the most common outcome of hybridization, followed by the transfer of adaptations (Buerkle et al., 2003). Note that these outcomes need not be exclusive—adaptations can be transferred across stable hybrid zones. In contrast to hybrid zone stability and adaptive introgression, homoploid hybrid speciation is infrequent in the absence of a hybrid habitat. Hybrid speciation does become much more common if there is an open habitat available for hybrids, but it still is rarer than the other two outcomes. Indeed, of all the proposed cases of homoploid hybrid speciation (Table 2), the critical link between hybrid phenotypes and reproductive isolation (Schumer et al., 2014) has only been shown in *Helianthus*. Until similar evidence is available for other proposed cases, we consider homoploid hybrid speciation to be rare. Likewise, speciation by reinforcement is believed for theoretical reasons to be uncommon (Barton, 2013; Servedio et al., 2013).

Empirical data appear to largely accord with theory. Numerous examples of apparently stable hybrid zones and adaptive trait introgression have been reported in plants, but convincing examples of homoploid hybrid speciation are rare. On the other hand, examples of reinforcement continue to be found (Hopkins and Rausher, 2011), so perhaps it is more important than suggested by theory. Andrew and Rieseberg (2013) recently detected a possible molecular signature of reinforcement in an incipient dune species of sunflower. If this putative signature can be validated, we might have a more rapid means for estimating the importance of reinforcement in natural populations of plants and animals.

Stebbins (1950, 1959) emphasized the importance of the genetic variation generated by introgressive hybridization for populations to explore new peaks of adaptation (sensu Wright, 1932). Evolution from standing genetic variation continues to be an important theme in evolutionary research (Barrett and Schluter, 2008; Rius and Darling, 2014), although it is not clear how much of this standing variation derives from hybridization. Nor is there strong support for Wright's shifting balance theory among contemporary evolutionary biologists. Hybrid variation likely does play an important role in purging genetic load found in rare or colonizing populations (Ellstrand and Schierenbeck, 2000; Peischl et al., 2013), but this possibility does not appear to have been considered by Stebbins or his contemporaries.

In the future, we expect that the widespread application of genomic data will allow us to more precisely estimate the frequency of hybridization in plants both currently and in the past. This information will allow us to more confidently identify the ecological and evolutionary factors that affect the propensity of

species to hybridize, assess the impact of hybridization on diversification rates in plants, and determine the frequency of the different outcomes of hybridization discussed. We also may be able to address the fundamental question: Is strict allopatric speciation rare in plants? That is, have most plant species experienced one or more episodes of homoploid hybridization during their recent evolutionary history?

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