Research article

Patterns of hybridization in plants

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ABSTRACT

Hybridization plays an important role in the evolution of many taxonomic groups, but large-scale phylogenetic patterns of hybridization are poorly known. Here, we investigate patterns of hybridization in vascular plants. Our dataset included 282 families, 3212 genera and $\approx$ 37,000 species accounts from eight regional floras covering continental Europe, two island regions, and parts of North America and Australia. Interspecific hybrids were common in the wild, occurring in 40% of families and 16% of genera, with an overall frequency of 0.09 hybrids per nonhybrid species. Taxon species richness explained a large amount of variation in the number of hybrids, but taxon bias (study effort) did not. We accounted for species richness in calculating hybridization propensities, and found that both families and genera differed in hybridization propensity. Hybridization propensity of a given group was generally consistent across regions (with the exception of Hawaii), suggesting that hybridization behavior may be determined more by intrinsic properties of a group than by environmental conditions. We found evidence of a strong phylogenetic signal ($\lambda = 0.93$) in hybridization propensity as hybrids were not uniformly distributed across orders of vascular plants. Characterization of the hybridization behavior of groups should lead to increased predictive power regarding their traits and evolutionary trajectories, and will allow comparative tests of the traits driving differences in hybridization propensity.

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Introduction

Hybridization is a phenomenon increasingly recognized as important in the evolution of plants, animals, and fungi (Gross and Rieseberg, 2005; Mallet, 2007; Schwenk et al., 2008; Mavarez and Linares, 2008; Giraud et al., 2008; Paun et al., 2009; Soltis and Soltis, 2009). Among many other potential and demonstrated effects, hybridization can result in new species of the same ploidy level (e.g., Rieseberg et al., 2003; Gompert et al., 2006) or different ploidy levels (e.g., Cronn and Wendel, 2004), the transfer of adaptive traits between species (e.g., Whitney et al., 2006, 2010; Campbell et al., 2009), and, in general, the "release" of genetic constraints on phenotypic evolution (Kalisz and Kramer, 2008). Some have even argued that hybridization is more important than mutation in generating genetic novelty within populations (Stebbins, 1959; Knobloch, 1972). Furthermore, hybridization can have major impacts on third parties not involved in hybridization *per se*; e.g., hybridization can mediate the spread of parasites such as *Wolbachia* to new hosts (Raychoudhury et al., 2009). Given its important role, understanding which groups of organisms are prone to hybridization and why are critical issues.

In plants, hybridization has long been considered widespread, but estimates of its prevalence can vary dramatically among regions and sources. Mallet (2005) used data from Mayr (1992) and Stace (1975, 1997) to estimate that 3.2% and 25.0% of plant species are involved in hybridization in the floras of Concord, Massachusetts and Great Britain, respectively. An alternate methodology counts hybrids rather than hybridizing parental species; here, "hybrid" refers to a hybrid type (or hybrid combination) derived from a unique combination of two parental species. Using this methodology, Ellstrand et al. (1996) recorded 1320 vascular plant hybrids when examining 12,033 species accounts across five regional floras, from which one can estimate a hybrid frequency of 0.11 hybrids per nonhybrid species. The data on which these hybridization estimates are based are entirely drawn from the United States and northern Europe, suggesting that wider sampling may be needed to adequately characterize patterns of hybridization.

Moving from a geographic to a taxonomic perspective, it has long been accepted that major groups of plants hybridize to different degrees (Focke, 1881 in Stebbins, 1959; Grant, 1981; Arnold, 1997). However, rigorous tests that control for factors such as opportunity (species richness of potential mates within a group) and taxon bias (differential scientific attention paid to different groups) are few. For example, Rieseberg and Wendel (1993) complied 165 case studies of introgression in plants and

noted that 85% of their cases involved dicot species, leading others to conclude that dicots hybridize at a higher frequency than monocots (Arnold, 1997). However, large differences in the relative species richness of dicots and monocots (Stevens, 2009) make this conclusion suspect. It is also unclear how stable (or consistent) hybridization behavior of a group is across different regions. For example, for the British flora, Stace (1975) reports that hybrids are rare in the Lamiaceae relative to the Rosaceae, but this pattern is apparently reversed in the California flora (Hickman, 1993). Better estimates of patterns of hybridization across taxa and regions will allow comparative analyses to sort through mechanistic explanations of why hybridization might vary in prevalence across groups and regions.

Here, we provide the largest survey to date of the frequency and distribution of naturally generated plant hybrids, examining ≈ 37,000 species accounts from 3212 genera and 282 families of vascular plants. Data are compiled from eight regional floras, taking advantage of a > 200 year history of careful attention to hybridization in floristic treatments (Stebbins, 1959). We account for opportunity for hybridization as well as potential taxon bias in study effort. We ask: (1) how common is plant hybridization, and how are recorded instances of hybridization distributed across regions? (2) Does the amount of observed hybridization increase with taxon species richness and/or with study effort? After accounting for these factors, do taxa differ in hybridization propensity? (3) Do taxa behave consistently across regions with respect to hybridization propensity? And, (4) does hybridization propensity exhibit phylogenetic signal?

Methods

Extent of hybridization

To characterize the extent of hybridization across vascular plant families, we analyzed eight floras generally following the methods of Ellstrand et al. (1996) and Whitney et al. (2009) (see details below). Floras included four North American regions: the Great Plains of the U.S. (Great Plains Flora Association, 1986), the Intermountain Region of the western U.S. (Cronquist et al., 1972–2005), the Northeastern U.S. (Magee and Ahles, 1999), and California (Hickman, 1993). In addition, we surveyed two island groups (British Isles: Stace, 1997; Hawai'i: Wagner et al., 1999 and Palmer, 2003) as well as Europe (Tutin et al., 1964–1980) and the state of Victoria, Australia (Walsh and Entwisle, 1994–1999). Note that the Intermountain flora (Cronquist et al., 1972–2005) has eight planned volumes; our analysis used the seven extant volumes.

For each vascular plant family present in each flora, the numbers of interspecific hybrids and the numbers of non-hybrid species were determined. For counting purposes, we follow Ellstrand et al. (1996) in defining a "hybrid" as a hybrid type derived from a unique combination of two parental species. Thus, in each flora, each pair of hybridizing species was counted as generating a single hybrid, even if there was evidence that the pair had hybridized multiple times. Occasionally, parental species generating hybrids were themselves hybrid in origin, thus the hybrid count included hybrid types such as allopolyploid–diploid crosses. To accommodate recent changes in phylogenetic hypotheses, we analyzed all floras at the generic level and reassigned those genera (with their associated counts of species and hybrids) to families and orders based on APGIII (Angiosperm Phylogeny Group, 2009) and Stevens (2009). Only native and naturalized taxa were considered. Taxa clearly resulting from anthropogenic crosses (e.g., "garden hybrids") and taxa only in cultivation were ignored. We tallied intra- and inter-generic hybrids separately,

and the latter were split between genera (e.g., half of each hybrid was assigned to each contributing genus). We treated apomictic microspecies conservatively, counting only those hybrids specifically listed in the flora. In some floras, particular genera (or, in the case of Rubus and Taraxacum, sections) were described as producing multiple hybrids without detailed specification of their numbers or the parental species involved. In these few cases we estimated the number of hybrids as 2% or 20% of the number of species present, whichever was greater. Finally, if a well-delineated group of species within a genus were described as interfertile and commonly producing hybrids, half of the possible combinations were tallied.

An alternative metric for assessing hybridization is the number of hybridizing parental species (as opposed to actual hybrids) (Grant and Grant, 1992; Mallet, 2005). This "hybridizing parents" metric focuses on the behavior of the parents while our metric focuses on the number of unique hybrid types generated; thus the two metrics may be appropriate for answering different questions. Unfortunately, with the exception of Europe, we did not score floras in such a way that the "hybridizing parents" metric could be calculated. We encourage future studies to score both metrics so that their relative advantages can be assessed. It appears, however, that the two metrics are very highly correlated: for the European flora (Tutin et al., 1964–1980), Spearman $\rho = 0.94$, $P < 0.0001$ ($n = 194$ hybridizing genera); for bird species of the world (Grant and Grant, 1992), Spearman $\rho = 0.99$, $P < 0.0001$ ($n = 15$ hybridizing orders).

Data analyses

We calculated summary statistics for the number of families and genera showing evidence of hybridization within and across floras. To describe the frequency of hybrids, the number of hybrids per nonhybrid species was calculated. We examined the influence of species richness on hybridization by regressing the absolute number of hybrids on nonhybrid species richness for both families and genera (SAS Proc Reg, SAS Institute, 2003). Because untransformed data did not meet normality assumptions, both variables were rank-transformed prior to analysis (Conover and Iman, 1981). We then asked whether additional variation in observed hybridization could be explained by bias in the amount of scientific attention paid to different groups. We defined study effort as the number of research articles on a given group in Biological Abstracts (Thomson Reuters). This database was queried on 4 June 2009 using JAVA scripts. For each genus in our database, the number of articles retrieved by the search "TA=genus AND Taxa Notes=(Plants) AND Timespan=1925–1999" was recorded. The time period was chosen to reflect scientific study prior to and during the completion of the floras, most of which were published during the 1990s. Study effort for families was calculated by summing the article numbers for the relevant genera. Study effort (rank-transformed) was then added to the regression models examining species richness (above).

A useful measure of hybridization propensity would reflect each group's propensity to produce hybrids once the opportunity for hybridization (the number of potential species with which to mate) is controlled. Thus we define hybridization propensity as the realized percentage of all possible hybrid combinations, i.e., for a genus of n nonhybrid species, hybridization propensity = $100 \times (\text{number of hybrids}/(n(n-1)/2))$. Because the vast majority of hybridization occurs within genera, hybridization propensities for families and orders were calculated as weighted averages of hybridization propensities of the component genera (weighted by species number).

To determine whether families and genera behave similarly across different regions with respect to hybridization, we calculated Spearman rank correlation coefficients for hybridization propensities across all possible pairwise combinations of regions (SAS Proc Corr, SAS Institute, 2003). This resulted in 56 correlation coefficients (28 for families and 28 for genera). We corrected for the multiplicity of tests using the Benjamini-Hochberg (1995) method. That is, we calculated sequential thresholds of significance as iq/m, where i is the rank of the observed P-value (ordered from smallest to largest, 1, 2, …, m), q is the assigned false-discovery rate (0.05), and m is number of tests conducted (56).

Finally, we examined whether hybridization propensity shows a phylogenetic signal in plants. For each of the 55 orders that contained ≥ two species in our global data set, we calculated hybridization propensity as a weighted average of the hybridization propensities of the component genera. We mapped hybridization propensity on an order-level tree (APGIII: Angiosperm Phylogeny Group, 2009) using the Parsimony Ancestral States method of Mesquite v. 2.6 (Maddison and Maddison, 2009). We then used BayesTraits (Pagel and Meade, 2009) to calculate λ (Pagel, 1999; Freckleton et al., 2002), which varies from 0 in cases of no phylogenetic signal to 1 in cases of complete phylogenetic dependence.

Results

How common is plant hybridization, and how are recorded instances of hybridization distributed across regions?

Across floras, we examined 282 families of vascular plants, comprising 3212 genera and species accounts for 36,940 nonhybrid species (the last figure is greater than the number of unique species examined, as some species are present in multiple floras). Regions differed substantially in recorded hybridization, with 21–39% of families and 5–19% of genera showing evidence of hybridization; the number of hybrids per nonhybrid species ranged from 0.04–0.26 (Table 1). Globally, we detected hybrids in 40.4% of families and 16.2% of genera (Table 1). Note that if only families containing ≥ 2 species in our data set are examined (i.e., the 47 families with no apparent opportunity for hybridization are excluded), nearly half of families (48.5%) contain hybrids.

Similarly, if genera containing one species are excluded, 22.8% of the remaining genera are involved in hybridization. We counted a total of 3437 hybrids, giving an overall hybrid frequency of 0.09 hybrids per nonhybrid species (Table 1).

Hybridization of species within genera was far more common than hybridization of species between genera. Of the 3437 hybrids recorded, only 121 (3.5%) represented intergeneric hybrids. Intergeneric hybridization was found in 13 families and was most commonly noted in the Poaceae, Asteraceae and Orchidaceae.

Does the amount of observed hybridization increase with taxon species richness and/or with study effort? After accounting for these factors, do taxa differ in hybridization propensity?

At the levels of both families and genera, more speciose taxa were associated with more recorded hybrids (Fig. 1; rank-transformed data; families $N=282$, $r=0.80$, $P<0.0001$; genera $N=3212$, $r=0.52$, $P<0.0001$). The smallest family producing hybrids contained four nonhybrid species in our data set. However, there was still substantial variation in hybridization behavior not explained by species richness, especially for genera (families $r^2=0.64$; genera $r^2=0.27$), which we interpret as evidence that taxa differ in hybridization behavior.

Study effort was significant when included in the regression models for both families and genera ($P=0.0409$ and $P<0.0001$, respectively), but the amount of additional variation in the number of hybrids explained was very slight (0.6% and 0.8%, respectively). For simplicity, in the rest of the analyses we ignore study effort and define hybridization propensity as the realized percentage of all possible hybrid combinations in a group. To aid in future research, we compiled graphics showing hybridization propensities of the 25 largest families in our survey, as well as the 25 families showing the greatest hybridization propensities (Figs. 2 and 3, respectively). Interestingly, some relatively speciose families showed no evidence of hybridization; these included the Santalaceae, Linaceae, Hydrocharitaceae and Urticaceae (Appendix A).

Do taxa behave consistently across regions with respect to hybridization propensity?

The hybridization propensity of a family or a genus in one region was generally predictive of its behavior in other regions (Table 2).

Table 1
Summary statistics on the recorded prevalence of natural hybridization in plants.

Region	Families			Genera			Nonhybrid Species Number	Hybrids	
	Number	Number with hybrids	% With Hybrids	Number	Number with hybrids	% With Hybrids		Number	Number per nonhybrid species
California, USA	171	51	29.8	1252	126	10.1	5996	389	0.065
Europe	184	58	31.5	1529	196	12.8	12,255	1340	0.109
British Isles	162	63	38.9	947	183	19.3	3009	770	0.256
Great Plains, USA	159	33	20.8	842	64	7.6	2856	153	0.054
Hawaii	164	40	24.4	715	59	8.3	1997	210	0.105
Intermountain West, USA[a]	110	33	30.0	742	86	11.6	3179	204	0.064
New England, USA	177	37	20.9	1018	54	5.3	3613	136	0.038
Victoria, Australia	177	37	20.9	1054	83	7.9	4035	235	0.058
Global totals	1304	352	27.0	8099	851	10.5	36,940	3437	0.093
Global totals (unique taxa)	282	114	40.4	3212	521	16.2	[b]	[b]	[b]

[a] Flora not yet complete; numbers reflect taxa in the published volumes only.
[b] Because data were collected at the generic level, the numbers of unique nonhybrid species and hybrids are not estimated.
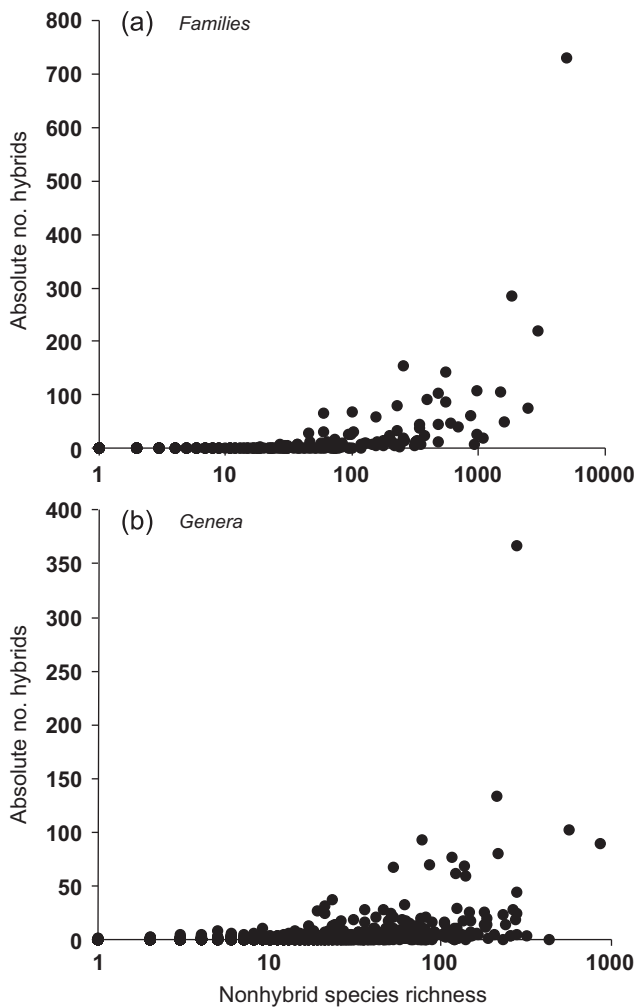
Fig. 1. The number of hybrids is positively correlated with nonhybrid species richness in (a) families and (b) genera. Data reflect counts summed across all regions. Note that plots are log-linear.

Fig. 2. Hybridization propensities in the 25 largest families surveyed. Hybridization propensities are weighted averages of the realized percentage of all possible hybrid combinations within the component genera.

For families, 22 of the 28 possible correlations were significantly positive. For genera, 20 of the 28 possible correlations were significantly positive. In general, Hawaiian groups appeared to be outliers; only 4 of 14 correlations involving Hawaii were significant, while hybridization propensities were significantly correlated across almost all other regions (38 of 42 pairwise correlations; Table 2).

Does hybridization propensity exhibit phylogenetic signal?

Hybridization propensities varied across plant orders (Fig. 4) and showed a strong phylogenetic signal: $\lambda = 0.93$. Likelihood ratio tests indicated that λ differed from 0.0 ($P < 0.001$) but not from 1.0 ($P > 0.1$). These results indicate strong phylogenetic dependence (Pagel, 1999; Freckleton et al., 2002).

Discussion

While molecular studies are increasingly important in understanding the frequency and consequences of hybridization, the morphological evidence from floras provides an unmatched large-scale survey of patterns of hybridization in plants. Detecting introgression via molecular data requires, e.g., multiple independent markers from the putative hybrid and putative parents
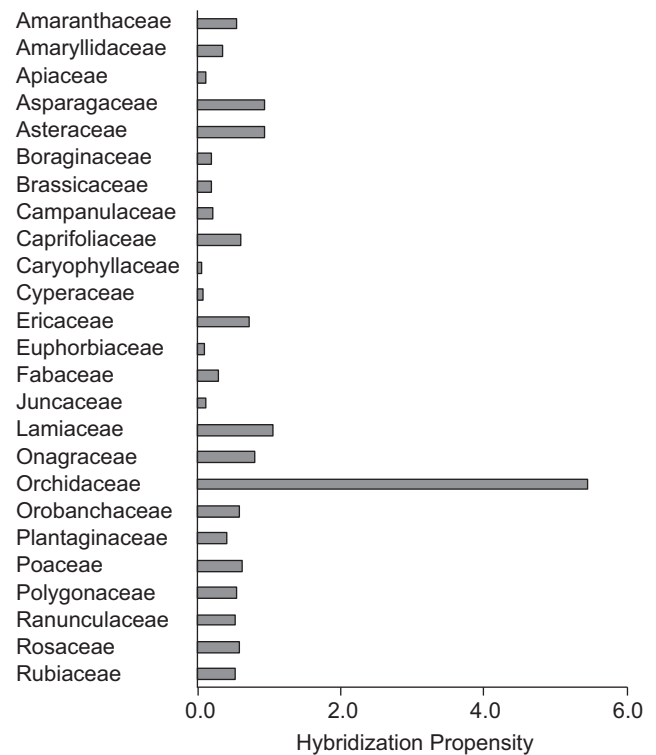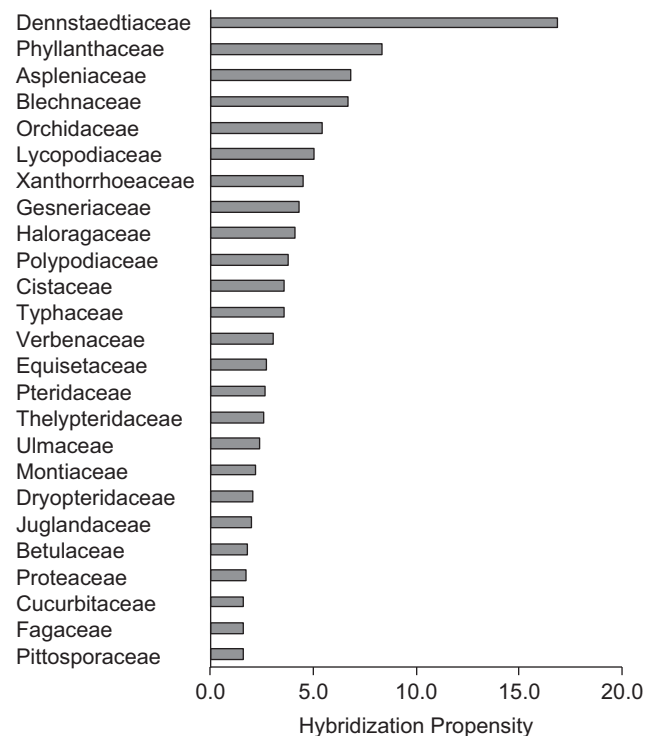

Fig. 3. The 25 most hybridization-prone families in our data set (families with < 10 species excluded from this figure). Hybridization propensities are weighted averages of the realized percentage of all possible hybrid combinations within the component genera.

Table 2
Hybridization propensity is correlated across regions. (A) Spearman rank correlation coefficients ρ for family-level (lower left) and genus level (upper right) hybridization propensities in each pair of regions. Correlations significant following Benjamini-Hochberg correction are shown in bold. (B) Sample sizes: number of shared families (lower left) and shared genera (upper right).

|	CA	EU	BI	GP	HI	IM	NE	VI
(A) Correlation coefficients								
California, USA		**0.22**	**0.20**	**0.24**	0.00	**0.37**	**0.22**	0.09
Europe	**0.39**		**0.46**	**0.25**	0.00	**0.27**	**0.24**	**0.20**
British Isles	**0.41**	**0.58**		**0.22**	0.02	**0.22**	**0.26**	**0.19**
Great Plains, USA	**0.29**	**0.36**	**0.33**		0.09	**0.35**	**0.29**	**0.17**
Hawaii	0.01	0.17	0.05	**0.20**		0.12	0.03	**0.16**
Intermountain West, USA	**0.41**	**0.45**	**0.43**	**0.51**	0.13		**0.24**	0.11
New England, USA	**0.31**	**0.52**	**0.28**	**0.47**	**0.22**	**0.43**		**0.17**
Victoria, Australia	**0.28**	**0.30**	**0.29**	**0.23**	0.20	0.20	0.16	
(B) Sample sizes								
California, USA		700	593	588	323	637	636	465
Europe	153		819	510	324	428	716	507
British Isles	142	151		423	265	369	622	457
Great Plains, USA	142	142	132		273	492	623	317
Hawaii	113	123	108	113		203	301	315
Intermountain West, USA	106	103	96	102	81		452	266
New England, USA	146	153	145	148	116	100		390
Victoria, Australia	128	136	126	123	122	91	126	
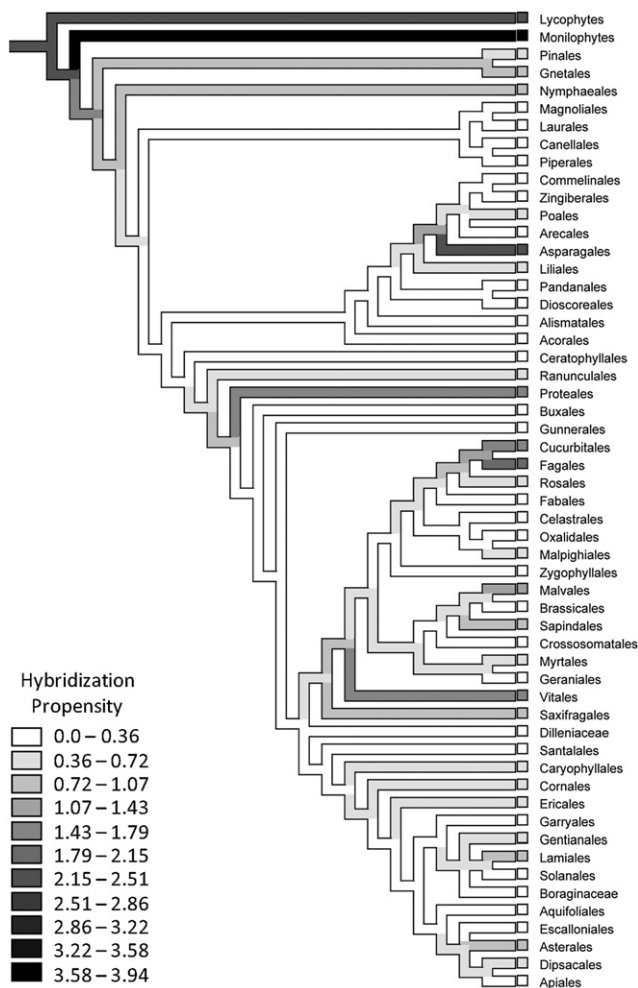
Fig. 4. Phylogenetic signal (λ=0.93) in vascular plant hybridization propensity. Hybridization propensity is the realized percentage of all possible hybrid combinations in a genus; order-level hybridization propensities shown here are weighted averages of the propensities of the component genera. Topology follows Angiosperm Phylogeny Group III (APG 2009).

(phylogenetic discordance analyses; Arnold, 2006), sequence data from multiple isolates (tests of intragenic mosaicism; Arnold, 2006), or expressed sequence tag (EST) libraries (the Introlog method; Barker and Rieseberg, 2008). Such extensive data are simply not yet available for the vast numbers of species available in floras. Importantly, morphology-based estimates provide a reliable indicator of plant hybridization: most putative hybrids identified via morphology that are then subject to molecular studies are confirmed as hybrids, both in plants (Cronn and Wendel, 2004) and animals (Mallet, 2005).

Hybridization is common and varies across regions

Overall, we found that hybrids are common, occurring in 40% of the plant families surveyed, at a frequency of 0.09 hybrids per nonhybrid species. These hybrids, however, are contained in relatively few genera (16%). Our results thus generally agree with those of Ellstrand et al. (1996) who concluded that plant hybrids are "common" but "not universal", with most instances of hybridization being concentrated in a relatively small group of genera. Importantly, however, numbers and frequencies of hybrids reported here are likely lower bounds. In general, surveys of hybridization and introgression (whether based on molecular markers, morphology, or other characters) are biased toward underestimation for several reasons. First and most obviously, few species can be thoroughly examined throughout their ranges; so many hybrids will not be encountered. Second, ongoing cases of hybridization will be more likely to be detected than cases that occurred in the recent or distant past. For example, in the case of molecular markers, the signal of hybridization may be diluted over time by mutations in the introgressed alleles, natural selection against introgressed alleles and genetic drift, all of which should make hybrids more difficult to identify (Rieseberg and Wendel, 1993). Third, cases of hybridization are unlikely to be suspected or described if the parents are not immediately obvious, e.g., when a parent has gone extinct, has undergone a range shift away from the hybrid populations, or has rapidly evolved a divergent phenotype. Finally, recent molecular work has identified 'cryptic' hybrids even in some groups with substantial barriers to interspecific contact, suggesting that

overall levels of hybridization may be higher than currently thought (Cronn and Wendel, 2004, Barker and Rieseberg, 2008).

Regions differed strongly in the numbers of recorded hybrids, but it is currently not possible to fully separate true biological differences from regional differences in study effort and/or flora editorial policies. It is perhaps informative that "the best-studied flora in the world" (Knapp, 2008, p. 20) – the British Isles (Stace, 1997) – has by far the greatest number of recorded hybrids per unit species richness (Table 1). However, our finding that hybridization propensity of a given family or genus is similar across regions indicates that regions differ in hybridization behavior at least in part because they contain different assemblages of families, genera and species.

Our finding that only 3.5% of hybrids represented intergeneric matings contrasts with a higher previous estimate of intergeneric hybridization. Knobloch (1972) recorded 2993 intergeneric hybrids in a pool of 23,675 hybrids, resulting in a figure of 12.6%. This much higher figure likely reflects the fact that the earlier study tallied both artificial and natural hybrids, with the former much more likely to be wide crosses involving different genera. Our figure of 3.5% is accordingly much more representative of natural hybridization, but again likely represents a lower bound.

Observed hybridization increases with taxon species richness, and taxa differ in hybridization propensity

We found that taxon species richness was a strong predictor of observed hybrids for both families and genera, consistent with a previous analysis using a smaller, family-level data set (Ellstrand et al., 1996). The hybrids tallied in this study are nearly all of recent (contemporaneous) origin, and most are not recognized as species in the richness totals, and thus cannot proximally cause high species richness in their respective taxa. Thus, we argue that high species richness likely causally affects hybrid numbers by providing opportunities for hybridization, in the form of species related closely enough to serve as potential mates. Of course, these considerations do not preclude the existence of higher-order factors that may causally affect both species richness and the number of hybrids. For example, colonization by a lineage of new habitats with 'empty niches' may induce an adaptive radiation, resulting in both high species richness and subsequent hybridization among genetically similar taxa. Alternately, it may be that hybridization is itself a key ingredient triggering adaptive radiation in such habitats, via the generation of large amounts of genetic and phenotypic novelty (Seehausen, 2004). Even without adaptive radiation, hybridization can elevate species numbers over evolutionary time via allopolyploidy (Meyers and Levin, 2006). There is thus the potential for positive feedback between species richness and hybridization rates during the diversification of a lineage.

Study effort as quantified by Biological Abstracts explained only a small amount of additional variation ($< 1\%$) in the numbers of hybrids. These results contrast with an analysis of hybridization patterns in 18 groups of animals (Schwenk et al., 2008). While for both studies ≈ 64–80% of the variation in hybrid numbers were explained by the combination of species richness and study effort, for animals 47% of the variation was explained by study effort, as estimated by hits in the Zoological Record (Schwenk et al., 2008). One possibility is that plant taxa are simply much more evenly studied (per unit species richness) than animal taxa, an idea supported in our data set by a positive correlation ($r^2 = 0.56$, $P < 0.0001$) between plant family species richness and study effort. Another possibility is that the Zoological Record is a better indicator of relevant study effort than Biological Abstracts, as the

former both spans a much longer time period and focuses more on primary systematics journals than does the latter.

Despite the strong relationship between species richness and number of hybrids, there was substantial unexplained variation, indicating that families and (especially) genera differ in hybridization propensity. The Dennstaedtiaceae, Phyllanthaceae and Aspleniaceae had the highest hybridization propensities (Fig. 3), while very low propensities were recorded for families such as the Santalaceae, Linaceae, Hydrocharitaceae and Urticaceae (Appendix A). In addition to opening up avenues for exploring why taxa differ in this regard (see Conclusions, below), knowledge about hybridization propensities might prove predictive about other important traits in plant groups. For example, given that hybridization can produce chemical novelty by 'mixing and matching' molecular components from the parents (Buschmann and Spring, 1995; Orians, 2000), groups with high observed hybridization propensities might have elevated diversities of secondary chemicals, with potential consequences for plant–herbivore and plant–pathogen interactions. Similarly, a recent finding that frequently hybridizing plant families have fewer members exhibiting invasive behavior (Whitney et al., 2009) may prove useful in predicting the identity of problematic invasive species. Hybridization propensities may be correlated with rates of adaptation or speciation. Finally, knowledge of the hybridization propensity of a group is clearly useful in assessing the risk of transgene escape from domesticated crops to wild relatives (Ellstrand, 2003; Hails and Morley, 2005).

Taxa behave consistently across regions with respect to hybridization propensity

The hybridization propensity of a group (family or a genus) tended to be similar across regions, with the exception of Hawaii. Of course, we expect that hybridization propensity will be highly correlated in proximal regions because some species will be shared, e.g., the Great Plains and Intermountain floras. We also expect hybridization propensity to be highly correlated in the single case in our analysis where one region is a subset of another, the floras of the British Isles and Europe. However, we found that behavior in even widely separated regions is correlated. For example, hybridization propensities in the floras of Victoria and Europe have Spearman correlation coefficients (ρ) of 0.20 and 0.30 ($n = 507$ shared genera and 136 shared families, respectively; Table 2), despite belonging to different hemispheres and being separated by $> 15,000$ km. Such patterns indicate that the hybridization behavior of a group may be determined more by intrinsic properties of the group than by the divergent environmental conditions encountered across different regions and continents.

Hybridization propensity exhibits strong phylogenetic signal

We found that recorded instances of hybridization are not uniformly distributed across orders of plants. High hybridization propensities are found in basal lineages (especially the Lycophytes and Monilophytes) and in scattered locations throughout the rest of the tree, e.g., in the Asparagales, Proteales, Fabids and Vitales. The presence of phylogenetic signal in hybridization propensities is an important finding, and suggests it will be necessary to incorporate phylogeny (e.g., via phylogenetically independent contrasts, Felsenstein, 1985; generalized least squares methods, Pagel, 1999; or spatial autocorrelation methods, Martins and Hansen, 1996) into comparative analyses correlating hybridization propensity with other family- or genus-level traits.

Conclusions

Our evidence suggests that hybridization behavior of a group may be determined more by its intrinsic properties than by environmental conditions. Characterization of the hybridization behavior of groups should lead to increased predictive power regarding their traits, from chemistry to invasiveness, and their evolutionary trajectories. Our results also highlight a lack of mechanistic understanding of why some groups hybridize more than others. Future comparative work building on this data set will use phylogenetically controlled methods to examine correlates (including perenniality, woodiness, mating systems, flower symmetry, genetic distance and other traits) potentially explanatory of hybridization propensity.

Acknowledgments

Appendix A.

Table A1.

Table A1
Largest 25 families with no reported hybrids in our data set.

Family	Number of species accounts examined
Santalaceae	100
Linaceae	94
Hydrocharitaceae	74
Urticaceae	74
Oxalidaceae	69
Ophioglossaceae	59
Melanthiaceae	46
Resedaceae	43
Zygophyllaceae	39
Selaginellaceae	38
Cleomaceae	37
Juncaginaceae	35
Acanthaceae	31
Arecaceae	31
Aristolochiaceae	31
Elatinaceae	30
Commelinaceae	29
Piperaceae	27
Cannabaceae	26
Hymenophyllaceae	24
Dilleniaceae	23
Elaeagnaceae	23
Pontederiaceae	23
Moraceae	22
Marsileaceae	20

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