

Hybridization-prone plant families do not generate more invasive species

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Abstract Many plant taxa are both hybrid-derived and invasive, suggesting a causal connection. However, given that hybridization is not rare in plants, we should expect some fraction of invasive taxa to be hybrids, even in the absence of an underlying causal relationship. Here, we test the hypothesis that hybridization leads to invasiveness by asking whether the number of hybrids and the numbers of naturalized, weedy, and invasive taxa are correlated across 256 vascular plant families. Data were derived from six regional floras and three global databases listing weeds and invasives. To account for phylogenetic nonindependence, we combined a supertree analysis with phylogenetically independent contrasts. After correcting for family size and phylogeny, we conclude that vascular plant families with a higher propensity for hybridization are not more likely to produce more naturalized, weedy, or invasive species than families less prone to hybridization. Instead, hybridization-prone families were in some cases associated with fewer naturalized species and invaders. We present two hypotheses for these patterns,

one based on Levin's (Syst Bot 31:8–12, 2006) ideas on reproductive interference and another based on Darwin's naturalization hypothesis. While these results do not preclude the possibility that hybridization generates weedy and invasive taxa with some frequency, they do suggest that the signal from the hybridization-invasion process may be relatively weak and easily obscured by other processes governing plant invasions.

Keywords Adaptation · Evolution of invasiveness · Introgression · Phylogenetically independent contrasts · Vascular plant hybrids · Weeds

Introduction

Ellstrand and Schierenbeck (2000) formalized the intriguing hypothesis that hybridization may play a role in generating weedy and invasive plants, extending a history of thought relating hybridization to adaptive evolution in plants. They documented 28 examples of invasive, hybrid-derived taxa, and suggested that hybridization may have spurred the evolution of invasive behavior in many of the examples (see also Vilà et al. 2000). Since the year 2000, additional plant cases have come to light (e.g., Greenwood et al. 2004), and cases of invasive hybrid animals are starting to be reported as well (e.g., Façon et al. 2005), suggesting that the proposed phenomenon could be widespread.

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General principles suggest that hybridization could affect invasiveness via several mechanisms. First, heterosis (hybrid vigor) may increase a species' competitiveness and colonization abilities (Stebbins 1985). Although usually transitory, heterosis can be fixed via allopolyploidy, apomixis, or clonal spread. Second, hybridization can result in increased genetic variation, which in turn can promote adaptive evolution (Anderson 1949; Anderson and Stebbins 1954; Stebbins 1959; Rattenbury 1962). Third, hybridization can generate novel genotypes (Stebbins 1969; Arnold 1997; Rieseberg et al. 2003) potentially matching the novel environment more closely than ancestral genotypes. Finally, it has been suggested that hybridization may provide a mechanism for purging accumulated genetic load, thereby producing a fitness boost and contributing to invasiveness (Ellstrand and Schierenbeck 2000).

Recent case studies have supported a causal connection between hybridization and invasion or range expansion in particular taxa. Campbell et al. (2006) examined the evolution of crop-wild hybrid radishes (*Raphanus*). Following three generations of natural selection in the field in Michigan, USA, lines introgressed with crop alleles achieved substantially higher fitness than non-introgressed lines when introduced to the novel environment of California, where naturally occurring hybrids have been invasive for over a century. In a second example, naturally occurring hybrid derivatives of two wild sunflower (*Helianthus*) species outperformed the parental species in common garden experiments (Whitney et al. 2006). Further work using synthetic hybrids indicated that cross-species transfer of herbivore resistance alleles could have aided the hybrid sunflower's historical southward expansion of its range limits (Whitney et al. 2006; Rieseberg et al. 2007). However, for most taxa in Ellstrand and Schierenbeck's (2000) list, the appropriate experiments have not yet been done to evaluate the link between hybridization and the evolution of invasiveness. Minimally, common garden experiments are required to demonstrate that hybrids are more fit or have higher population growth rates than parental taxa in the invasive range (Vilà et al. 2000; Pilson and Prendeville 2004).

If the hybridization-invasion link is real, is it common enough to generate patterns at regional or global scales? Given the fairly widespread nature of hybridization among plant taxa (Ellstrand et al. 1996)

and the high rate of plant introductions (Rejmánek et al. 2005), it is clear that we should expect a certain fraction of invasive taxa to be hybrids due to chance alone. Looking across families of vascular plants, there is variation both in the frequency of hybridization (Ellstrand et al. 1996) and in the number of weedy or invasive taxa (Daehler 1998; Pyšek 1998). Thus, we have the opportunity to examine whether the patterns are correlated. In this paper, we bring together data on hybridization frequencies in plant families with data on the frequencies of naturalized, weedy and invasive taxa in those families. We also take phylogeny into account, as any relationship found could be the result of shared ancestry (Felsenstein 1985). To illustrate, suppose that hybridizing families were all found in a single clade because they reflect retention of a trait (elevated hybridization propensity) that evolved once in an ancestral group. Suppose that this ancestral group also evolved an elevated tendency to produce invasive species, and that this trait value was also retained following diversification. Under this scenario, there would be just one evolutionary association between hybridization propensity and invasiveness, and to treat each modern-day family in this clade as evidence of a causal/evolutionary association would be akin to pseudoreplication. Therefore, we construct supertrees and employ phylogenetically independent contrasts in our analyses. We ask:

- (1) Within a region, are families exhibiting more extensive hybridization represented by more naturalized species?
- (2) Across regions, do families exhibiting more extensive hybridization have more members present on global lists of weeds and invasives?

Methods

Extent of hybridization

To characterize the extent of hybridization across vascular plant families, we analyzed six floras generally following the methods of Ellstrand et al. (1996), who examined regional biosystematic floras for evidence of hybridization (but who were not concerned with the question of invasion). We analyzed one of the original Ellstrand et al. source

floras (the Great Plains of the U.S., Great Plains Flora Association 1986), updated and/or expanded editions of three additional Ellstrand et al. floras (British Isles, Stace 1997; Hawai'i, Wagner et al. 1999; the Intermountain Region of the western U.S., Cronquist et al. 1972–2005) and two new floras (Northeastern U.S., Magee and Ahles 1999; California, Hickman 1993). In addition, we expanded our consideration of Hawaiian vascular plants by analyzing a new treatment of ferns and lycophytes (Palmer 2003). Note that the Intermountain flora (Cronquist et al. 1972–2005) has seven planned volumes; our analysis utilized the six 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. 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 based on Stevens' (2006) Angiosperm Phylogeny Website. Only native and naturalized taxa were considered; taxa only in cultivation were ignored. We did not count hybrids among subspecies or probable primary intergradation as suggested by the floras. 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. We treated apomictic microspecies conservatively, counting only those hybrids specifically listed in the flora. In contrast to Ellstrand et al. (1996), we also counted naturalized hybrids mentioned in a flora that apparently arose outside the region covered by the flora (in addition to those arising inside the region), as we did not wish to discriminate against some of the very taxa whose presence would support a hybridization-invasion link (i.e., we wanted a liberal test of the hypothesis). Finally, in some floras (Great Plains, Intermountain, California, British Isles), particular groups (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. This improves upon the Ellstrand et al. (1996) practice of assigning four hybrids to such groups, as that practice clearly overestimates the number of hybrids for small groups (e.g., four hybrids should not be

possible for a group of three non-hybrid species) and likely underestimates the number of hybrids for large groups (e.g., *Ceanothus* in California).

Numbers of naturalized, weedy and invasive species

We follow Richardson et al. (2000) in recognizing naturalized species as non-native species able to survive and reproduce in their new range without human assistance; invasive species as those naturalized species that demonstrate spread from their sites of introduction; and weedy species as plants (including both natives and non-natives) that have harmful environmental or economic effects. We compiled data on the prevalence of these types of species in each family. First, data on the numbers of naturalized species in each family were extracted from each of the floras under consideration. Next, we counted the number of weeds and/or invasive taxa in each family from three databases of global scope. The Global Compendium of Weeds (Randall 2002, 2007) lists (as of July, 2007) >24,000 species described as weedy; these include both native and non-native species found in both agricultural and natural areas. Weber's (2003) treatment of plant invasives contains 450 species, all of which are invasive in natural areas and which have "significant negative effects" on native communities. The IUCN Global Invasive Species Database (ISSG 2007) is a more restricted list that (as of July, 2007) included 221 species of invasive vascular plants.

Regional and global analyses of hybridization versus naturalized/weedy/invasive status

Regional analyses asked whether, within the area covered by a particular flora, families that produced more hybrids also included more naturalized species. We use naturalized species as a rough proxy for invasives because numbers of the former are a good predictor of numbers of the latter (Rejmánek and Randall 2004) and because the floras did not allow us to consistently distinguish true invasives from non-invasive but naturalized species. Counts of hybrids and naturalized species are expected to be strongly positively correlated with species richness within a family (here termed family size), and indeed those patterns were significant in all datasets (data not shown). Therefore we removed the influence of

family size via initial regressions of both the independent (no. hybrids) and dependent (no. naturalized species) variables on family size. We used two types of family sizes: “regional family size” refers to the total number of non-hybrid species + hybrid taxa within a region (determined from the floras), while “global family size” is the total number of species from all continents (determined from Stevens 2006). Hybrid counts were regressed on regional family size as more confamilial taxa in a region should provide more opportunities for hybrids to form. Counts of naturalized species were regressed on both regional family size and global family size in multiple regression analyses as both of these variables should contribute to the regional number of naturalized taxa. The resulting residuals for counts of hybrids and naturalized taxa were regressed against each other to test the regional hypotheses. All statistical analyses utilized SAS (SAS Institute 2003).

Global analyses asked whether families exhibiting more extensive hybridization had more of their members present on three global lists of weeds and invasives. For each family, a hybridization index was calculated by summing hybrid counts across all floras analyzed. No attempt was made to avoid ‘double counting’ of hybrids formed from the same parents in different regions. Thus, the index incorporates information on both the number of hybridizing taxa and the frequency with which they hybridize in different regions. Our assumption is that the six regions taken together are representative of global patterns of hybridization; this is clearly an assumption which would benefit from more data and closer analysis when these data become available. While our sample regions do span 160° of longitude, they underrepresent the tropics and furthermore leave several continents unsampled. As in the regional analyses, the influence of family size was removed via initial regressions; “family size” with respect to the hybridization index was the total number of non-hybrid species plus the number of hybrid taxa across all floras. The residuals for counts of weeds and invasives were then regressed on residuals for the hybridization index.

Supertree construction and phylogenetically independent contrasts

To account for the phylogenetic nonindependence of our observations, we revisited the regional and global

analyses (previous section) using phylogenetically independent contrasts (PICs; Felsenstein 1985). We employed Phylomatic (Webb and Donoghue 2005) using the Davies et al. (2004) angiosperm supertree to construct base family-level phylogenies for each flora. Phylogenies were imported to Mesquite v. 1.12 (Maddison and Maddison 2006), where non-angiosperm (lycophyte, monilophyte, gymnosperm, and gnetophyte) families were added by hand, based on their position in the Phylomatic “maximally resolved seed plant tree” (Webb and Donoghue 2005; accessed June 2007) and other sources (ferns: Smith et al. 2006). Because of incomplete phylogenetic information, 7 of 263 families could not be placed; these included the Apodanthaceae, Dipsacaceae, Garryaceae, Gerrardinaceae, Sparganiaceae, Taccaceae, and Turneraceae. Phylogenies are available from the lead author on request.

Phylogenetically independent contrasts (PICs; Felsenstein 1985) were generated using the PDAP: PDTREE module in Mesquite (Garland et al. 1993; Midford et al. 2002). Actual branch lengths are unknown, but diagnostics indicated that branch lengths of 1.0 were adequate in all analyses; furthermore, the method is generally robust to this assumption (Martins and Garland 1991; Garland et al. 1999). Standardized contrasts were obtained by dividing the raw contrasts by their standard deviations. Then, as above, the influence of family size on each variable was removed via regression, and the residuals were used in the final regressions comparing measures of hybridization and weedy/invasive behavior among families.

Results

Across floras, we examined 263 families of vascular plants, comprising 2,389 genera and species accounts for 20,235 non-hybrid species (the last figure is greater than the number of unique species examined, as some species are present in multiple floras). We counted a total of 1,904 hybrids. As noted by Ellstrand et al. (1996), we found that the propensity to hybridize was distributed nonrandomly across families. This and other general patterns of hybridization in this dataset will be examined in greater detail in future studies. Of the 263 families, 256 (>97%) were present in phylogenies and formed the basis of our analyses, below.

Relationships between hybridization and naturalized taxa: regional analyses

For the 256 families in our analyses, the floras recorded 5,868 instances of naturalized taxa, of which 5,523 were non-hybrids and 345 were hybrids. On a percentage basis, hybrids were less well represented among naturalized taxa (5.9%) than among native taxa (9.6%). Examination of the raw (phylogenetically uncorrected) patterns of hybridization propensity and numbers of naturalized taxa found two negative relationships and one weakly positive relationship (Table 1, Fig. 1). After phylogenetic correction (Table 1, Fig. 2), only the two negative relationships remained. Strikingly, for both the British Isles and Hawai'i, families with greater hybridization propensity were associated with lower than average numbers of naturalized species (Fig. 2a, d), with substantial amounts of variation explained ($r^2 = 0.39, 0.21$, respectively; Table 1). No significant relationships were apparent for California, the Great Plains, the Intermountain Region, or New England.

Families with small regional family sizes (low species richness within a region) might be expected to heavily influence the results for two reasons. First, these families should have few hybrids, reflecting the lack of confamilial partners with which to hybridize. Second, they may also consist largely of naturalized

plants; e.g., for Hawaii, 60% of the 90 families with fewer than five species contain no native members, compared with only 12% of the larger families. To test whether small families introduced bias, we re-ran the analyses three times, excluding families with regional richness of <2 , <5 , and <10 species, respectively. None of these results differed qualitatively (in terms of significance levels or the signs of slopes) from the analyses of the full datasets (data not shown).

Relationships between hybridization and weeds and invasives: global analyses

For the families in our analyses, the global databases contained 23,554 weed species (Global Compendium of Weeds; Randall 2002, 2007), 444 'Weber invasives' (Weber 2003), and 219 'IUCN invasive' species (IUCN Global Invasive Species Database; ISSG 2007). In the raw data analyses, there were no significant relationships between the hybridization index for a family (the total number of hybrids recorded across the six floristic regions) and the numbers of weedy or invasive species, although the trend in all three datasets was slightly negative (Table 1, Fig. 3a–c). After phylogenetic correction (Table 1, Fig. 3d–f), the negative hybridization/invasive relationship became significant for the IUCN

Table 1 Results of regression analyses of the number of naturalized taxa on the number of hybrids within a vascular plant family (for regional analyses) or of the number of weedy or invasive taxa on a hybridization index (for global analyses)

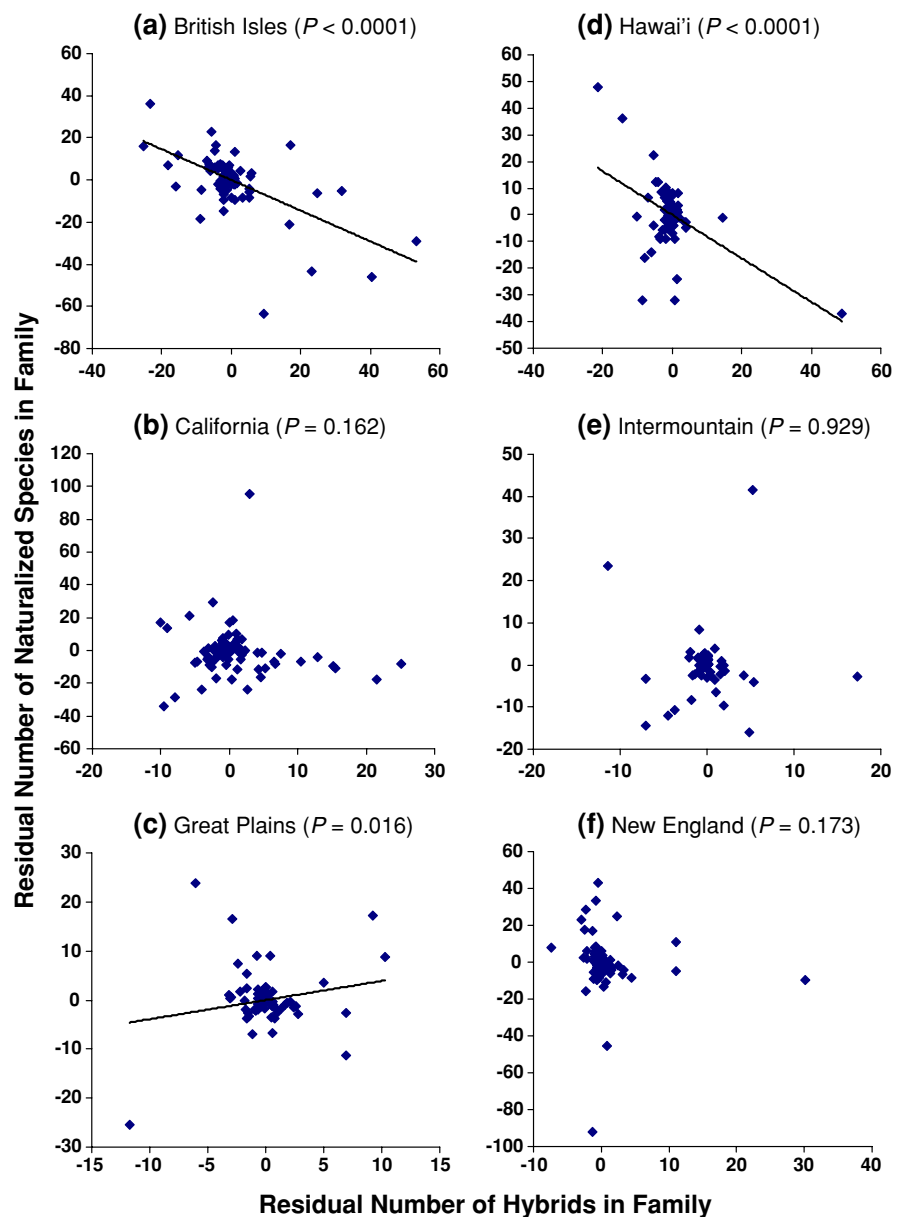
Analysis/dataset	N^a	Corrected for family size			Corrected for family size and phylogeny		
		Slope	r^2	P	Slope ^b	r^2	P
Regional							
British Isles naturalized	174	−0.729	0.36	<0.001	−0.745	0.39	<0.001
California naturalized	175	−0.273	0.01	0.162	−0.258	0.01	0.183
Great Plains naturalized	162	0.390	0.04	0.016	0.286	0.02	0.058
Hawai'i naturalized	162	−0.816	0.25	<0.001	−0.745	0.21	<0.001
Intermountain naturalized	98	−0.020	0.00	0.929	−0.009	0.00	0.970
New England naturalized	184	−0.371	0.01	0.173	−0.338	0.01	0.218
Global							
GCW weeds	256	−1.657	0.01	0.072	−1.691	0.01	0.062
Weber invasives	256	−0.037	0.01	0.134	−0.042	0.01	0.097
IUCN invasives	256	−0.021	0.01	0.057	−0.027	0.02	0.012

^a Number of plant families

^b Constrained through (0,0)

Significant relationships ($P < 0.05$) are indicated in bold font

Fig. 1 Uncorrected relationships between hybridization and the number of naturalized species in each of six regions (the ‘regional analyses’). Each *point* represents a plant family. The numbers of hybrids and naturalized species are presented as residuals from regressions removing the influence of family size (see “Methods”)



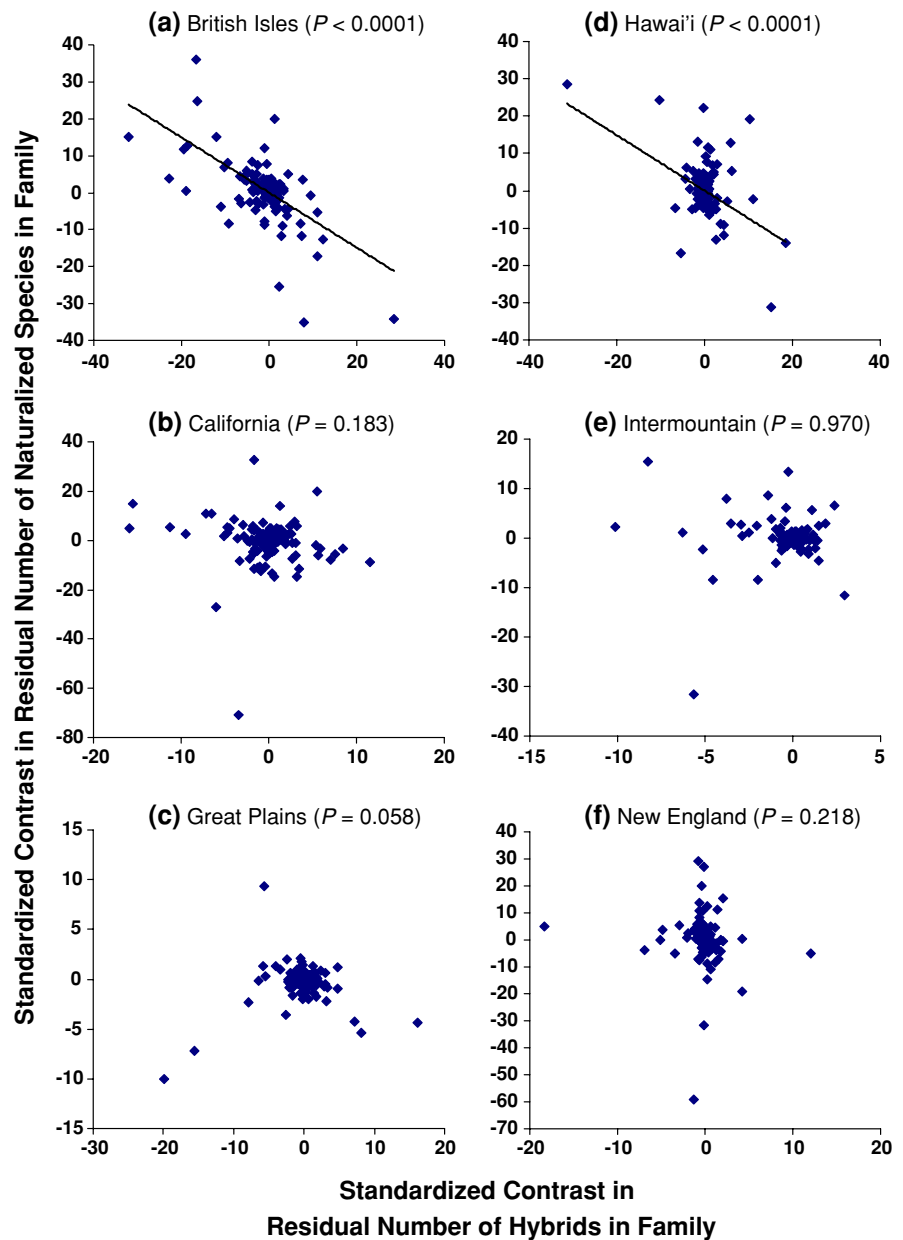
invasive dataset (Fig. 3f), although explanatory power was quite low, with an r^2 value of only 0.02 (Table 1).

Discussion

Both within regions and globally, we found no evidence that vascular plant families with a higher propensity for hybridization are more likely to produce more naturalized, weedy, or invasive species than families less prone to hybridization. In some

cases, hybridization-prone families are actually associated with fewer naturalized species (British Isles, Hawai'i) and fewer globally recognized invaders (IUCN invasives). At first glance, it might seem that regionally speciose families should both hybridize frequently (due to opportunity) and have a high resistance to invasion as a result of niche filling and/or lack of enemy release (Strauss et al. 2006), and therefore could drive the negative patterns. However, family size has been factored out of the analysis, so this explanation is untenable. Instead, we currently

Fig. 2 Phylogenetically corrected relationships between hybridization and the number of naturalized species in each of the six regions. Each *point* represents a plant family. The numbers of hybrids and naturalized species were subjected to regressions removing the influence of family size, and phylogenetically independent contrasts were based on the residuals



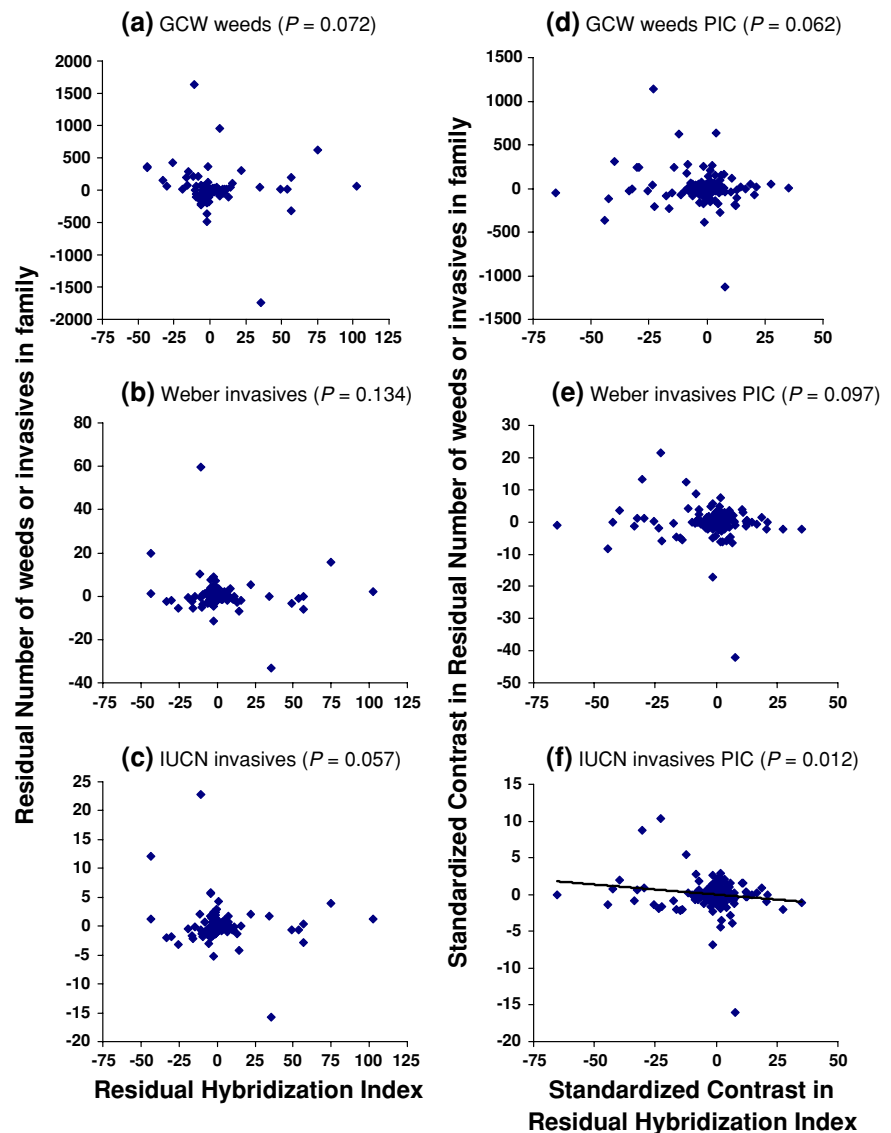
have two hypotheses to explain these unexpected negative relationships.

First, hybridization itself may prevent the invasion by confamilial species via reproductive interference (Levin 2006). In this scenario, an introduced species would be subject to pollen swamping from closely related native species with which it hybridizes. Assuming a large enough degree of hybrid inviability, hybrid sterility, and/or gamete wastage, rapid extinction of the rarer taxon (presumably, the newly

introduced species) could result (Levin et al. 1996; Levin 2006). If this scenario were played out across many nascent invasions, it could generate a negative relationship between hybridization propensity and the number of successful invasive species within a family. Although this line of thought is intriguing, we have little data on how frequently invasions fail because of such reproductive interference.

The second hypothesis for our patterns invokes Darwin's naturalization hypothesis, the idea that

Fig 3 Relationships between hybridization and the occurrence of globally recognized weedy or invasive species in 256 plant families (the ‘global analyses’). Each *point* represents a plant family. The hybridization index is derived by summing counts of hybrids from all six floras analyzed. “GCW weeds” are 23,554 species listed in an extensive database of global weeds (Randall 2002, 2007); “Weber invasives” are 444 species of plants recognized as invasive in natural areas on a global scale (Weber 2003); “IUCN invasives” are 219 species of vascular plants recognized as invasives on a global scale (ISSG 2007). As in Figs. 1 and 2, data have been corrected for family size (all panels) and for phylogenetic relationships (panels d–f)



species congeneric with natives should face particular barriers to invasion, because they will be phenotypically similar and have similar niches to the natives (Darwin 1859). Recent studies are consistent with this hypothesis (Strauss et al. 2006). If species in a group that hybridizes extensively are genetically more similar to each other than those in an average group, this could translate into higher than average phenotypic/niche similarity and thus higher resistance to invasion by another member of the group. Thus, like phylogenetic similarity (Webb et al. 2002), hybridization frequency could be a reliable indicator of phenotypic/niche similarity. A first step in

investigating this hypothesis could be to examine the correlation between hybridization propensity and mean phylogenetic similarity across groups (genera or families).

Caveats

Whereas most of the hybridization recorded in the floras takes place within genera (data not shown), this study was conducted at the family level. Therefore, it could be possible that patterns of hybridization and invasion within genera are obscured in the analysis of family level patterns. We did perform generic-level

analyses on genus-size corrected (but not phylogenetically corrected) data and found patterns very similar to those at the family level: genera more prone to hybridization did not contain greater numbers of naturalized taxa (data not shown). However, it is not known if these patterns are robust to phylogenetic correction. It is currently not possible to do phylogenetically controlled analyses of large numbers of genera (e.g., the $\approx 2,400$ genera in the current study) due both to software limitations and, more importantly, to the lack of information on phylogenetic relationships for many plant genera.

A second caveat is that our sampling of floristic regions may not be representative of more general patterns of hybridization. As new floras are published that include information on hybrids, it will be possible to increase the sampling breadth and gain greater confidence that our estimates of family level parameters are reasonable. Furthermore, it would be informative to examine hybridization frequencies in a particular source region and compare them to weedy/invasive behavior in a known sink or invaded region. For example, given that many North American invaders are derived from Eurasia (Baker 1986; Cadotte et al. 2006; Guo et al. 2006), one could examine appropriate European or Asian floras (if they exist) for evidence of hybridization and relate that data to patterns of invasion in North America.

Finally, a flora-based approach may underestimate the prevalence of hybridization simply because of observer bias (Ellstrand et al. 1996), and thus may dilute any link between hybridization propensity and the generation of naturalized, weedy or invasive taxa. Across floras, the frequency of reported hybrids varied widely, from 20.8% of all taxa (non-hybrids + hybrids) in the Flora of the British Isles to 4.1% in the New England flora. Interestingly, floras in relative geographical proximity tended to have similar frequencies of reported hybrids (e.g., 5.2 and 4.1% for Great Plains and New England, respectively; 6.2 and 6.5% for California and Intermountain, respectively), perhaps suggesting that observer bias was not substantial. It should also be noted that the British Isles flora has been extensively examined for hybrids (Stace 1975, 1997) and still did not support a positive relationship between hybridization and naturalization.

Conclusions

Our results do not support the idea that increased hybridization propensity results in increased numbers of naturalized, weedy or invasive taxa detectable at the scale of plant families. Importantly, however, these results do not preclude the possibility that hybridization regularly generates weedy and invasive taxa. Indeed, we are accumulating a growing list of examples in which hybridization can be mechanistically linked to particular phenotypes that increase a plant's invasive potential (Campbell et al. 2006; Whitney et al. 2006). Many of the invasive hybrid taxa described in Ellstrand and Schierenbeck (2000) may indeed turn out to be examples of this phenomenon, after the appropriate tests are done. Common garden experiments are required to demonstrate that hybrids are more fit or have higher population growth rates than parental taxa in the invasive range; then, molecular and/or phenotypic analyses must identify particular alleles, traits or trait combinations unique to hybrids and associated with their invasive success.

However, the current results do suggest that the signal from the hybridization-invasion process is relatively weak, and is obscured by other processes governing the success of plant invasions (e.g., propagule pressure, Lockwood et al. 2005; reproductive interference, Levin 2006; exclusion due to niche overlap, Darwin 1859). This is consistent with a main thrust of the current invasion literature emphasizing that invasion is multicausal (Rejmánek et al. 2005); different invasions across different taxa and locations are unlikely to be linked to a single 'smoking gun.'

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