

Patterns, Predictors, and Consequences of Dominance in Hybrids

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ABSTRACT: Compared to those of their parents, are the traits of first-generation (F_1) hybrids typically intermediate, biased toward one parent, or mismatched for alternative parental phenotypes? To address this empirical gap, we compiled data from 233 crosses in which traits were measured in a common environment for two parent taxa and their F_1 hybrids. We find that individual traits in F_1 s are halfway between the parental midpoint and one parental value. Considering pairs of traits together, a hybrid's bivariate phenotype tends to resemble one parent (parent bias) about 50% more than the other, while also exhibiting a similar magnitude of mismatch due to different traits having dominance in conflicting directions. Using data from an experimental field planting of recombinant hybrid sunflowers, we illustrate that parent bias improves fitness, whereas mismatch reduces fitness. Our study has three major conclusions. First, hybrids are not phenotypically intermediate but rather exhibit substantial mismatch. Second, dominance is likely determined by the idiosyncratic evolutionary trajectories of individual traits and populations. Finally, selection against hybrids likely results from selection against both intermediate and mismatched phenotypes.

Keywords: hybridization, speciation, phenotypic mismatch, opposing dominance.

Introduction

When divergent populations occur in sympatry, they might mate and form hybrids (Mallet 2005). If those hybrids are

viable and fertile, whether they survive and reproduce depends on their ability to persist under prevailing ecological conditions. Because selection against hybrids limits gene flow between parents (Harrison 1993), understanding the mechanisms underlying hybrid performance in the field is key to understanding postzygotic isolation (Barton and Hewitt 1985; Gompert et al. 2017). Quantifying general patterns of phenotype expression in hybrids would clarify mechanisms of natural and sexual selection that act against hybrids. For example, if hybrids resemble one parent, they could thrive in that parent's niche and readily backcross (Mallet 1986). Alternatively, if hybrids are phenotypically intermediate for all traits or possess mismatched trait combinations due to dominance in opposing directions (i.e., they resemble parent 1 for trait x but parent 2 for trait y), they might be unable to survive and reproduce in the available niche space (Hatfield and Schluter 1999; Matsubayashi et al. 2010; Arnegard et al. 2014; Cooper et al. 2018). Currently, little is known about general patterns of trait expression in hybrids.

Previous synthetic studies investigating hybrid phenotypes have conflicting conclusions. Some authors suggest that hybrid intermediacy is the rule (Hubbs 1940, 1955), whereas others find that hybrids are better described as mosaics of parental and intermediate characters (Rieseberg and Ellstrand 1993). Such previous studies typically lacked a quantitative framework and/or focused on a single taxon (e.g., fish or plants), limiting our ability to arrive at general conclusions. In addition, previous studies of hybrid phenotype expression tend to use data from domesticated taxa, wherein dominance is often elevated compared to natural populations (Fisher 1931; Crnokrak and Roff 1995). Here, we use a geometric approach to quantify patterns of hybrid

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phenotypes across a broad range of wild (or recently wild) plant and animal taxa in a way that is comparable across studies. By quantifying the parent bias across each pair of traits, we determine the extent to which hybrids are intermediate or tend to resemble one parent more than the other. And by quantifying the mismatch (or opposing dominance; Matsubayashi et al. 2010), we can determine the extent to which hybrids have mismatched combinations of divergent parental traits.

In this article, we systematically document patterns of phenotype expression in hybrids, investigate the possible predictors of these patterns, and use experimental data to explore the fitness consequences of trait interactions in the field. We first summarize the results of 198 studies that compared the phenotypes of hybrids and parents in a common environment and test whether features of a cross—such as the genetic distance between or taxon of the parents—are associated with dominance (“Patterns and Predictors of Dominance”). We then use data from an experimental planting of recombinant hybrid sunflowers to evaluate whether patterns of pairwise parent bias and mismatch predict fitness in hypothesized directions (“Fitness Consequences of Parent Bias and Mismatch in Recombinant Sunflowers”). Our results provide insight into the mechanisms that might commonly underlie selection against hybrids in nature.

Patterns and Predictors of Dominance

Methods

In this section, we provide a brief summary of our methodology for collecting and analyzing data on hybrid trait expression from the literature and then describe the patterns evident in the data. A detailed explanation of all methods is given in the “Supplementary Methods” section of the supplemental PDF (available online).

Systematic Review of Dominance Patterns in F₁ Hybrids. We conducted a systematic literature search and identified 198 studies from which we could collect data of at least one divergent phenotypic trait measured in two parent taxa and their F₁ hybrids in a common environment. We included studies that conducted crosses between wild-collected parental populations or laboratory populations with ≤ 10 generations of captivity. Crosses in the data set are both intraspecific (43%) and interspecific (57%). Data from wild hybrids (i.e., not from controlled crosses) were included only if hybrids were genotyped to confirm hybrid status and generation. We aimed to include only traits with environment-dependent effects on fitness—traits plausibly under divergent selection between populations and stabilizing selection within populations—rather than directional selection in the same direction in both populations. Said another way, we attempted

to include only traits that could be characterized as nonfitness traits (Merilä and Sheldon 1999) or ordinary traits (Orr and Betancourt 2001). For example, traits such as embryo viability are almost certainly under directional selection and were not included in our database. We excluded likely fitness components because such traits in hybrids are often affected by developmental difficulties resulting from hybrid incompatibilities or heterosis resulting from outbreeding (Coyne and Orr 2004). This choice to exclude fitness traits likely renders our analysis on dominance more conservative since hybrid breakdown or heterosis would manifest as a transgressive phenotype (see Stelkens and Seehausen 2009). By contrast, traits such as limb length might have particular values best suited to some environments and genetic backgrounds—it is implausible that such traits would always be selected to a maximum or minimum value. Data from backcross (BC₁ only) and F₂ hybrids were collected when available but were used in a previous publication to test a theoretical prediction about pleiotropy (Thompson 2020). The studies in our analysis spanned a range of taxa but included mostly vascular plants (~34%), vertebrates (~30%), and arthropods (~30%), with the few remaining studies using annelids (<1%), echinoderms (<1%), red algae (Rhodophyta; <1%), and molluscs (~2%).

We restricted our data set to traits where parents had divergent phenotypes. We retained all traits for which the parents were >1 phenotypic standard deviation (SD) apart, which was the case for 71.7% of measured traits (using the smaller of the two parental SDs). We also retained traits for which the parents were <1 SD apart but had statistically distinguishable phenotypes (*t*-test, $P < .05$), which accounted for an additional 9.4% of measured traits. The data for the remaining 18.9% of traits for which we collected data were discarded (see fig. S1; figs. S1–S16 are available online). In total, data used for the analysis of dominance patterns come from 233 unique crosses.

After filtering traits, we converted all trait data that were published with a transformation applied (e.g., $\ln(x)$, \sqrt{x}) to their original measurement scale, because expectations are not the same on a log or square-root scale as for raw units. This choice to analyze all traits in their original measurement units influences the dominance patterns because traits that are intermediate on the raw scale might be dominant on a log scale, or vice versa, but results in greater comparability among traits and studies. We then put all traits in all studies on a common scale where one (arbitrarily determined) parent had a value of 0 for all traits and the other had a value of 1 (see fig. 1). Under an expectation of additivity, an F₁ hybrid would have a trait value of 0.5 for all traits. Because we do not make any assumptions about which trait value is ancestral or derived, we cannot distinguish between dominance and recessivity. For example, a trait’s degree of dominance is the same whether the hybrid trait

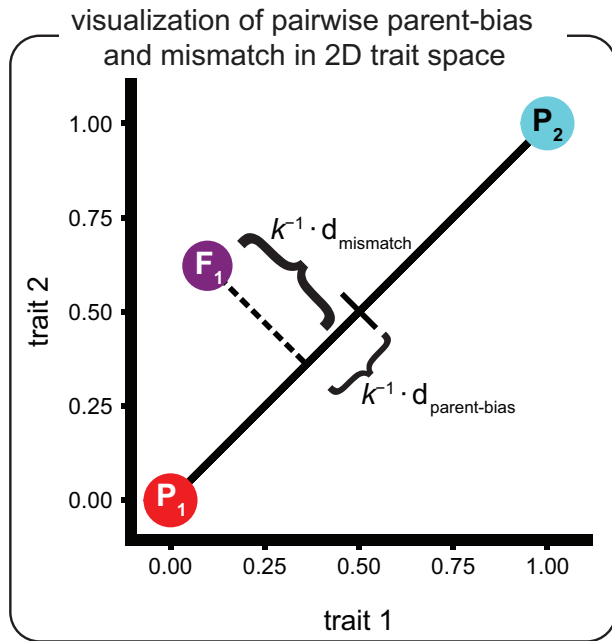


Figure 1: Visual overview of how two-dimensional dominance metrics were calculated. When studies contained two or more divergent traits, we calculated pairwise parent bias ($d_{\text{parent-bias}}$) and mismatch (d_{mismatch}) of the hybrid phenotype (F_1) with respect to the line connecting the two parent phenotypes (P_1 and P_2 ; note that which parent is called P_1 or P_2 is arbitrary). This procedure was repeated for every pair of traits. The scaling factor, k , renders the maximum value observed without transgression (i.e., d_{mismatch} when F_1 trait values are $[0, 1]$ or pairwise $d_{\text{parent-bias}}$ when F_1 trait values are $[0, 0]$) equal to 1. For two traits, $k = \sqrt{2}$. Dominance values >1 can result when traits are transgressive. In this hypothetical example, $d_{\text{parent-bias}}$ is ~ 0.25 and d_{mismatch} is ~ 0.5 ; see table 1 for other possible F_1 two-dimensional hybrid phenotypes and their corresponding dominance values.

value is 0.2 or 0.8. Importantly, however, hybrids having two traits with values 0.2 and 0.8 have an arithmetic mean phenotype of 0.5, but this hybrid is mismatched rather than intermediate. This failure of simple averaging highlights the need for geometry-based dominance metrics.

Quantifying Dominance in F_1 Hybrids. We quantified three metrics of dominance. Within a cross, each dominance metric was scaled such that values of 0 indicate no dominance, values of 1 indicate the maximum dominance without transgressing the parental trait range, and values greater than 1 result from transgression (see table 1 for hypothetical hybrid phenotypes and corresponding dominance values for all three metrics).

The first dominance metric is univariate dominance ($d_{\text{univariate}}$), which considers traits individually. The $d_{\text{univariate}}$ metric measures the deviation of trait values from the ad-

ditive expectation of 0.5, regardless of direction. For a single trait, this was calculated as

$$d_{\text{univariate}} = 2(|z_i - 0.5|), \quad (1)$$

where z_i is the scaled mean phenotype of trait i . A $d_{\text{univariate}}$ value of 0 results when a trait is exactly intermediate ($z_i = 0.5$; the mean of the parental trait values, 0 and 1); a $d_{\text{univariate}}$ value of 0.5 results when the F_1 's mean trait value is halfway between intermediate and that of one parent (i.e., $z_i = 0.25$); and a $d_{\text{univariate}}$ value of 1 results when the F_1 hybrid mean equals that of one of the parents (i.e., $z_i = 0$ or $z_i = 1$). Transgressive traits have $d_{\text{univariate}}$ values >1 . We averaged $d_{\text{univariate}}$ values across traits within each cross to obtain estimates of cross mean $d_{\text{univariate}}$.

The remaining two dominance metrics consider pairs of traits at a time and are therefore calculated in two dimensions (for a general overview, see fig. 1; for examples from the data set, see fig. S2). We consider all pairs of traits, instead of all traits together, to increase the comparability of dominance values among studies measuring different numbers of traits. For crosses where three or more divergent traits were measured, we calculated two-dimensional dominance metrics for each trait pair and then took the mean of all pairwise estimates as the value for that cross.

The second metric of dominance is pairwise parent bias ($d_{\text{parent-bias}}$), which captures deviation from bivariate intermediacy in the direction of either parent. Imagine a cross between two plant species, one of which has flowers that are narrow (mean width = z_1) and red (color = z_2), representing the bivariate phenotype of $[0, 0]$, and where the other species has wide yellow flowers, represented by a bivariate phenotype of $[1, 1]$. If their F_1 hybrid's standardized phenotype is $[0, 1]$ (i.e., narrow yellow flowers), then the mean $d_{\text{univariate}} = 1$ but pairwise $d_{\text{parent-bias}} = 0$. A $d_{\text{parent-bias}}$ of 0 would also result if the F_1 hybrid was exactly intermediate between the parents (i.e., $[0.5, 0.5]$). The $d_{\text{parent-bias}}$ has a minimum value of zero when dominance is equally strong in the direction of both parents and increases indefinitely as dominance increases in a manner that is biased toward one parent. For each pair of traits, we first determined the

Table 1: Hypothetical examples of possible F_1 trait values and corresponding values for cross mean $d_{\text{univariate}}$, $d_{\text{parent-bias}}$, and d_{mismatch}

F_1 phenotype	Mean $d_{\text{univariate}}$	$d_{\text{parent-bias}}$	d_{mismatch}
[.5, .5]	0	0	0
[0, 1]	1	0	1
[1, 1]	1	1	0
[.25, .75]	.5	0	.5
[.5, 1]	.5	.5	.5
[1.25, 1]	1.25	1.25	.25

Note: Parent phenotypes are scaled to $[0, 0]$ and $[1, 1]$.

scalar projection, b , of the hybrid phenotype onto the line connecting parents. This projection is calculated as

$$b = \frac{z_1 + z_2}{k}, \quad (2)$$

where z_1 and z_2 are the hybrid values for traits 1 and 2. We then calculated pairwise parent bias as

$$d_{\text{parent-bias}} = k \cdot \left| \frac{k}{2} - b \right|, \quad (3)$$

where b is the scalar projection from equation (2), k is a scaling factor ($k = \sqrt{2}$) used to give a hybrid a phenotype with parental values for both traits (i.e., [0, 0] or [1, 1]) a $d_{\text{parent-bias}}$ value of 1, and $d_{\text{parent-bias}}$ cannot exceed $d_{\text{univariate}}$.

The third and final metric of dominance is pairwise mismatch (d_{mismatch}), which captures the perpendicular distance between the mean hybrid phenotype and the line connecting parental mean phenotypes (fig. 1). When the hybrid phenotype is on the line connecting parents (i.e., when both hybrid traits in the pair are equally displaced toward the same parent), d_{mismatch} has a minimum value of zero, and it increases indefinitely as the variance in dominance among traits increases. Returning to the earlier example of a cross between plants with divergent floral traits, d_{mismatch} values of 0 would characterize hybrids with phenotypes that are varying degrees of intermediate (e.g., [0.5, 0.5] or [0.75, 0.75]) or recover parental phenotypes [0, 0] or [1, 1]. A d_{mismatch} value of 1 results when dominance is complete but in opposite directions [0, 1] or [1, 0], which corresponds to narrow yellow flowers or wide red flowers. For each pair of traits, we calculated mismatch as

$$d_{\text{mismatch}} = k \cdot \sqrt{z_1^2 + z_2^2 - b^2}, \quad (4)$$

where z_1 and z_2 are as in equation (1) and b and k are as in equation (3).

Evaluating Patterns Caused by Sampling Error. The above metrics of dominance, applied to data, are a product of both biology—net dominance effects of genes—and measurement and/or sampling error. Such error around an intermediate phenotype would appear as dominance because we calculate dominance as the difference between the observed mean phenotype and the midparent value. In addition, a given amount of error is more likely to result in high (e.g., $d > 1$) dominance estimates when the parents involved in a cross are phenotypically similar than when they are more divergent. It is therefore important to quantify the magnitude of dominance observed due to sampling error alone.

To quantify patterns of dominance due to sampling error, we generated 1,000 simulated data sets that had an

identical structure to the raw data but where hybrid mean phenotypes were replaced with means calculated from a simulated distribution. Specifically, we generated random normal vectors (using the `rnorm` function) for each trait measured in F_1 hybrids with a length equivalent to the number of hybrids measured by authors and the original trait SD but an expected mean that was exactly intermediate between the parents (i.e., `rnorm`; $n = n_{F_1}$, $\text{mean} = \mu_{(P_1, P_2)}$, $\text{sd} = \text{SD}_{F_1}$). We then took the mean of each random vector and replaced the observed hybrid mean with the simulated mean. The simulated mean can differ from strict intermediacy due only to sampling error. We calculated each of the three dominance metrics for each cross in all simulated data sets and compared the distribution of estimates to what we observed in the original data.

Testing Possible Predictors of Dominance in F_1 Hybrids.

We explored several possible predictors of dominance motivated by previous results and theoretical predictions. For example, previous studies have determined that genetic distance between cross parents affects the frequency with which hybrid traits transgress the parent range (Stelkens and Seehausen 2009), a pattern that should be captured by our $d_{\text{univariate}}$ metric.

To determine whether genetic distance affects our dominance metrics, we computed genetic distance using gene sequence data and tested whether it was associated with any metric of dominance. To maximize the number of crosses for which we could estimate genetic distance, we used cytochrome *b* for animals and the internal transcribed spacer I and II for plants. Because the species in our data set can hybridize, it is possible that we might underestimate genetic divergence if there is hybridization and introgression in nature—this problem might be especially pronounced for the mitochondrial cytochrome *b*. We could not obtain sufficient nuclear data for animals, so the genetic distance data should be interpreted with this limitation in mind because mtDNA often seems to introgress more readily than nuclear genes (e.g., Bachtrog et al. 2006; Wang et al. 2020). Genetic distance was calculable for less than one-quarter of all crosses and only three intraspecific crosses, so we also compared dominance metrics between intraspecific and interspecific crosses—the underlying assumption being that genetic distance between parents is lower in the former compared to the latter.

Various taxon-specific reviews have arrived at different conclusions about the extent of dominance observed in hybrids. For example, Rieseberg and Ellstrand (1993) considered plants only and concluded that dominance is common in hybrids, whereas Hubbs (1955) worked on fish and concluded that dominance in hybrids is rare. To test whether there might be variation in dominance between taxa, we built a phylogeny encompassing nearly all crosses

in our data set (fig. S3) and tested for phylogenetic signal in dominance metrics. We also tested whether there are differences in dominance between predefined taxonomic groups such as plants and animals.

Finally, we tested for parent-of-origin effects. If parent-of-origin effects are common and have some systematic basis, then hybrid trait values might, for example, tend to resemble the maternal parent more than the paternal; this is testable in the present data set because many crosses ($n = 96$) were conducted in both directions.

Results

Patterns of Dominance in F_1 Hybrids. We used data gathered from the literature to generate estimates of dominance in F_1 hybrids. We first consider each trait individually and then calculate mean univariate dominance ($d_{\text{univariate}} \pm 1$ SE) for each unique cross in the data set. Considering all cross mean $d_{\text{univariate}}$ estimates together, the mean $d_{\text{univariate}}$ for traits measured in F_1 hybrids was 0.79 ± 0.078 (fig. 2A [see fig. S4 for the same figure with the X-axis extended]; median = 0.55), which suggests that the average trait is not intermediate but rather more than halfway between intermediate and parental. In $\sim 20\%$ of crosses (and 20% of individual traits), the mean $d_{\text{univariate}}$ was >1 , indicating transgression.

In addition to $d_{\text{univariate}}$, we calculated two complementary two-dimensional dominance metrics to investigate whether hybrids tend to be biased toward one parent over the other

($d_{\text{parent-bias}}$) or have mismatched combinations of divergent traits (d_{mismatch}). These metrics are different from $d_{\text{univariate}}$ because high single-trait dominance could be either in the same direction for both traits (leading to more parent bias) or in opposite directions (leading to more mismatch). We find that the mean pairwise $d_{\text{parent-bias}}$ among crosses was 0.68 ± 0.01 (fig. 2B; median = 0.44), implying that, for a given pair of traits, hybrids, on average, resemble one parent $\geq 68\%$ more than the other. The mean pairwise d_{mismatch} was 0.60 ± 0.10 (fig. 2C; median = 0.31), implying that the average hybrid is about 60% as mismatched, as is maximally possible without transgression for a given pair of traits. Mismatch did not differ between pairs of traits that were both in the same category and pairs of traits from different categories ($F_{1,102.47} = 0.0199$, $P = .88$).

We generated simulated data sets to estimate the magnitude of dominance we would expect from sampling error alone. We find that the simulation-based estimates of all three dominance metrics were approximately one-third as large as what is observed in the real data, with little variation among replicate simulations (see fig. S6). These simulation results indicate that the majority of our signal is biological rather than caused by sampling error.

Predictors of Dominance in F_1 Hybrids. We next investigated whether dominance patterns in F_1 hybrids are associated with genetic distance and phylogeny. We found no significant associations between any metric of dominance and any metric of genetic distance (see detailed results in

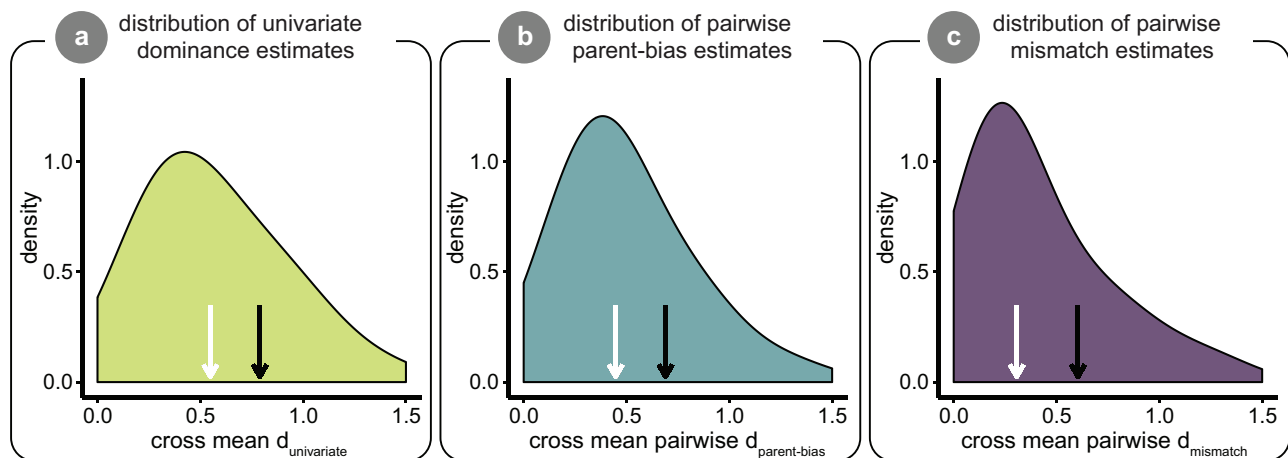


Figure 2: Patterns of dominance in F_1 hybrids. The density plots (Y-axis standardized across panels) show the three main dominance metrics contained herein, with each cross contributing at most a single value per panel. For all three dominance metrics, values of 0 indicate no dominance, values of 1 indicate the maximum without transgression, and values >1 reflect transgression. The X-axis is truncated at 1.5, but the means (black arrows) and medians (white arrows; values given in text) are calculated from the whole data set (see fig. S5 for a summary of patterns when each cross contributes a median rather than mean value). Panel a shows univariate dominance ($d_{\text{univariate}}$; eq. [1]), panel b shows parent bias (pairwise $d_{\text{parent-bias}}$; eq. [3]), and panel c shows mismatch (pairwise d_{mismatch} ; eq. [4]). Panel a contains one value from all crosses ($n = 233$), while panels b and c contain only information from crosses wherein two or more traits were measured ($n = 165$).

figs. S7–S9). In addition, there was no evidence for phylogenetic signal in any dominance metrics (all $\lambda < 1 \times 10^{-5}$, all $P = 1$) and no difference in any dominance metrics in comparisons of major clades (fig. S9). We found that dominance is lower when the parental populations have larger differences in their phenotype coefficients of variation and greater when parents are more variable, although each of these factors explains less than 1% of the variance in $d_{\text{univariate}}$ (see fig. S10). Trait type generally did not affect dominance, although chemical traits (e.g., pheromones) seemed to have higher dominance and transgression than all other trait types (fig. S11). Some caution is warranted here, however, because chemical traits were the least well-represented category in the data.

Because many crosses were conducted reciprocally (i.e., hybrid crosses were conducted with each parent species serving as dam), we could evaluate parent-of-origin effects on trait values. We found that 25.6% of traits differed significantly (at $P = .05$) between cross directions. The mean magnitude of phenotypic difference between cross directions was 0.65 SDs (units of smaller parental SD). Within each cross that was conducted in two directions, we calculated the fraction of traits that exhibited maternal bias and tested whether this fraction deviated significantly from 0.5. We found that traits of F_1 hybrids tend to resemble the maternal parent about 57% of the time. ($t_{94} = 2.034$, $P = .0447$, 95% CI = [0.502, 0.657]), suggesting that cytoplasmic or maternal effects are slightly more common than paternal effects.

Fitness Consequences of Parent Bias and Mismatch in Recombinant Sunflowers

The above analyses were motivated by the hypothesis that, compared to a hybrid that is a perfect intermediate, hybrids resembling parents should fare relatively well and hybrids exhibiting trait mismatches should fare relatively poorly. However, it is not possible to test the fitness consequences of parent bias and mismatch in the data synthesized from the literature because no studies in our data set have both individual-level phenotype and lifetime fitness data collected in the field. In addition, studies of F_1 hybrids would have limited power to detect fitness effects of parent bias or mismatch because there is little genetically based phenotypic variance among F_1 s within a cross. Comparisons across systems are undesirable because of methodological and biological variation among studies and systems. The optimal way to investigate the fitness effects of parent bias and mismatch is to examine an experimental population of recombinant hybrids—wherein there is quantitative among-individual variation in the degree of parent bias, mismatch, and fitness—and then to use these resulting data to test whether dominance metrics are associated with fitness.

Methods

Study System and Experimental Design. To evaluate the fitness effects of parent bias and mismatch, we leveraged data from a field experiment in annual sunflowers (*Helianthus*). The two parent species of the cross were *H. annuus* ssp. *annuus* (hereafter, simply *H. annuus*) and *H. debilis* ssp. *cucumerifolius* (hereafter, *H. debilis*). *Helianthus annuus* is an annual, self-incompatible diploid that is weedy and widely distributed in its native North America. *Helianthus debilis*, by contrast, is a small sunflower endemic to central Texas. The two species are highly divergent in many traits (see tables S1, S2, available online). Compared to *H. debilis*, *H. annuus* is much larger and has a slower life cycle, greater longevity, higher water-use efficiency, thicker leaves, more leaf trichomes, larger ligules and phyllaries, and a different branching architecture (Whitney et al. 2006, 2010).

After 4 weeks of growth in a greenhouse, 503 *H. annuus* \times *H. debilis* BC_1 hybrid seedlings were planted alongside individuals of both parental species in central Texas. Fitness (seed number) as well as 30 architectural, floral, eco-physiological, phenological, and herbivore resistance (e.g., trichome density) traits were measured. Of the 503 BC_1 individuals, we retained 475 in the analyses. Fifteen were excluded because of labeling mistakes and/or oversights resulting in missing trait data; we expect these exclusions were random with respect to trait and fitness values. An additional 13 plants died before some traits could be measured and were also excluded. Thus, any effects of dominance on fitness detected in our experiment reflect fertility selection rather than viability selection. Of course, dominance could also affect viability, but we could not evaluate this relationship within the current study design. We applied the same trait selection and filtering criteria as in the systematic review and retained 19 traits (see table S1 for trait details). The data from this experiment have been previously published (Whitney et al. 2006, 2010).

Quantifying Dominance Metrics in the Sunflowers. For each plant, we calculated pairwise $d_{\text{parent-bias}}$ and d_{mismatch} (eq. [3], [4]) and then took the average across all trait pairs. Mean pairwise $\ln(d_{\text{parent-bias}})$ and $\ln(d_{\text{mismatch}})$ are positively correlated in this data set ($r = 0.81$, $P < .001$; fig. S12) because the traits of many BC_1 individuals are transgressive and because high single-trait dominance sets the upper limit of both parent bias and mismatch. Therefore, we investigated their respective effects on fitness using multiple linear regressions of the form

$$\ln(W_i) = \beta_0 + \beta_1 \cdot \ln(d_{\text{parent-bias}}) + \beta_2 \cdot \ln(d_{\text{mismatch}}), \quad (5)$$

where W_i is an individual's absolute fitness (in this case, number of seeds), and $d_{\text{parent-bias}}$ and d_{mismatch} are the mean individual dominance values averaged across each trait pair

(residual error term omitted for clarity). We natural log transformed the fitness component and dominance metrics because residuals exhibited severe heteroskedasticity when the raw values were used, although the qualitative conclusions do not change if untransformed data are analyzed. Diagnostics of the regression model indicated that, in spite of the correlation between the predictors, our analysis does not suffer from multicollinearity (variance inflation factor = 4.19; maximum condition index = 8.19). We also ran the same multiple regression for each trait pair separately and asked whether the signs of regression coefficients (β_1 and β_2) were consistent with those observed in the analysis of mean pairwise $d_{\text{parent-bias}}$ and d_{mismatch} .

Results

In the BC₁ sunflowers, $d_{\text{parent-bias}}$ was positively associated with seed count ($\hat{\beta}_1 = 1.75 \pm 0.26$ [SE], $F_{1,472} = 44.68$, $P = 6.56 \times 10^{-9}$; fig. 3A), whereas d_{mismatch} had a negative association ($\hat{\beta}_2 = -2.95 \pm 0.16$, $F_{1,472} = 77.26$, $P < 2.80 \times 10^{-17}$; fig. 3B). The multiple regression explained 20% of the variation (i.e., r^2) in $\ln(\text{seed count})$. Both main effects remained significant and in the same direction if an interaction term was specified in the model. In this data set, the fitness consequences of a unit change in d_{mismatch} were larger than the fitness consequences of an equivalent unit change in pairwise $d_{\text{parent-bias}}$ ($|\hat{\beta}_1| \neq |\hat{\beta}_2|$; $F_{1,472} = 40.86$, $P = 3.94 \times 10^{-10}$). We note that pairwise trait correlations were typically quite low in these data (mean $|\rho| = 0.16$; fig. S13).

We also evaluated dominance-fitness relationships for each pair of traits separately. This analysis is heuristic because pairs of traits are not independent, but we present it to complement the above results. Considering only sta-

tistically significant coefficients, pairwise $d_{\text{parent-bias}}$ improved fitness for 67% of trait pairs and d_{mismatch} reduced fitness for 81% of trait pairs (fig. S14; see also fig. S15 for a graphical example of the trait pair with the most negative fitness consequences when mismatched). Both of these percentages are significant departures from 50%, as determined by exact binomial tests (71 of 106 significant $d_{\text{parent-bias}}$ coefficients positive, $P = 6.1 \times 10^{-4}$; 72 of 89 significant d_{mismatch} coefficients negative, $P = 3.2 \times 10^{-9}$). Thus, the fitness consequences of pairwise $d_{\text{parent-bias}}$ and d_{mismatch} are consistent between analyses of an individual's mean value averaged over all trait pairs and when considering pairs of traits individually.

We last evaluated whether the fitness effects of parent bias and mismatch were driven by individuals with transgressive dominance values. We first removed all individuals from the data set with mean pairwise d_{mismatch} values > 1 and then conducted the same multiple regression analysis as above. We find that both main effects remain significant and in the same direction as above (results not shown but included in the R scripts deposited in the Dryad Digital Repository [<https://doi.org/10.5061/dryad.d7wm37q09>; Thompson et al. 2021]; $n = 430$ plants). When conducting the analysis after removing individuals with transgressive mean pairwise $d_{\text{parent-bias}}$ values, the main effect terms were in the same direction as above, but only mean pairwise d_{mismatch} remained significant ($n = 163$ plants).

Discussion

In this article, we compiled data from studies that measured phenotypic traits in F₁ hybrids to characterize general patterns of hybrid trait expression. We then investigated whether the observed dominance could be predicted by genetic distance

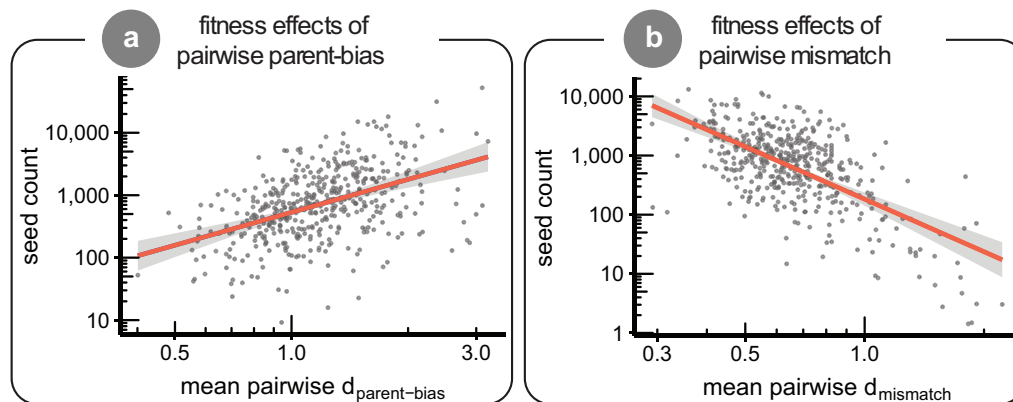


Figure 3: Effect of parent bias and mismatch on fitness in *Helianthus annuus* × *Helianthus debilis* backcross (BC₁) hybrid sunflowers growing in the field. The points are partial residuals extracted from a multiple regression using visreg (Breheny and Burchett 2017). Each point represents one individual hybrid plant ($n = 475$). Both axes are \log_{10} transformed. Panel *a* illustrates the effect of parent bias, and panel *b* illustrates the effect of mismatch.

between the parents or phylogeny. Last, we tested whether parent bias and mismatch were associated with fitness in a field experiment with recombinant hybrid sunflowers. The systematic review reveals that dominance is common: individual traits in F_1 hybrids are typically halfway between the parental midpoint and one parent's phenotype. This dominance of individual traits causes hybrids to resemble one parent more than the other and to be mismatched. Neither genetic distance nor phylogeny predicted any metric of dominance, indicating that it will be difficult to make accurate predictions about the patterns of dominance for any individual cross. In the sunflower data, pairwise parent bias improved fitness and mismatch reduced fitness. We discuss these results in the context of previous research on dominance and trait expression in hybrids and highlight the implications for speciation research.

Genetic Underpinnings of Dominance and Mismatch

Although dominance is commonly observed in F_1 hybrids, we do not know which trait values are derived versus ancestral and therefore cannot relate our data to most theories on the evolution of dominance (e.g., Haldane's [1924, 1927] sieve). In any case, interpopulation phenotypic divergence in most traits is likely underpinned by many quantitative trait loci (QTL; Otto and Jones 2000), and our results hint at two general features of such QTL. First, high dominance in F_1 s implies that, for many alleles underlying adaptation, the heterozygote phenotype is not simply the arithmetic mean of the alternative homozygote phenotypes. Such patterns have been documented in many QTL-mapping studies. For example, Miller et al. (2014) quantified dominance of QTL underlying marine-freshwater phenotypic divergence in threespine stickleback (*Gasterosteus aculeatus*) and found that the majority of QTL underlying marine-freshwater divergence in threespine stickleback had partial dominance effects. Second, the QTL underlying different traits seem to have unequal mean dominance coefficients—dominance for some traits is biased toward one parent, and dominance in other traits is more intermediate or biased toward the other.

Any specific value of dominance is likely particular to the environment in which study organisms are measured. Dominance of individual loci has long been understood to depend on the environment (Hersh 1934), and substantial evidence suggests that hybrid phenotypes vary depending on prevailing environmental conditions (e.g., Demuth and Wade 2007). Although the results of each individual study are likely influenced by gene-by-environment interactions ($G \times Es$), we can think of no reason why the overarching patterns documented here would change in any particular way if $G \times Es$ did not play a role.

In F_1 hybrids, transgressive trait expression might result from epistasis, although additive gene action seems more

common in reviews of the topic (Rieseberg et al. 1999). Many traits in our data set transgressed the parental range, but we caution that this does not necessarily hint at one underlying genetic architecture over another. Dominance values in an F_1 are the net effects of dominance at multiple individual loci plus additive and epistatic effects between loci, with transgressive effects at the tail of the distribution of possible outcomes. We therefore see our results in figure 2 as a documentation of pattern and do not speculate further about underlying causes.

Patterns and Predictors of Dominance

Our results corroborate some previous findings but are inconsistent with others. Hubbs (1940) suggested that fishes show additive inheritance “as a very general rule,” whereas Rieseberg and Ellstrand (1993) suggested plant hybrids are best characterized as being “a mosaic of both parental and intermediate morphological characters rather than just intermediate ones” (205). Our quantitative analysis paints a picture more akin to mosaicism than strict intermediacy. In addition, we find no evidence for any major differences in dominance among taxonomic groups, which suggests that the choice of study taxon does not bias estimates of dominance.

Stelkens and Seehausen (2009) found that the genetic distance between parents was positively correlated with transgression frequency—the tendency for traits to fall outside the range of parental values. We used an almost entirely independent data set and found that genetic distance did not predict transgression or any other aspect of trait expression in hybrids. Perhaps the most likely cause of this discrepancy is that, in addition to ordinary traits like those considered herein, Stelkens and Seehausen (2009) also considered more traditional fitness traits. Transgression in such traits could reflect intrinsic hybrid incompatibility (e.g., small body size due to poor condition or low seed production due to inviable ovules) and heterosis (e.g., larger body size or high seed count due to overcoming inbreeding depression in parents). Incompatibility increases with parental genetic divergence (Orr 1995; Matute et al. 2010; Moyle and Nakazato 2010; Wang et al. 2015), and heterosis seems to as well, until inviability becomes substantial (Wei and Zhang 2018). Importantly, such inviability and heterosis would manifest as high $d_{\text{univariate}}$ or transgression using our approach. Because we consider traits that are putatively under stabilizing selection within populations, the mechanisms linking genetic distance with transgression in earlier studies do not apply to the present data set.

Although we specifically excluded traits that are directly linked to fitness, it remains possible that hybrid incompatibilities underlie some patterns documented herein. For example, one study conducted crosses between wild *Drosophila melanogaster* and *Drosophila simulans*. Male hybrids of

this cross are (typically) inviable, and so David et al. (2002) report only data for females in parent species. If there is inviability that is undetected in some studies, this might influence estimates of dominance. A lack of relationship between genetic divergence and dominance, however, suggests that incompatibility is not likely the primary driving force of the observed patterns.

Fitness Consequences of Mismatch

Our results clarify the potential for dominance to have a role in driving progress toward speciation. The data collected from the literature challenge the conjecture that reduced F_1 fitness is due only to phenotypic intermediacy and hybrids falling between parental niches (Coyne and Orr 2004; Nosil 2012). Rather, F_1 hybrids often possess novel multivariate phenotypes that are mismatched for divergent traits. In nature, the phenotype of an organism is an integrated suite of traits that function together to influence performance and, ultimately, fitness (Arnold 1983; Brodie 1992). Because mismatch, caused by dominance in conflicting directions among traits, breaks up suites of integrated traits, mismatched hybrids might be poorly suited to any environment.

In the sunflower data, we found that pairwise parent bias improved fitness and that mismatch reduced fitness. Importantly, mismatch was more detrimental than parent bias was beneficial. Meanwhile, F_1 hybrids are likely closer in phenotype to one parent than the other and yet also have some traits resembling the less-similar parent that might render them unable to survive and reproduce in the similar-parent's niche or perhaps in any niche at all. At present, it is not clear how general this finding is. It would be valuable to conduct more field experiments with recombinant hybrids to arrive at generalities in the ways that parent bias and mismatch affect fitness.

It is informative to examine the trait pairs that had the highest fitness consequences when mismatched (fig. S14). The most negative fitness effects resulted when development duration was mismatched with height of the uppermost branch (fig. S15). *Helianthus annuus* has a more prolonged phenology than *Helianthus debilis*, taking about 28 days longer to initiate inflorescence formation in this experiment (table S2). In addition, *H. annuus* is a tall plant with branches distributed throughout the main stem (uppermost branch height above ground: mean = 133 cm), whereas *H. debilis* is a much shorter plant, with branches clustered at the base (uppermost branch: mean = 17 cm). Plants that mature slowly (like *H. annuus*) but are short and compact (like *H. debilis*) have lower fitness than rapid-developing compact plants (fig. S15). The parental phenotypes apparently reflect a trade-off, where the benefits of being a compact plant are compromised by a prolonged development.

Due to the segregation of divergent alleles, individual backcross and F_2 hybrids might be more mismatched on average than F_1 s. Such increased mismatch would result in ecological hybrid breakdown—where recombinant hybrids have lower fitness than F_1 s due to increased trait mismatches (Arnegard et al. 2014). In the present study, we were limited to comparing cross mean data. It would be valuable to compile data for hybrid crosses raised in a common environment where data for individual hybrids can be analyzed. In particular, quantifying how the magnitude of phenotypic mismatch observed in backcross and F_2 hybrids compares to F_1 s would allow us to infer the likely strength of mismatch-based hybrid breakdown. Although F_2 s are more variable than F_1 s (East 1916), if divergent traits are linked in the genome (e.g., Westram et al. 2018) or are controlled by the same pleiotropic allele (e.g., Rennison et al. 2015), then segregation might not result in increased mismatch.

Conclusion

In this study, we synthesized data from 198 studies to describe general patterns of phenotype expression in F_1 hybrids. Compared to previous studies with a similar goal, the distinguishing features of our analysis are that we used quantitative trait data rather than bins of “parental” versus “intermediate,” looked across several major clades, and examined divergently selected traits in wild organisms. For individual traits, reasonably high dominance is the rule rather than the exception. Previous studies have documented the phenomenon where dominance acts in opposite directions for different traits (Matsubayashi et al. 2010). We built on these previous studies by quantifying mismatch using simple geometry and demonstrating that mismatch affects the average hybrid to a fairly substantial degree.

Previous authors have qualitatively drawn a link between trait mismatches and hybrid fitness (e.g., Arnegard et al. 2014; Cooper et al. 2018), and we add to these earlier results by directly linking individual-level mismatch metrics to fitness in sunflowers. This result contributes to a growing literature on trait interactions in hybrids, and we suggest that future studies use our approach (or a complementary approach) to test the fitness consequences of mismatch directly. Such trait interactions are similar to Bateson-Dobzhansky-Muller hybrid incompatibilities (BDMIs), with fitness consequences mediated via ecology. Ecological BDMIs have the opportunity to affect many F_1 hybrids and could be a major mechanism of extrinsic postzygotic isolation. Only field observations and experiments can provide the data that are necessary to test this hypothesis.

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Statement of Authorship

K.A.T. conceived of the systematic review and designed the protocol with input from M.U.-C. and D.S. K.A.T. and M.U.-C. screened studies and collected data, and K.A.T. contacted authors for data if necessary. K.A.T. checked all data for accuracy. K.D.W. had the idea to explore the fitness effects of parent bias and mismatch in sunflowers, and K.D.W. and L.H.R. contributed sunflower data. K.A.T. analyzed the data and wrote the paper with input and contributions from all authors.

Data and Code Availability

All data and analysis code used in this article have been deposited in the Dryad Digital Repository (Thompson et al. 2021; <https://doi.org/10.5061/dryad.d7wm37q09>).

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Photograph of the common garden of *Helianthus annuus* × *H. debilis* backcross hybrids, at Ladybird Johnson Wildflower Center in Austin, Texas. Photo: Ken Whitney.