

REVIEW AND SYNTHESIS

Hybridisation is associated with increased fecundity and size in invasive taxa: meta-analytic support for the hybridisation-invasion hypothesis

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Abstract

The hypothesis that interspecific hybridisation promotes invasiveness has received much recent attention, but tests of the hypothesis can suffer from important limitations. Here, we provide the first systematic review of studies experimentally testing the hybridisation-invasion (H-I) hypothesis in plants, animals and fungi. We identified 72 hybrid systems for which hybridisation has been putatively associated with invasiveness, weediness or range expansion. Within this group, 15 systems (comprising 34 studies) experimentally tested performance of hybrids vs. their parental species and met our other criteria. Both phylogenetic and non-phylogenetic meta-analyses demonstrated that wild hybrids were significantly more fecund and larger than their parental taxa, but did not differ in survival. Resynthesised hybrids (which typically represent earlier generations than do wild hybrids) did not consistently differ from parental species in fecundity, survival or size. Using meta-regression, we found that fecundity increased (but survival decreased) with generation in resynthesised hybrids, suggesting that natural selection can play an important role in shaping hybrid performance – and thus invasiveness – over time. We conclude that the available evidence supports the H-I hypothesis, with the caveat that our results are clearly driven by tests in plants, which are more numerous than tests in animals and fungi.

Keywords

Adaptive evolution, colonisation, hybridisation, introgression, invasion genetics, phylogenetic meta-analysis, polyploidy, range expansion, weeds.

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INTRODUCTION

The study of what determines invasion success in non-native organisms has a long history (Elton 1958; Baker 1974), although not always a successful one (Perrins *et al.* 1992; Mack 1996). Genetic and evolutionary factors have been considered important (Baker & Stebbins 1965; Crawford & Whitney 2010), including the hypothesis that interspecific hybridisation may promote invasiveness (Stebbins 1985; Abbott 1992). This Hybridisation-Invasion (H-I) hypothesis has received particular attention in the past decade-and-a-half following the publication of Ellstrand & Schierenbeck (2000). In addition to summarising the mechanisms by which hybridisation could enhance invasiveness, Ellstrand and Schierenbeck compiled preliminary support for the hypothesis via a list of 28 taxa in which hybridisation has preceded invasiveness. This original list has since been expanded to 35 hybrid taxa (Schierenbeck & Ellstrand 2009), contributing to the increasing acceptance of the idea that hybridisation can be a driver of biological invasions (e.g. Darling *et al.* 2008; Le Roux & Wicczorek 2009; but see Whitney *et al.* 2009). As species are transported globally with increasing frequency, invasive hybrids will continue being introduced to new regions, and new opportunities for interspecific mating will undoubtedly result in the formation of novel hybrid taxa. The hypothesised connection between hybridisation and invasiveness is,

therefore, likely to remain a critical issue, both for conservation and for better understanding the evolutionary ecology of colonising species. However, despite rapidly growing interest in this topic, we currently lack a comprehensive assessment of the evidence either supporting or refuting a causal link between hybridisation and invasiveness.

Ellstrand & Schierenbeck (2000) outlined several, non-mutually exclusive, mechanisms by which hybridisation could enhance invasiveness; we highlight them briefly here (see also Rieseberg *et al.* 2007). First, hybridisation can create novel phenotypes relative to the parental taxa, increasing the likelihood of survival and establishment success in novel habitats. Such novelty includes transgressive phenotypes, where hybrids exhibit trait values that fall outside the range of their parents (Rieseberg *et al.* 1999), as well as novel combinations of parental phenotypic traits (Hovick *et al.* 2012). Second, hybridisation can lead to increased phenotypic and genetic variation relative to the parental taxa, which may help hybrids better cope with environmental stochasticity and increase their evolutionary potential (Anderson & Stebbins 1954; Stebbins 1959). Heterosis is a special case of increased genetic variation, where hybrids (particularly F₁s) experience performance gains due to increased heterozygosity. When hybridisation is accompanied by mechanisms that stabilise heterotic lineages (i.e. polyploidy, clonal growth or agamospermy), the resulting hybrids may experience increased invasiveness (e.g. Parepa

et al. 2014). Finally, if the parental taxa are relatively isolated and occur in small populations, hybridisation could lead to the purging of genetic load, and the resulting fitness boost could increase invasiveness (Ellstrand & Schierenbeck 2000). To our knowledge, this final mechanism has not yet been demonstrated empirically.

Establishing a causal relationship between hybridisation and invasiveness can be challenging. A first challenge is that, because many hybrid taxa are sterile, performance assessments cannot always rely on fecundity as an indicator of potential population growth rates. Second, the outcomes of performance comparisons between hybrids and parents frequently depend on which hybrid class (F_1 , BC_1 , etc.) is examined (Arnold & Hodges 1995; Arnold & Martin 2010). For example, hybrids experiencing heterosis in the F_1 generation may experience hybrid breakdown as segregating genes in subsequent generations lead to decreasing fitness (Hooftman *et al.* 2007). Even within the same hybrid class, hybrid individuals can be highly variable, resulting in biologically meaningful differences among lineages with differing parental backgrounds (Pyšek *et al.* 2003; Hartman *et al.* 2013). Third, the environmental context can determine relative performance of hybrids vs. parents (Arnold & Martin 2010), and in at least one case, hybrids outperform their parental taxa by way of different traits in different environments (Hovick *et al.* 2012). These considerations suggest that the performance metric, the choice of hybrid material and the environmental setting all need to be carefully considered to provide meaningful tests of the H-I hypothesis.

A further challenge in evaluating the H-I hypothesis is that observational studies documenting increasing frequencies of hybrids relative to their parental taxa tell us nothing definitive about *relative* hybrid performance and therefore invasiveness. Even in the absence of a hybrid advantage, interspecific mating will often lead to at least low levels of introgression of selectively neutral alleles, creating hybrid swarms (e.g. Hasselman *et al.* 2014). Yet, some studies of hybrid invaders interpret high abundances of hybrids relative to their parental taxa as evidence that hybridisation has promoted invasiveness in that taxon (e.g. Urbanska *et al.* 1997; Moody & Les 2002; Tavalire *et al.* 2012; Wu *et al.* 2013). This practice can result in unsubstantiated claims regarding the role of hybridisation being propagated throughout the literature.

Because of these challenges, testing the H-I hypothesis clearly requires an experimental approach. At the most basic level, these experiments must compare hybrid performance with that of the parental taxa in a common environment in order to remove the effects of environmental variation and historical chance while focusing on genetically based performance differences among taxa. In any such experiment, the proper parental taxa must be used as benchmarks for comparison with hybrid performance. Ideally, both parents would be included in any such tests, but at a minimum the more invasive parental taxon must be. For example, if an invasive hybrid results from hybridisation between a relatively benign native species and an introduced invasive species, then performance assessments that exclude the invasive parent are unlikely to be informative: the invasive parent may have been capable of spreading just as rapidly and

achieving the same densities even if hybridisation had not occurred. Unfortunately, a surprising number of studies fail to include comparisons to the more invasive parent (see Discussion, below).

Previous compilations of taxa that are both invasive and hybrid-derived (Ellstrand & Schierenbeck 2000; Schierenbeck & Ellstrand 2009) represent a vital first step in determining whether hybridisation and invasiveness are causally related. However, these compilations were not intended to be exhaustive. More importantly, given that hybridisation is not rare (animals: Schwenk *et al.* 2008; plants: Whitney *et al.* 2010a; fungi: Giraud *et al.* 2008), we should expect some fraction of invasive taxa to be hybrids, even in the absence of an underlying causal relationship. Our aims are to clarify the criteria needed for evaluating the H-I hypothesis and to evaluate tests meeting these criteria that have been conducted to date. We perform a systematic review to address three questions: (1) based on a comprehensive evaluation of the literature, how frequently has hybridisation been associated with invasiveness in plants, animals, and fungi? (2) to what extent has the H-I hypothesis been evaluated experimentally? and (3) do those evaluations support or refute the H-I hypothesis? We expand earlier compilations of invasive hybrids (Schierenbeck & Ellstrand 2009) by including a number of new hybrid taxa. In addition, we present recommendations for designing future tests of whether hybridisation promotes invasiveness.

METHODS

To investigate the H-I hypothesis, we carried out a systematic review (*sensu* Liberati *et al.* 2009) that included meta-analyses. In doing so, we followed the PRISMA statement (Liberati *et al.* 2009) to the extent possible; note that PRISMA was developed for systematic reviews in medicine and thus not all provisions are relevant here. Our first step was to conduct an exhaustive literature review in an attempt to identify all plant, animal, and fungal taxa for which interspecific hybridisation is postulated to have enhanced invasiveness or contributed to geographic range expansions. We then assessed the extent to which this hypothesis has been tested experimentally, and then quantified the effects of hybridisation on invasiveness using meta-analysis. Following Richardson *et al.* (2000), we define invasiveness as a measure of the ability of a species, without human assistance, to increase in population size and spatial distribution following introduction. However, here we have relaxed the 'introduction' criterion to also include a handful of systems where both parents are native to the region from which a hybrid has subsequently spread. Thus, our dataset includes putatively invasive hybrids originating via a number of possible scenarios: (1) hybridisation in the native range, followed by local or regional range expansion, (2) hybridisation in the native range, followed by introduction to a novel region, (3) hybridisation in the novel range between two (or more) introduced parents, and (4) hybridisation in the novel range between one introduced and one native parent. These scenarios are not mutually exclusive because in some systems hybrids have been introduced repeatedly to novel regions and/or the parental taxa recurrently hybridise.

Literature search criteria

On May 10, 2012 (and again on August 5, 2013 to update our dataset), we searched Thomson Reuters Web of Science (<http://apps.webofknowledge.com>) for the keywords 'hybrid*' and 'inva*', subsequently limiting our records to those in the following categories (to minimise references from the medical literature): Ecology, Evolutionary Biology, Plant Sciences, Marine and Freshwater Biology, Entomology, Zoology, Fisheries and Agronomy. This search yielded 945 references. On the same days, we also conducted a forward citation search on three seminal papers that address the implications of hybridisation for biological invasions (Stebbins 1985; Abbott 1992; Ellstrand & Schierenbeck 2000); this added 593 references to our list. We read all 1538 abstracts and every study in which an invasive or weedy species had been determined to be a hybrid, retaining studies in which hybridisation was linked to invasiveness. Additional relevant references cited by these studies were added to our database as we encountered them. We kept a running list of hybrid systems that fit our criteria (see following paragraph), and once we had finished reviewing the studies in our database we conducted one additional taxon-specific search for each of the 72 hybrid systems identified (last updated August 5, 2013) to ensure we had not overlooked any experimental parent-hybrid comparisons in those systems. These study selection steps are summarised in Appendix 1, and Appendix 2 presents the resulting list of 72 systems in which hybridisation has a presumed link to invasiveness. We then confirmed that the use of a single search engine did not result in appreciable numbers of relevant studies being missed (Appendix 3).

Our search included hybrid plant, animal and fungal taxa (including the 'fungoid' stramenopiles; bacteria were omitted). We excluded hybrids that have only been synthesised experimentally (i.e. have no analogues in nature), and we excluded transgenic hybrids where hybrid advantage is linked to transformed genes such as those providing herbicide resistance. While there are many fascinating systems where intraspecific hybridisation (i.e. 'wide crossing') may have enhanced invasiveness (Lavergne & Molofsky 2007; Culley & Hardiman 2009; Geiger *et al.* 2011), we limited our review to interspecific hybridisation. Finally, one interspecific hybrid system identified previously (Schierenbeck & Ellstrand 2009) as a potential example of the H-I process was excluded because recent evidence argues against its hybrid origin ('strawhull' rice: Reagon *et al.* 2011; Sun *et al.* 2013).

Assessing the literature: what do we know about hybrid invaders?

For each hybrid system we recorded basic biological information (see Appendix 2) including growth form (for plants: tree, herb, grass), life history (e.g. annual, perennial) and ploidy of the parental and hybrid taxa. We recorded whether the parental taxa had commercial origins (i.e. horticulture, agriculture or the pet trade), the provenance of parental taxa (native or introduced) and whether hybridisation occurred before or after introduction to a novel region.

Lastly, for each system we collected information about the strength of evidence supporting the H-I hypothesis. We noted

whether such inferences were based on *ad hoc* observations, observational studies (measurements taken in naturally occurring populations), lab- or greenhouse-based experimental studies, or field-based experimental studies conducted in a common environment (including common garden and mesocosm experiments). We recorded the metrics by which hybrid performance was assessed and the parental taxa to which hybrid performance was compared. Finally, we recorded which hybrid class(es) were investigated.

Meta-analysis: do hybrids outperform parents?

For the meta-analysis, we identified every study in our dataset conducting an experimental hybrid-parent performance comparison, including field-, greenhouse-, and lab-based experiments. We excluded non-experimental observations from natural populations, as this approach does not permit taxon-specific (i.e. genetic) effects to be separated from environmental effects. We also excluded performance comparisons that were unable to test the H-I hypothesis because of uninformative benchmarks (e.g. studies failing to compare a hybrid with its most invasive parental taxon). We extracted performance data for hybrids and their parental taxa, grouping performance metrics into three categories: fecundity (including for *Lactuca*, the product of germination rate, survival rate and seed output plant⁻¹; see Hooftman *et al.* 2005), survival and organism size. We consider these individual performance metrics to be potential components of population growth rates and thus proxies for invasiveness, while acknowledging that they can be imperfect indicators (see Discussion). For plants, roughly half of the reported fecundity estimates included values of zero for individuals that died before setting seed (*Helianthus*, *Lactuca* and *Sorghum*), while other estimates excluded pre-reproduction mortality (*Reynoutria*, *Senecio vulgaris* and *Senecio squalidus*); *Raphanus* fecundity estimates in our database represent a combination of both approaches. Estimates including pre-reproduction mortality are likely to be more robust indicators of population growth rates (see Discussion), but we included both types of estimates for meta-analyses. For the two hybrid fungal pathogens in our dataset only pathogenicity was reported, and we considered this a fecundity proxy for our meta-analysis. We extracted means and standard deviations (or the data needed to calculate them) from tables and figures, using in the latter case the object measurement tool in Adobe Acrobat Professional version 7 (Adobe Systems Inc., San Jose, CA, USA).

We used Hedges' *d* as our effect size metric:

$$d = \frac{\bar{Y}_{Hyb} - \bar{Y}_{Par}}{s} J,$$

where \bar{Y}_{Hyb} and \bar{Y}_{Par} are mean performance of the hybrid and parental taxa, *s* is the pooled standard deviation and *J* is a small-sample correction factor (Rosenberg *et al.* 2013). Positive values for *d* thus indicate hybrids that outperform their parents, as predicted by the H-I hypothesis. If multiple hybrid classes were considered in a single experiment, we extracted data separately by hybrid class (e.g. resynthesised F₁ vs. wild hybrids). Some of the studies in our meta-analysis reported data from both parental taxa, in which case we calculated

Hedges' d twice, once for the hybrid relative to the more 'invasive' parent (i.e. that with higher fecundity, larger size or higher survival), and a second time for the hybrid relative to mean performance of both parents.

We performed a series of data-aggregation steps to minimise non-independence in our dataset. When multiple performance metrics fitting one of our categories were reported in a single study, we selected the most comprehensive (e.g. total biomass instead of aboveground biomass). For studies conducted using multiple experimental treatments, we selected the treatment most closely approximating natural conditions in the field (i.e. herbivores present); lacking an obvious selection on that basis, we chose one at random. We used fixed-effect meta-analysis with inverse variance weighting to aggregate effect sizes from multiple sites or habitats within a single study (Mengersen *et al.* 2013), doing so separately for each parental taxon and hybrid class. We used weighted means to aggregate data from multiple hybrid classes within an experiment, using two alternative aggregation approaches. In the first, we simply combined data from all hybrid classes; this can be used to calculate an overall hybrid effect, but it ignores meaningful distinctions between the types of hybrids used across studies. Thus, in the second approach we distinguished three hybrid categories: (1) naturally occurring, or 'wild' hybrids usually assumed to be advanced-generation hybrids, (2) resynthesised F_1 hybrids from experimental crosses, and (3) resynthesised post- F_1 hybrids from experimental crosses (a broad category, ranging from F_2 and BC_1 to F_{10} hybrids). Finally, for hybrid taxa that had been studied in multiple studies, we aggregated effect sizes using one final fixed-effects meta-analysis, yielding no more than one effect size per species in every analysis. We conducted random-effect meta-analyses with inverse variance weighting on these data in R (version 3.0.2; R Development Core Team 2013) using the *metafor* package (version 1.9-3; Viechtbauer 2010). As a measure of heterogeneity in our analyses we present I^2 values for each model (Higgins & Thompson 2002). I^2 ranges from 0 to 100% and can be interpreted as the proportion of variability in a given effect size estimate due to between-study heterogeneity.

Because we expected the group of resynthesised post- F_1 hybrids to be a heterogeneous sample, we also created a subset of our full dataset for more detailed analyses using meta-regression (Mengersen *et al.* 2013). For the few hybrid taxa in which performance data from multiple hybrid classes were reported, we re-aggregated effect sizes within and among studies (as above) to yield a single effect size per taxon and per hybrid class. This gave distinct effect sizes for wild hybrids, F_1 s, generation 2 hybrids (including F_2 , BC_1 and progeny of selfed F_1 s), generation 3 hybrids (including F_3 , BC_2 and progeny of selfed F_2 s) and so on. We included hybrid class as a continuous, fixed effect in meta-regressions, which tested for significant increases or decreases in effect size across generations. Because hybrid class is unknown for wild hybrids in the dataset, we omitted them from these analyses. To account for multiple effect sizes per species, we used a multivariate approach in *metafor* (the *rma.mv* command), specifying hybrid taxon as a random factor and adding a study-level random variable to achieve a random-effects meta-regression. Where

the hybrid class effect was significant it was sometimes inconsistent across taxa, so in these cases we re-ran random-effects meta-regressions separately for each hybrid taxon in the dataset (note that data are lacking to assess taxon \times class interactions statistically). All meta-regressions included an intercept, although we report only on inferences regarding significance of the slopes.

Because all species have a shared evolutionary history, non-independence among species is an important consideration for meta-analyses where effect sizes can be mapped onto phylogenies (Lajeunesse 2009; Chamberlain *et al.* 2012). We conducted phylogenetic meta-analyses using PhyloMeta version 1.3 (Lajeunesse 2011) to account for this non-independence. A phylogeny was constructed as follows: a base topology of plant taxa was derived from Phylomatic v.3 (Webb & Donoghue 2005) using tree R20120829; resolution within Asteraceae was added using topologies in Funk *et al.* (2009); animal and fungal taxa were added based on Maddison & Schulz (2007). We aged internal nodes for the phylogeny of plant taxa based on Wikström *et al.* (2001), using the *bladj* algorithm in Phylocom to interpolate ages of undated nodes (Webb *et al.* 2008). We added ages to all remaining nodes using the Expert Result dates from Hedges *et al.* (2006). This base tree with all taxa and node ages is presented in Appendix 4. Phylogenetic meta-analysis results did not differ qualitatively from non-phylogenetic results. Because of this concordance and because PhyloMeta does not support meta-regression, for the sake of consistency and ease of interpretation we present results only from non-phylogenetic meta-analyses and meta-regressions in the main text; see Appendix 4 for phylogenetic meta-analysis results.

The results we present make no distinction between experiments conducted in the field vs. lab or greenhouse experiments. Where sample sizes were large enough to run analyses using only field-collected data, outcomes were similar to those using the more complete dataset (data not shown); heterogeneity tests also indicated similar effect sizes in field- vs. lab-based investigations (Appendix 5; see Table 1 for Field/Lab designations). Because of limited sample sizes, we present comparisons between hybrids and their 'more invasive' parent only. Comparisons of hybrid performance to the average performance of both parents yielded similar results, although with slightly larger effect sizes (data not shown); the results presented below can therefore be considered conservative.

RESULTS

Including those that have been identified in previous reviews (Ellstrand & Schierenbeck 2000; Schierenbeck & Ellstrand 2009), we found 72 hybrid systems (i.e. a hybrid taxon and its two or more parental species) for which hybridisation has been putatively associated with invasiveness, weediness or range expansion (Appendix 2). The vast majority are plants ($n = 59$ systems), followed by fungal pathogens (including fungi and stramenopiles; $n = 8$) and animals ($n = 5$). Plant hybrids in our database come from 20 families, primarily Asteraceae ($n = 16$), Poaceae ($n = 8$) and Brassicaceae ($n = 6$).

Table 1 Experimental studies included in meta-analyses.

Hybrid Taxon	Parental Taxa	Field/ Lab	Hybrid Classes [§]	Fecundity	Survival	Size	Reference
Plant taxa							
<i>Carpobrotus</i> hybrids [¶]	<i>C. edulis</i> ^E × <i>C. chilensis</i> ^E	Field	Wild		W>P1>P2 [†]	P2=P1=W	Vila & D'Antonio 1998b
		Field	Wild		W=P2=P1	W=P1=P2	Vila & D'Antonio 1998a
		Field	Wild		W=G ₂ =P2>P1	P2 ^a =P1 ^{ab} =W ^b	Weber & D'Antonio 1999
<i>Helianthus annuus texanus</i>	<i>H. a. annuus</i> ^N × <i>H. debilis</i> ^N	Field	Wild, BC ₁	W>P1 ^a =P2 ^{ab} =G ₂ ^b	W=G ₂ =P2>P1	P1=W=G ₂ >P2 [†]	Whitney <i>et al.</i> 2006, 2010b
		Field	Wild, BC ₁ , BC ₇	G ₇ =W=P1>P2>G ₂	W ^a =P2 ^{ab} =G ₂ ^{ab} =P1 ^b >G ₇	W=P1>G ₇ >G ₂ >P2	Hovick <i>et al.</i> unpub. (see Appendix 6)
		Field	Wild, BC ₁ , BC ₄	W=P1=G ₄ >G ₂	P1 ^a =G ₂ ^a =G ₄ ^{ab} =W ^b	P1 ^a =G ₄ ^{ab} =G ₂ ^b =W ^b	Whitney <i>et al.</i> unpub. (see Appendix 6)
<i>Lactuca</i> hybrids	<i>L. serriola</i> ^N × <i>L. sativa</i> ^E	Field	BC ₁ , S ₁	G ₂ >P2=P1	G ₂ >P2>P1	P2=G ₃ =P1	Hartman <i>et al.</i> 2013
		Field	F ₁ , S ₁₋₃ , BC ₁ S ₁ , BC ₁₋₃	G ₁ ^a =G ₂ ^{ab} =G ₃ ^{bc} =P1 ^{bc} =G ₄ ^c >P2	G ₁ ^a =G ₂ ^{ab} =G ₃ ^b =G ₄ ^b	W>P1	LaRue <i>et al.</i> 2013
<i>Myriophyllum</i> hybrids [¶]	<i>M. spicatum</i> ^E × <i>M. sibiricum</i> ^E	Field	BC ₁ S ₁	P1=G ₃ >P2	G ₃ =P1>P2	G ₃ >P1	Campbell & Snow 2007
<i>Raphanus</i> hybrids	<i>R. raphanistrum</i> ^E × <i>R. sativus</i> ^E	Field	G ₃	P1>G ₃ [*]	G ₄ >P1	G ₃ >P1*	Campbell <i>et al.</i> 2006;
		Field	G ₄	G ₄ >P1	G ₄ >P1	G ₄ >P1	Campbell <i>et al.</i> 2006;
		Field	G ₄	W>P1>P2	W>P1>P2	P1=G ₄ *	Hovick <i>et al.</i> 2012
		Field	F ₁	P1>G ₁ [*]	P1>G ₁ ^{*,†}	W=P2>P1	Ridley & Ellstrand 2009
		Field	F ₂ , F ₁₀	P1=G ₂ ; G ₁₀ =P1			Snow <i>et al.</i> 2001
<i>Reynoutria × bohemica</i> [¶]	<i>R. japonica</i> ^E × <i>R. sachalinensis</i> ^E	Field	Wild		P1=W=P2 ^{*,†}	P2=W=P1	Snow <i>et al.</i> 2010*
		Field	Wild		P1=W>P2*		Pyšek <i>et al.</i> 2003
		Field	Wild		W=P1=P2 ^{*,†}		Brabec & Pyšek 2000
<i>Senecio vulgaris</i> var. <i>hibernicus</i>	<i>S. squallidus</i> ^E × <i>S. vulgaris</i> var. <i>vulgaris</i> ^N	Field	F ₁ , BC ₁ , F ₂	G ₂ =G ₁ =P1			Gammon <i>et al.</i> 2010
<i>Senecio squallidus</i>	<i>S. aethnensis</i> ^E × <i>S. chrysanthemumifolius</i> ^E	Lab	Wild		W=P1=P2*	W>P2=P1*	Parepa <i>et al.</i> 2014
		Lab	Wild			W=P1*	Richards <i>et al.</i> 2008
		Lab	Wild			P1=W*	Roufied <i>et al.</i> 2011
<i>Sorghum alnum</i>	<i>S. halepense</i> ^E × <i>S. bicolor</i> ^E	Field	Wild	P1=W=P2	W=P1=P2*	P2=W=P1	Hawkes <i>et al.</i> 2010
<i>Spartina</i> hybrids [¶]	<i>S. alterniflora</i> ^E × <i>S. foliosa</i> ^N	Lab	Wild	P2=W>P1		P2 ^a =W ^{ab} =P1 ^b	Brennan <i>et al.</i> 2012
<i>Typha × glauca</i> [¶]	<i>T. angustifolia</i> ^E × <i>T. latifolia</i> ^N	Field	Wild	G ₁ =P1		G ₁ =P1*	Arriola & Ellstrand 1997
		Field	Wild			W=P1>P2	Ayres <i>et al.</i> 2004
		Field	Wild			W>P2=P1	Sullivan <i>et al.</i> 2010

(continued)

Table 1. (continued)

Hybrid Taxon	Parental Taxa	Field/ Lab	Hybrid Classes [§]	Fecundity	Survival	Size	Reference
Fungal taxa <i>Melampsora</i> × <i>columbiana</i>	<i>M. medusae</i> ^N × <i>M. occidentalis</i> ^N	Lab	Wild	P2>W>P1			Newcombe <i>et al.</i> 2000
<i>Pythium</i> hybrids	<i>P. arrhenomanes</i> ^E (or similar) × <i>P. phragmitidis</i> ^N	Lab Lab	Wild Wild	W=P1>P2 W=P1>P2*			Newcombe <i>et al.</i> 2001 Nechwatal & Mendgen 2009
Animal taxa <i>Ambystoma</i> hybrids	<i>A. tigrinum mavortium</i> ^E × <i>A. californiense</i> ^N	Field	F ₁ , F ₂ , BC ₁		P2=P1=G ₁ =G ₂	P1=G ₁ =G ₂ >P2	Ryan <i>et al.</i> 2009
<i>Cyprinella</i> hybrids	<i>C. lutrensis</i> ^E × <i>C. venusta</i> ^N	Lab	Wild, F ₁ , F ₂ , BC ₁ F ₁		P1>G ₁ =G ₂ >P2>W G ₁ >P1=P2*	P1>G ₂ ^a =W ^{ab} =G ₁ ^b >P2	Johnson <i>et al.</i> 2010 Blum <i>et al.</i> 2010

*Significant differences as reported in references; otherwise, significance reflects means separated by >2 SEM, based on our aggregated data.

†Excluded from meta-analysis because variability not reported.

‡G₂ and G₁₀ hybrids assessed in separate experiments.

§All hybrid classes used (S_x = selfed F_xs; BC_x = backcrossed F_xs; BC₁S₁ = selfed BC₁s).

¶Capable of clonal growth (Flora of North America Editorial Committee 1993+).

For each entry, significant differences are indicated by inequality signs and superscript letters, where necessary (taxa sharing the same letter do not differ). Differences are from referenced studies or our data aggregations (see footnote) and were not used in meta-analysis. Parental taxa are denoted P1 and P2, reflecting their order in the 'Parental Taxa' column; P1 is the more invasive/higher performing parent used for meta-analyses. Parents are denoted as native (N) or exotic (E), relative to the region where hybrids are invasive.

Experimental tests of the H-I hypothesis

From our full list of 72 hybrids, we found 18 hybrid taxa for which experimental hybrid-parent performance comparisons utilizing the relevant parent(s) have been conducted (reported in 40 studies and two unpublished datasets), either in the field (24 studies plus our unpublished datasets) or in the lab or greenhouse (16 studies). Only 14 of the 59 plant hybrids in our dataset (23.7%) have been assessed experimentally in such a way as to test the H-I hypothesis (Appendix 2). Nine of the 14 hybrid systems have been assessed in the field, with the remainder tested only in the lab or greenhouse. These experiments compare hybrid performance to that of the relevant parental taxa, either both parents (e.g. Vila & D'Antonio 1998b; Hooftman *et al.* 2005; Sullivan *et al.* 2010) or, if one parent is clearly more invasive or a superior competitor (i.e. if the inferior parent has not become naturalised despite opportunity), the superior parent (e.g. Hovick *et al.* 2012). For 11 of the remaining 45 taxa that have not been adequately tested, observational or incomplete experimental data have been reported that are suggestive of hybrid performance gains; these include some studies comparing hybrids with their inferior competitor parent only (e.g. Grosholz 2010) and some studies comparing hybrids with only one parent, either because the second is not clearly inferior (Van Grunsven *et al.* 2009), or because the second parent is not yet known (Henery *et al.* 2010; Hahn *et al.* 2012). For the remaining 34 of these 45 plant hybrids, hybridisation has been confirmed and also suggested as the underlying driver of weediness or invasiveness, but we have found no data on which to judge the latter claim.

For fungal pathogens, two hybrids have been assessed sufficiently to yield experimental tests of the H-I hypothesis: the rust *Melampsora* × *columbiana* (Newcombe *et al.* 2000, 2001) and a *Pythium* hybrid found on European *Phragmites australis* (Nechwatal & Mendgen 2009). All such investigations have been conducted in the lab, thus the relative performance of hybrid pathogens in the field is not known.

Of the five invasive animal hybrids in our dataset, two systems have been investigated experimentally. *Ambystoma* hybrids have been assessed both in field (Ryan *et al.* 2009) and lab tests (Johnson *et al.* 2010) and *Cyprinella* hybrids have been assessed in the lab only (Blum *et al.* 2010).

For our meta-analyses, we excluded eight of the 42 studies reporting experimental data, either because they failed to report some measure of variability or because they only reported data (percent germination, photosynthesis-related traits and walking speed) not fitting with our three performance categories; this exclusion eliminated three hybrid plant taxa from subsequent analyses (*Sarcocornia* hybrids, *Sphagneticola* hybrids and *Viola* × *tatrae*), cutting our final list to 15 hybrid taxa (11 plant, two animal and two fungal hybrids; see Table 1 and Appendix 4).

Meta-analysis: does hybridisation lead to hybrid performance gains?

Many of the 34 studies included in our meta-analyses used multiple hybrid classes, reported data from multiple unique experiments or established experiments across multiple loca-

tions. Thus, we calculated a total of 47 fecundity-based, 52 size-based and 42 survival-based effect sizes from experimental hybrid-parent performance comparisons. In all analyses, effect-size heterogeneity (I^2) among taxa was substantial, which likely contributed to non-significant differences in heterogeneity tests comparing F_1 , post- F_1 and wild hybrids (fecundity: $Q = 3.32$, $P = 0.190$, $I^2 = 86.1\%$; survival: $Q = 1.18$, $P = 0.553$, $I^2 = 93.3\%$; size: $Q = 2.54$, $P = 0.280$, $I^2 = 96.2\%$; all d.f.=2). We thus conducted analyses on all hybrid classes combined; however, because of an *a priori* interest in relative performance by each group and because these categories represent hybrid populations with distinct histories of genotypic filtering and selective pressures, we also conducted analyses separately for each hybrid class. This approach is also supported by (less conservative) fixed-effects analyses, which found significant differences between hybrid classes (results not shown). We found no indication of publication bias based on funnel plots and rank correlation tests for funnel plot asymmetry (see Appendix 5).

Do hybrids out-reproduce their parental taxa?

Meta-analyses of fecundity indicated that naturally occurring wild hybrids significantly outperformed their 'more invasive' parental taxon ($Z = 2.79$, $P = 0.005$, $n = 6$, $I^2 = 72.1\%$; see 'Overall M-A results' in Fig. 1a). Within individual taxa, wild hybrids were uniformly more fecund than their more invasive parents, with the effect reaching statistical significance in *Raphanus* and *Senecio squalidus* (and nearly reaching statistical significance in *Helianthus*, with a 95% confidence interval of $[-0.034, 0.281]$, Fig. 1a). For all hybrid classes considered together, hybrids were also significantly more fecund than their more invasive parent ($Z = 2.04$, $P = 0.042$, $n = 9$, $I^2 = 64.1\%$; Fig. 1a). However, resynthesised F_1 and later-generation (post- F_1) hybrids did not have significantly enhanced fecundity (F_1 : $Z = -0.73$, $P = 0.468$, $n = 4$, $I^2 = 92.7\%$; post- F_1 : $Z = 0.72$, $P = 0.470$, $n = 4$, $I^2 = 85.2\%$; Fig. 1a).

Our meta-regression of fecundity responses indicated a marginally significant generation effect across all three taxa, with relative hybrid fecundity increasing over subsequent generations ($\beta_{\text{gen}} \pm \text{SE} = 0.106 \pm 0.058$, $Z = 1.83$, $P = 0.067$, $I^2 = 95.6\%$), although this relationship varied across taxa (Fig. 2a). When taxa were assessed separately with linear models, the generation effect was marginally significant and positive for *Helianthus*, not significant for *Raphanus*, and significantly negative for *Lactuca* (*Helianthus*: $\beta_{\text{gen}} = 0.218 \pm 0.117$, $Z = 1.87$, $P = 0.062$, $I^2 = 93.2\%$; *Raphanus*: $\beta_{\text{gen}} = 0.132 \pm 0.108$, $Z = 1.223$, $P = 0.221$, $I^2 = 93.7\%$; *Lactuca*: $\beta_{\text{gen}} = -0.067 \pm 0.032$, $Z = -2.13$, $P = 0.033$, $I^2 = 74.6\%$). Despite apparent nonlinearity in the scatterplot (Fig. 2a), a polynomial relationship was not supported for all three taxa combined (polynomial model $P = 0.101$, $\beta_{\text{gen}} P = 0.133$ and $\beta_{\text{gen}}^2 P = 0.286$). In contrast, a polynomial model did fit the combined *Helianthus* and *Raphanus* data well (polynomial model $P = 0.004$; $\beta_{\text{gen}} = 0.688 \pm 0.259$, $Z = 2.66$, $P = 0.008$; $\beta_{\text{gen}}^2 = -0.049 \pm 0.023$, $Z = -2.162$, $P = 0.031$, $I^2 = 93.9\%$), indicating that hybrid relative fecundity for these two taxa increased rapidly over the first few generations before reaching a point where hybrids outperformed their parents (Fig. 2a).

Do hybrids outlive their parental taxa?

Meta-analyses of survival indicated that none of our three hybrid classes differed from their parental taxa (wild: $Z = 0.36$, $P = 0.718$, $n = 4$, $I^2 = 81.9\%$; F_1 : $Z = 0.76$, $P = 0.446$, $n = 3$, $I^2 = 92.0\%$; post- F_1 : $Z = -0.12$, $P = 0.901$, $n = 4$, $I^2 = 96.2\%$; Fig. 1b), but we note that small sample sizes for these analyses limit our power to detect any true effects. The combination of all hybrid classes gave the same non-significant result ($Z = 0.79$, $P = 0.429$, $n = 8$, $I^2 = 93.9\%$). Unlike our other performance metrics, relative survival of hybrids tended to vary more among taxa than among hybrid classes within taxa. Regardless of hybrid class, all *Lactuca*, *Raphanus*, *Senecio vulgaris* and *Cyprinella* hybrids had significantly higher survival than their parents, whereas all *Reynoutria* and *Ambystoma* hybrids had significantly lower survival (Fig. 1b).

Across the three systems for which data are available, relative hybrid survival significantly decreased across generations ($\beta_{\text{gen}} = -0.122 \pm 0.048$, $Z = -2.55$, $P = 0.011$; $I^2 = 93.3\%$; Fig. 2b). This pattern was similar for *Helianthus* and *Lactuca* when analysed separately (*Helianthus*: $\beta_{\text{gen}} = -0.097 \pm 0.022$, $Z = -4.41$, $P < 0.001$, $I^2 = 0.0\%$; *Lactuca*: $\beta_{\text{gen}} = -0.077 \pm 0.042$, $Z = -1.82$, $P = 0.068$, $I^2 = 86.8\%$; note that *Ambystoma* had too few data points to be assessed separately).

Are hybrids larger than their parental taxa?

In addition to being more fecund, wild hybrids were also significantly larger than their more invasive parent ($Z = 2.00$, $P = 0.046$, $n = 9$, $I^2 = 89.4\%$; Fig. 1c). In contrast to the fecundity data, effect size variation among wild hybrid taxa for organism size was much greater (89.4 vs. 72.1%), with a broader range of effect size estimates (Fig. 1c) and two influential outlier genera with large wild hybrids relative to their parents (the plants *Typha* and *Myriophyllum*; Cook's $D > 0.34$ and $D_{\text{ffits}} > 0.65$ for both). Because relative size advantages may be particularly relevant for species that persist and spread by clonal growth, we re-analysed the wild hybrid size data by clonal growth category (present vs. absent; see Table 1). Although effect sizes for these two groups were not significantly different from each other ($Q = 2.36$, d.f.=1, $P = 0.124$), only wild hybrids capable of clonal growth were larger than their parental taxa (clonal: $Z = 2.18$, $P = 0.029$, $n = 5$, $I^2 = 88.0\%$; non-clonal: $Z = 0.55$, $P = 0.581$, $n = 4$, $I^2 = 90.8\%$; Fig. 1c). At the level of individual clonal taxa, hybrids were significantly larger than parents in *Myriophyllum*, *Reynoutria* and *Typha* but not in *Carpobrotus* or *Spartina*. For resynthesised F_1 s and post- F_1 s, hybrids were smaller than their parental taxa on average, but with large confidence intervals that overlapped zero (F_1 : $Z = -0.99$, $P = 0.325$, $n = 2$, $I^2 = 97.8\%$; post- F_1 : $Z = -0.77$, $P = 0.444$, $n = 4$, $I^2 = 98.5\%$). When all hybrid classes were considered together, hybrid and parental size did not differ ($Z = 0.50$, $P = 0.620$, $n = 12$, $I^2 = 97.1\%$).

Among the three resynthesised hybrid taxa that have been assessed, relative hybrid size did not vary across generations ($\beta_{\text{gen}} = -0.023 \pm 0.078$, $Z = -0.30$, $P = 0.768$, $I^2 = 98.1\%$; Fig. 2c).

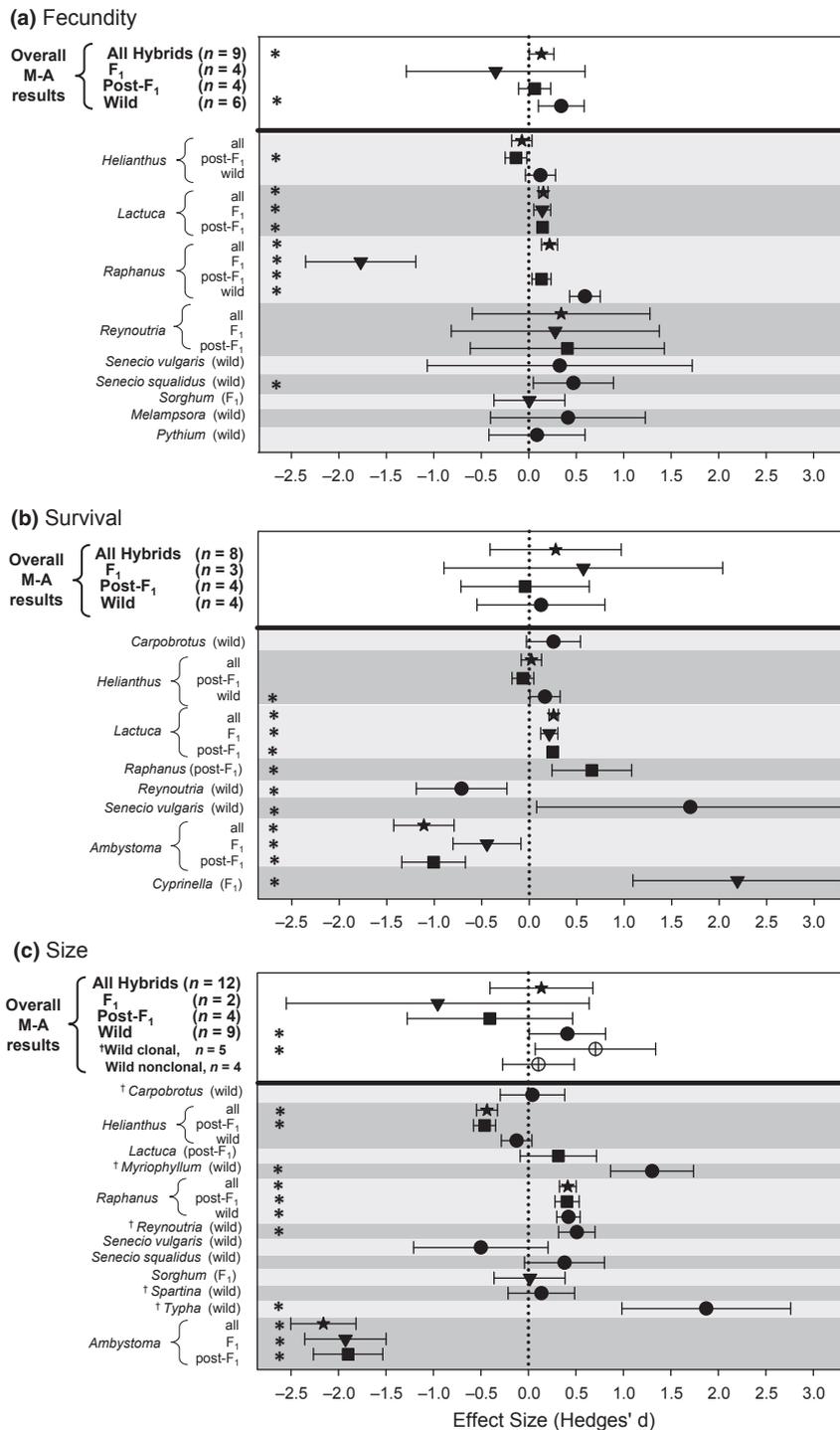


Figure 1 Meta-analysis results, showing effect sizes and 95% confidence intervals for hybrid vs. parental performance for (a) fecundity, (b) survival and (c) size. Effects greater than zero (dotted vertical line) indicate greater hybrid performance relative to their 'more invasive' parental taxon. Confidence intervals excluding zero are noted with an asterisk along the left side of the panel. Overall effect sizes shown in the non-shaded region at the top of each panel are from random effect meta-analyses conducted separately for (1) all hybrid classes combined, (2) resynthesised F₁ hybrids, (3) resynthesised post-F₁ hybrids and (4) wild hybrids. In panel C, separate overall effect sizes are also shown for wild hybrids that are capable vs. incapable of clonal growth. Individual effect sizes are shown beneath the solid horizontal line, with taxa separated by alternate shading and symbols indicating different hybrid classes.

DISCUSSION

We found moderate support for the hypothesised connection between interspecific hybridisation and increased invasiveness.

Quantitative data from experimental performance comparisons that could be used to test the H-I hypothesis were available for roughly 21% of all invasive or weedy hybrid taxa in our dataset. Not surprisingly, among-study heterogeneity was

high in all cases, reflecting species-specific responses to hybridisation in addition to likely variation in the design of experiments and performance assessments. The strongest evidence supporting the H-I hypothesis was found in fecundity-based performance assessments involving wild (as opposed to resynthesised) hybrids; evidence was strongest in plants but weaker in the few animal and fungal taxa for which data were available. Although fecundity relative to parents was on

average low in resynthesised hybrids, it increased significantly over time in two of the three systems for which we could assess the pattern; in these systems, resynthesised hybrids outperformed their parents by approximately the fifth generation post-hybridisation. Hybrid survival was more variable among taxa, and although no overall effect was seen in the meta-analysis, hybrid survival relative to parents tended to be high for plants and inconsistent between the two animal systems evaluated (note that tests in animal systems have only focused on resynthesised, instead of wild, hybrids). For resynthesised hybrids, there was an overall pattern of decreasing relative survival over time post-hybridisation. Finally, with respect to size, the meta-analysis revealed that wild hybrids were larger than their parental taxa, a pattern that was particularly strong for taxa in which hybrids are capable of clonal growth.

Designing experiments to test the H-I hypothesis: two basic criteria

One of the clearest patterns from our review is that many studies appearing to test the H-I hypothesis have not adequately done so. At a minimum, we argue that an informative test must meet two basic criteria. First, it must compare the performance of hybrids to that of the most invasive parent to ensure that hybrid performance is assessed relative to the correct benchmark. Where two introduced or two native species have hybridised, typically both parents must be included in the assessment to determine whether hybridisation has enhanced invasiveness. Where hybrids result from crossing one native taxon with one introduced and invasive taxon, the introduced parent must be included in any assessment for meaningful comparisons. If the most relevant parent is omitted, then inferences regarding the H-I hypothesis are impossible. For example, California *Spartina* is often cited as a case where hybridisation is associated with invasiveness (e.g. Ayres *et al.* 2008; Grosholz 2010). However, we found no experimental tests comparing fecundity or survival of the hybrid to the invasive parent, and a test of size found no difference between the taxa (Table 1). A test of resistance to goose herbivory found decreased palatability in the hybrid relative to the native parent *S. foliosa* (Grosholz 2010). This pattern was interpreted as support for the H-I hypothesis, via the suggestion that hybrids 'may pose a greater risk to natural systems than the parent species.' Again, however, no comparison was made to the invasive parent *S. alterniflora*. It could be that the invasive

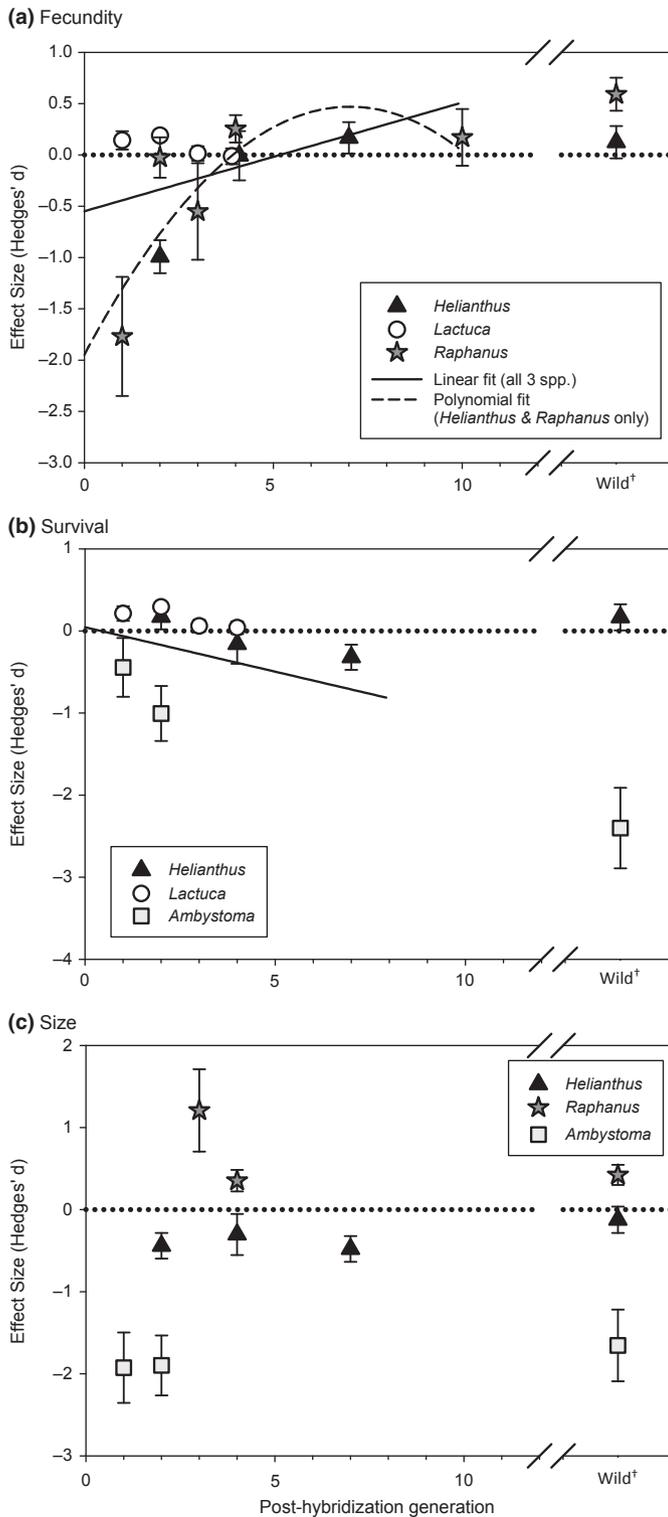


Figure 2 Meta-regression results, showing effect sizes (hybrid vs. parental performance) by hybrid generation for (a) fecundity, (b) survival and (c) size. Effects greater than zero (above the dotted horizontal line) indicate greater hybrid performance relative to their 'more invasive' parental taxa. Error bars indicate 95% confidence intervals. The best-fit lines in panels A and B show significant relationships between hybrid generation and Hedges' d for fecundity and survival based on meta-regression parameter estimates; the meta-regression for size in panel C was not statistically significant. In addition to the linear best-fit line, panel A also depicts the nonlinear relationship between hybrid generation and relative fecundity supported for *Helianthus* and *Raphanus* (considered apart from *Lactuca*; see Results). Note that effect sizes for naturally occurring wild hybrids were not included in the analysis, but are shown in the figure for comparison.

parent has equal (or even lower) palatability relative to the hybrid, in which case hybridisation could have nothing to do with performance or invasiveness in this system.

In some cases, accurate identification of both parental taxa is a barrier to our first criterion for testing the H-I hypothesis. For example, a tetraploid cytotype of spotted knapweed (*Centaurea stoebe* s.l.) has been recorded as invasive in North America, with molecular analyses pointing to an allopolyploid origin between the diploid *Centaurea stoebe* s. str. and an unknown parent (Mraz *et al.* 2012). Robust common garden experiments have been conducted in this system (Henery *et al.* 2010; Hahn *et al.* 2012), but without knowing the second parent's identity inferences regarding the H-I hypothesis are moot. Similar challenges exist in other systems (e.g. Kim *et al.* 2008; Inderbitzin *et al.* 2011), emphasising the continued importance of phylogenetic and taxonomic research in putative cases of hybridisation-induced invasiveness.

We suggest that a second criterion for testing the H-I hypothesis is that performance assessments be conducted experimentally in a common environment, as observations of hybrid performance or abundance in naturally occurring populations are not unambiguously interpretable. This criterion is not satisfied by a handful of key studies often cited in support of the H-I hypothesis that document increased abundances of hybrids relative to their parental taxa (Urbanska *et al.* 1997; Moody & Les 2002). Abundant hybrids could indeed result from enhanced invasiveness, but the same patterns could also result from chance dispersal events or simply from the introgression of neutral alleles from one parental genome into the other.

Fitness components vs. population growth rates as measures of invasiveness

In our meta-analyses, the degree to which the H-I hypothesis was supported varied with the fitness component (fecundity, survival or size) examined. In some cases, this pattern may reflect expected life-history tradeoffs: for example, resynthesised *Helianthus* hybrids displayed an increase in relative fecundity but a decrease in relative survival over time post-hybridisation (Fig. 2a,b). This issue highlights the importance of knowing how individual fitness components are related to the population growth rate (λ), which determines invasiveness. While fitness components are expected to generally be positively correlated with λ , the details matter. For instance, if populations are establishment (microsite) limited rather than propagule limited (Poulsen *et al.* 2007), then beyond a certain point, increased fecundity will not necessarily result in increased λ .

Female fecundity alone could be misleading in tests of the H-I hypothesis if male fitness (i.e. pollen or sperm viability) is severely depressed in hybrids relative to their parents. Because we only found pollen viability data for four taxa representing a variety of hybrid classes (*Sorghum*, *Reynoutria*, *Raphanus* and *Senecio squalidus*), a meaningful meta-analysis was not possible. However, for resynthesised *Raphanus* hybrids the change in pollen viability over time is similar to the changes in *Raphanus* fecundity we identified using meta-regression; that is, pollen viability is depressed in the F_1 generation but then recovers by approximately generation 3–6, eventually reaching values

equal to or greater than that of its parental taxon (Snow *et al.* 2010). It remains unknown whether male fitness responds similarly in other invasive hybrids and to what extent such patterns might influence population growth rates.

Four studies (of two hybrid systems) included in our meta-analyses do report λ for hybrids vs. parent populations (Hooftman *et al.* 2005, 2007; Campbell *et al.* 2006; Hartman *et al.* 2013). In *Raphanus*, λ did not differ between paired field populations of resynthesised hybrids and their better performing parental taxon over the second through fourth years post-hybridisation in Michigan (Campbell *et al.* 2006). From the perspective of testing the H-I hypothesis, this finding concurs with a common garden experiment in the same region where fourth-generation hybrids did not outperform their parental taxon (hybrids were significantly less fecund and had similar survival to the parent; Campbell *et al.* 2006). In *Lactuca*, λ was estimated from experimental populations of hybrids and both parental taxa by multiplying germination and survival rates by seed output plant^{-1} (Hooftman *et al.* 2005, 2007; Hartman *et al.* 2013); in all cases, differences in λ between taxa reflected differences in survival but not in seed output, suggesting that for *Lactuca*, survival is a better indicator of λ than is fecundity. Unfortunately, without estimates of λ and individual fitness components from other systems, questions remain about the degree to which these alternative performance metrics may indicate differences in population growth rates. Overall, future tests of the H-I hypothesis for sexually-reproducing species would be better served if λ (rather than fitness components alone) were estimated as the measure of invasiveness.

For some taxa, size (or vegetative growth rate) may be the most relevant measure of invasiveness. Many invasive plants reproduce primarily via clonal spread (Pyšek & Richardson 2007); and indeed clonality has been identified as an important mechanism by which heterosis achieved in the F_1 (which is normally broken down by recombination in sexual species) can be stabilised in hybrid lineages, potentially increasing invasiveness (Ellstrand & Schierenbeck 2000). Invasive populations of hybrid *Myriophyllum*, *Reynoutria* and *Typha* can reproduce clonally, have been shown to be largely composed of F_1 individuals (Kirk *et al.* 2011; Bailey 2013; LaRue *et al.* 2013), and in our analyses were all significantly larger than their parents (Fig. 1c). For taxa such as these, size may be a relevant measure of invasive potential; thus a pattern in which hybrids are larger than parents can be interpreted as support for the H-I hypothesis. Conversely, although *Carpobrotus* and *Spartina* hybrids also exhibit clonal growth, sexual reproduction (and thus recombination) appears to be common in these systems (Gallagher *et al.* 1997; Ayres *et al.* 2008), and hybrids were not larger than their parental taxa (Fig. 1c). The contrasting patterns expressed by these two groups of hybrid taxa illustrate the critical importance of measuring performance in a way that captures invasive potential appropriately for each particular system.

How does within-taxon variation in relative hybrid performance affect our understanding of the H-I hypothesis?

Hybrid taxa are often highly variable, and our review highlights three key aspects of this variability that have direct

bearing on how the H-I hypothesis is conceived, interpreted and tested. These non-mutually exclusive sources of variation can be distinguished as habitat effects, generation effects and lineage effects.

Habitat effects: genotype by environment ($G \times E$) interactions influence hybrid invasiveness

Habitat-specific performance advantage can lead to a complicated mosaic of peaks in hybrid relative performance. For example, *Carpobrotus* hybrids had higher relative growth rates than both of their parental taxa in backdune (but not bluff scrub) habitats, yet hybrid survival in response to herbivory was greatest in the bluff scrub (Vila & D'Antonio 1998b). At a larger geographic scale (North America), *Raphanus* hybrids have been shown to outperform their weedy parental taxa in California, where they are currently invasive (Campbell *et al.* 2006; Ridley & Ellstrand 2009), and in Texas, where they do not yet occur naturally (Hovick *et al.* 2012), but not in Michigan (Campbell *et al.* 2006). Although hybrids were traditionally thought to occur only in intermediate hybrid zones (Anderson 1948; Barton & Hewitt 1985), mounting evidence suggests that genome shuffling following hybridisation can result in phenotypes that are able to thrive in non-intermediate and even non-parental habitats (Rieseberg *et al.* 1999, 2007). Site-specific variation in hybrid relative performance will make it more difficult to reject the null hypothesis of no difference between hybrids and their parents if some common (but not ubiquitous) combination of biotic and abiotic factors exists that favours hybrid invaders. These considerations suggest there may be great value in assessing performance across a range of conditions.

Generation effects: not all hybrid generations are created equal

In most cases, assessments of hybrid relative performance depend greatly on which hybrid class(es) are investigated. Our meta-analyses indicate that wild (presumably later-generation) hybrids are more likely to outperform their parental taxa than are resynthesised (mostly early-generation) hybrids, on average. This pattern conforms to long-held expectations that hybrid performance should increase in post- F_1 hybrid classes as poorly adapted genotypes are filtered from the population by natural selection (reviewed by Arnold & Hodges 1995). Similarly, based on our meta-regressions, relative fecundity increased over subsequent generations post-hybridisation (Fig. 2a), and in many cases, the earliest-generation (F_1) hybrids performed worse than their parents and all other hybrid classes (Fig. 1a–c). Hybrid survival also varied by generation but in the opposite direction, decreasing over time post-hybridisation (Fig. 2b). This pattern may reflect a survival-fecundity life history tradeoff (cf. *Helianthus* from Fig. 2a and b).

These considerations mean that the choice of hybrid class used in testing the H-I hypothesis is a crucial one. On one hand, resynthesising hybrid lineages for testing the H-I hypothesis is the cleanest way to isolate the effects of hybridisation from other evolutionary factors such as population admixture and bottlenecks. On the other, tests using early-generation hybrid populations will often include poorly adapted genotypes (e.g. Snow *et al.* 2010) and thus may give

misleading answers about whether hybrids are capable of outperforming the parental species. Early-generation hybrid populations often have low average fitness but with high variance and a small number of well-adapted individuals (e.g. Whitney *et al.* 2006). The composition of these populations can therefore change substantially in only a few generations, making tests with only early-generation hybrids suspect. These problems are avoided if resynthesised lineages are first allowed to evolve in natural conditions post-hybridisation (Campbell *et al.* 2006; Whitney *et al.* 2006), thus letting natural selection filter out poorly adapted genotypes and mimicking naturally occurring hybridisation/invasion events.

Lineage effects: variable outcomes among hybridisation events

Hybrid lineages derived from the same pair of parental species, but formed with input from different parental individuals, can differ substantially in traits and performance (Pyšek *et al.* 2003; Hartman *et al.* 2013). Such variability can also play out at the population level, which means that source populations must be chosen carefully for experimental comparisons (or for resynthesising hybrid lineages). For instance, a hybrid-parent comparison that draws parental individuals from far beyond the supposed range of hybrid formation may be uninformative, particularly where parental taxa are themselves highly variable.

Strong associations between hybridisation and polyploidy for weedy and invasive hybrids

In many systems where the H-I hypothesis has been invoked, hybridisation is also closely associated with polyploidy (Stebbins 1985). In our dataset, 37 of 59 plant hybrids (63%) are reported to be polyploid, and of these nearly half have increased ploidy relative to their parental taxa (16 of 37; see Appendix 2). Polyploidy is not as well studied in fungal pathogens (Albertin & Marullo 2012), but two fungal hybrids from our database are also reported to be polyploid (*Verticillium longisporum* and *Phytophthora alni alni*). Because polyploidy alone may contribute to invasiveness (Pandit *et al.* 2011; te Beest *et al.* 2012), an important future research direction is disentangling the effects of hybridisation from those of polyploidy.

A robust 'gold standard' design for experimentally separating the effects of hybridisation from those of polyploidy in systems experiencing both phenomena would be to create resynthesised hybrid lineages in which both effects are manipulated independently. That is, experimental crosses would be exposed (or not) to chromosome doubling agents such as colchicine to create homoploid hybrid descendants, allopolyploid (hybrid) descendants, and autopolyploid (non-hybrid) descendants from the same set of parents. Performance could then be compared among parental taxa and their descendant lineages to disentangle the phenotypic effects of hybridisation and polyploidy. Such experiments with invasive polyploid taxa would benefit by considering the same sources of variation discussed above (habitat, generation and lineage effects), making strong inferences on the roles of hybridisation and polyploidy for polyploid invaders possible.

The H-I hypothesis: conclusions and future directions

Based on experiments that have been reported to date, the H-I hypothesis is moderately supported across taxa, with strong support in some systems (particularly plants) and little support in others for which it has been postulated (e.g. *Senecio vulgaris* var. *hibernicus*). Overall, our results suggest an important but variable effect of hybridisation in triggering or allowing invasions, although we note that these inferences rely on estimates of fecundity, survival and size as proxies of population growth rates and thus of invasiveness. Variability in outcomes (i.e. whether hybridisation triggers invasiveness or not) is consistent with a main theme of the current invasion literature emphasising that invasion is multicausal (Rejmánek *et al.* 2005); as historic, species-specific and environment-specific factors can predominate, different invasions across different taxa and locations are unlikely to be linked to a single 'smoking gun.'

The list of invasive hybrids initially compiled by Ellstrand & Schierenbeck (2000) continues to grow (see Appendix 2); however, in most systems we still lack well-designed experiments to test the H-I hypothesis. Critical components of future tests include ensuring that: (1) hybrid performance is compared to the correct benchmark, i.e. the more invasive parent, (2) tests are experimental and carried out in a common environment, (3) species-specific performance metrics are used that accurately reflect the invasiveness of species with different life histories, and (4) more tests in animal and fungal taxa are attempted.

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AUTHORSHIP

Designed the study, reviewed the literature, reconstructed phylogenies, and wrote the manuscript: SMH and KDW. Compiled data for the meta-analyses and performed all statistical analyses: SMH.

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