1 Heterosis indices: What do they really measure?

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18 Unlike dominance indices, heterosis indices, with one exception, do not
19 properly measure the level of deviation from additivity, thus making them
20 unsuitable for comparative analyses.

21 Abstract

22 Heterosis (hybrid vigour) is a universal phenomenon of crucial agro-economic
23 and evolutionary importance. We show that the most common heterosis
24 indices do not properly measure deviation from additivity because they
25 include both a component accounting for "real" heterosis and a term that
26 is not related to heterosis since it is derived solely from parental values.
27 Therefore, these indices are inadequate when the aim of the study is to
28 compare heterosis levels between different traits, environments, genetic
29 backgrounds or developmental stages, as these factors may affect not only
30 heterosis but also parental values. The only relevant index for such com-
31 parisons is the so-called "potence ratio". These observations argue for the
32 careful choice of heterosis indices depending on the purpose of the work.

33 **Key words:** Flowering, growth rate, heterosis index, hybrid vigour, maize,
34 non-additivity, yield.

35 Introduction

36 Non-linear processes are extremely common in biology. In particular,
37 genotype-phenotype or phenotype-phenotype relationships frequently dis-
38 play concave behaviours, resulting in the dominance of "high" over "low"
39 alleles (Wright, 1934) and in positive heterosis for a wide range of poly-
40 genic traits (Fiévet *et al.*, 2018; Vasseur *et al.*, 2019). Properly quantifying
41 the degree of non-additivity is an essential prerequisite for interpreting and

42 comparing genetic studies and for making predictions in plant and animal
43 breeding. However, most of the classical heterosis indices do not meet this
44 requirement.

45 First, let us recap how the degree of dominance is measured. There are
46 two classical dominance indices:

47 (i) Wright (1934) defined:

$$D_W = \frac{z_2 - z_{12}}{z_2 - z_1}$$

48 where z_1 , z_2 and z_{12} are respectively the phenotypic values of genotypes
49 A_1A_1 , A_2A_2 and A_1A_2 , with $z_2 > z_1$. D_W varies from 0, when A_2 is
50 fully dominant over A_1 , to 1, when A_2 is fully recessive with respect to
51 A_1 . $D_W = 0.5$ corresponds to semi-dominance or additivity ($z_{12} = \frac{z_1+z_2}{2}$)
52 (Table 1). Note that D_W is strictly equivalent to the dominance coefficient
53 h used in evolutionary genetics (Crow & Kimura, 1970).

54 (ii) Falconer (1960) proposed the following index:

$$D_F = \frac{z_{12} - \bar{z}}{\frac{z_2 - z_1}{2}}$$

55 where $\bar{z} = \frac{z_1+z_2}{2}$. D_F varies in the opposite direction to D_W : its value is 1
56 if $z_{12} = z_2$ (complete dominance of A_2 over A_1), -1 if $z_{12} = z_1$ (A_2 is fully
57 recessive with respect to A_1) and 0 if there is additivity. In the case of
58 overdominance, $D_W < 0$ and $D_F > 1$, and in the case of underdominance,
59 $D_W > 1$ and $D_F < -1$ (Table 1).

60 The D_W and D_F indices are linearly related:

$$D_F = 1 - 2D_W$$

61 Thus, dominance can be quantified with either index, both of them giving
62 the position of the heterozygote relative to the parental homozygotes. The

two indices merely vary in opposite directions, with D_W decreasing when dominance increases.

For polygenic traits, either index could be used to quantify non-additivity, *i.e.* real heterosis, without any ambiguity. Actually, one finds five heterosis indices in the literature (see their characteristic values in Table 1).

The two most popular indices are the best-parent (BP) and mid-parent (MP) heterosis indices (*e.g.* Gowen, 1952; Frankel, 1983):

$$H_{BP} = \frac{z_{12} - z_2}{z_2}$$

$$H_{MP} = \frac{z_{12} - \bar{z}}{\bar{z}}$$

where z_2 , z_{12} and $\bar{z}$ are respectively the phenotypic values of the parent 2 (with $z_2 > z_1$), of the parent 1 $\times$ parent 2 hybrid and of the parental mean.

In some instances, the authors do not normalize the difference between the hybrid and the best- or mid-parent value:

$$H_{bp} = z_{12} - z_2$$

$$H_{mp} = z_{12} - \bar{z}$$

Finally, the so-called "potence ratio" (Mather, 1949) has the same expression as Falconer's dominance index:

$$H_{PR} = \frac{z_{12} - \bar{z}}{\frac{z_2 - z_1}{2}}.$$

A value of 0 indicates additivity, 1 indicates $z_{12} = z_2$ (hybrid value = best-parent value), -1 indicates $z_{12} = z_1$ (hybrid value = worst-parent value) and > 1 (resp. < -1) indicates best-parent (resp. worst-parent) heterosis (Table 1). H_{PR} includes the values of the three genotypes, whereas the other indices lack one of the parental values (H_{BP} and H_{bp}) or both (H_{MP}

and H_{mp}). From a genetic point of view, H_{PR} is explicitly expressed in terms of the five genetic effects contributing to heterosis (Supplementary Table S1). Thus, the potence ratio, which is still by far the least used heterosis index, is the only one that informs us of the exact position of the hybrid value relative to the parental values. Wright's dominance index has the same property, but its inverse direction of variation, which makes comparisons less easy, probably explains why it is not used in this context.

Relationship between the potence ratio and the other heterosis indices

It is easy to show that the relationship between H_{PR} , hereafter noted h_{P} for simplicity, and the other indices is (with $z_2 > z_1$):

$$H_{\text{MP}} = h_{\text{P}} \left(\frac{z_2 - z_1}{z_1 + z_2} \right) = h_{\text{P}} z_{\text{m}} \quad (1)$$

$$H_{\text{BP}} = \left(\frac{-1 + h_{\text{P}}}{2} \right) \left(\frac{z_2 - z_1}{z_2} \right) = \left(\frac{-1 + h_{\text{P}}}{2} \right) z_{\text{b}} \quad (2)$$

$$H_{\text{mp}} = h_{\text{P}} \left(\frac{z_2 - z_1}{2} \right) = h_{\text{P}} \bar{z} z_{\text{m}} \quad (3)$$

$$H_{\text{bp}} = \left(\frac{-1 + h_{\text{P}}}{2} \right) (z_2 - z_1) = \left(\frac{-1 + h_{\text{P}}}{2} \right) z_2 z_{\text{b}} \quad (4)$$

where $z_{\text{m}} = \frac{z_2 - z_1}{z_1 + z_2}$ is the variation coefficient (σ/μ) of the trait in the parents and $z_{\text{b}} = \frac{z_2 - z_1}{z_2}$ is the difference between the parents normalized by the best-parent value (or $z_{\text{b}} = 2\sigma/z_2$).

For a given h_{P} value, the indices H_{MP} and H_{BP} are linearly related to z_{m} and z_{b} , respectively, *i.e.* they depend on the scale of the parental values. More specifically, the relationship between H_{MP} and z_{m} is negative when $h_{\text{P}} < 0$ and positive when $h_{\text{P}} > 0$, while the relationship between H_{BP} and z_{b} is negative when $h_{\text{P}} < 1$ and positive when $h_{\text{P}} > 1$. As z_{m} and

100 z_b are positive, we see from equation 1 that for $h_P \neq 0$, we have

$$0 < H_{MP} < h_P \quad \text{if } h_P > 0 \quad (\text{positive mid-parent heterosis})$$

101 and

$$h_P < H_{MP} < 0 \quad \text{if } h_P < 0 \quad (\text{negative mid-parent heterosis})$$

102 Regarding H_{BP} , we see from equation 2 that for $h_P \neq 1$, we have

$$0 < H_{BP} < \left(\frac{-1 + h_P}{2} \right) \quad \text{if } h_P > 1 \quad (\text{positive best-parent heterosis})$$

103 and

$$\left(\frac{-1 + h_P}{2} \right) < H_{BP} < 0 \quad \text{if } h_P < 1 \quad (\text{negative best-parent heterosis})$$

104 If $h_P = 0$ (resp. $h_P = 1$), H_{MP} (resp. H_{BP}) = 0.

105 Numerical applications performed with nine h_P values, from $h_P = -2$
 106 to $h_P = 2$, show that the same H_{MP} or H_{BP} value can be observed for very
 107 different h_P values (Supplementary Figure S1). For instance, $H_{MP} \approx 0.4$
 108 can correspond to both mid-parent heterosis ($h_P = 0.5$, $z_m \approx 0.8$) and
 109 best-parent heterosis ($h_P = 2$, $z_m \approx 0.21$).

110 We illustrate this using experimental data from maize. We measured
 111 six traits (flowering time, plant height, ear height, grain yield, thousand-
 112 kernel weight and kernel moisture) in four crosses (B73×F252, F2×EP1,
 113 F252×EP1, F2×F252) grown in three different environments in France
 114 (Saint-Martin-de-Hinx in 2014, Jargeau in 2015 and Rhodon in 2015). We
 115 computed h_P , H_{MP} and H_{BP} for the 72 trait-cross-environment combina-
 116 tions. Fig. 1A,B shows that the relationship between h_P and the other two
 117 indices is very loose, if any. A given h_P value can correspond to a wide range

118 of H_{MP} or H_{BP} values, and vice versa. We performed the same analyses
 119 using the data published by Shang *et al.* (2016), who measured five traits
 120 in two crosses of cotton grown in three environments. The same loose rela-
 121 tionship between h_P and either heterosis index was observed (Fig. 1C,D).
 122 This means that the trait variation coefficients or the normalized difference
 123 between the parents, which are not related to heterosis since they do not
 124 include values from the hybrids, markedly affect H_{MP} and H_{BP} .

125 Regarding the H_{mp} and H_{bp} indices, which are not dimensionless, they
 126 only provide the direction of heterosis. For a given h_P value, H_{mp} can vary
 127 from $-\infty$ to 0 when $h_P < 0$ and from 0 to $+\infty$ when $h_P > 0$, and H_{bp}
 128 can vary from $-\infty$ to 0 when $h_P < 1$ and from 0 to $+\infty$ when $h_P > 1$
 129 (equations 3 and 4).

130 Let us examine the possible interpretation errors that may result from
 131 the use of the most common heterosis indices.

132 **The pitfalls of the most commonly used heterosis in-** 133 **indices**

134 The non-univocal relationship between h_P and the most commonly used
 135 heterosis indices has two consequences. (i) Comparing index values for a
 136 given trait in different crosses and/or environments and/or developmental
 137 stages leads to erroneous conclusions whenever these factors have an effect
 138 on the scale of the trait and/or on the difference between the parental
 139 values (*i.e.* on z_m or z_b). Possible differences in actual heterosis levels
 140 between these conditions cannot be detected. (ii) This problem is even
 141 more pronounced when studying different traits because each trait has its
 142 own scale of variation, making H_{MP} and H_{BP} (and to a greater extent H_{mp}
 143 and H_{bp}) useless for comparing the real levels of heterosis of these traits.

144 These pitfalls can easily be illustrated from our maize dataset. Fig. 2A

shows that classifying a set of traits according to their degree of heterosis can give markedly different results depending on whether one uses the h_P index or one of the two indices H_{MP} and H_{BP} . For instance, in the F252×EP1 cross, flowering time displays moderate heterosis according to H_{MP} and H_{BP} even though this trait actually has the highest h_P value. Conversely, plant height is the second most heterotic trait according to H_{MP} and H_{BP} , but not according to h_P . Similarly, comparing heterosis of a given trait in different hybrids results in index-specific rankings: heterosis of ear height measured with h_P is highest in the B73×F252 hybrid, whereas according to H_{MP} and H_{BP} the highest values are found in the F252×EP1 hybrid (Fig. 2B). Finally, the effect of the environment on heterosis reveals the same discrepancies between h_P on the one hand and H_{MP} or H_{BP} on the other hand (Fig. 2C).

It is also informative to compare the variation of heterosis indices for a trait measured during development or growth. We fitted the percentage of flowering individuals over time in the W117×F192 and W117×F252 hybrids and their parents, using the Hill function:

$$y = \frac{ax^n}{b + x^n}$$

where n is the Hill coefficient. We then computed the variation of heterosis for the percentage of flowering individuals estimated from the fitted curves (Fig. 3). Again, h_P tells a different story compared to H_{MP} and H_{BP} . Both H_{MP} and H_{BP} decrease as flowering progresses because the variation coefficient also decreases. This masks the evolution of real heterosis, which actually increases.

Similar results were observed in a simulation describing the increase in population size of a unicellular organism, which exhibits logistic growth.

170 We used:

$$y = \frac{K}{1 + a e^{-r\theta}}$$

171 where y is the size of the population, K the carrying capacity, a a constant,
 172 r the growth rate and θ the time. We assumed that the parents differed
 173 only in their growth rate r and that there is additivity for this parameter.
 174 Results show that the variations over time of H_{MP} and H_{BP} index values for
 175 population size are clearly not congruent with that of h_P (Supplementary
 176 Figure S2).

177 Discussion

178 If H_{MP} and H_{BP} (and their non-normalized forms H_{mp} and H_{bp}) do not
 179 provide reliable information on non-additivity, why are they so commonly
 180 used? There are probably both historical and technical reasons: (i) The
 181 first scientists who quantified heterosis were plant breeders (Shull, 1908;
 182 East, 1936). From an economic perspective, the goal was, and still is, to de-
 183 velop hybrids that are "better" than the best- or mid-parent values for the
 184 desired agronomic traits, and not to know where the hybrid value is rela-
 185 tive to the parental values. Heterosis indices have been defined accordingly
 186 and the habit has remained; (ii) The indices giving the right non-additivity
 187 values, h_P ($= H_{PR}$) for heterosis and D_W or D_F for dominance, can take
 188 on high to very high values when the parents are close, due to the small
 189 differences $z_2 - z_1$ in the denominator of the fractions. This can produce
 190 extreme values that are not easy to represent and manipulate for statistical
 191 treatments. Nevertheless, such values are biological realities that convey
 192 precisely the inheritance of the traits under study, something that H_{MP} ,
 193 H_{BP} , H_{mp} and H_{bp} do not. In addition, from a practical point of view, a
 194 single index is sufficient to know the position of the hybrid relative to the
 195 mid- or best-parent, whereas in a number of studies the authors compute

196 and comment both H_{MP} and H_{BP} (or H_{mp} and H_{bp}). More importantly, to
 197 compare the amplitude of heterosis between traits, developmental stages,
 198 crosses or environmental conditions, there is no other choice but to use
 199 the only heterosis index – H_{PR} – that is not affected by the scale of the
 200 parental values and that accounts for the position of the hybrid in the
 201 parental range.

202 **Supplementary data**

203 Table S1. Heterosis indices expressed as functions of genetic effects.
 204 Fig. S1. Influence of the scale of the parental values on H_{MP} and H_{BP} for
 205 different values of the potence ratio h_P .
 206 Fig. S2. Heterosis for population size (simulations).

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215 **Author contributions**

216 Conceptualization: DdV. Maize experiments: JBF. Data analyses and nu-
 217 merical applications: DdV and JBF. DdV and JBF wrote the manuscript.

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Table 1. Dominance and heterosis indices. D_W : Wright's dominance index. D_F : Falconer's dominance index. H_{mp} , H_{MP} , H_{PR} , H_{bp} and H_{BP} : heterosis indices. Subscripts: mp or MP, mid-parent; PR, potence ratio; bp or BP, best-parent. In the equations of the text, H_{PR} is also noted h_P for simplicity. z_1 (resp. z_2): the phenotypic value of parental homozygote 1 or of parent 1 (resp. 2). z_{12} : the heterozygote or hybrid value. $\bar{z}$: the mean parental value. By convention, $z_2 > z_1$.

Reference	Index	Index scales with their characteristic values
High homozygote	$D_W = \frac{z_2 - z_{12}}{z_2 - z_1}$	$+\infty \text{ --- } \frac{z_{12} = z_1}{1} \text{ --- } \frac{z_{12} = \bar{z}}{0.5} \text{ --- } \frac{z_{12} = z_2}{0} \text{ --- } -\infty$ <p>Underdominance Recessivity Additivity Dominance Overdominance</p>
Mean homozygote	$D_F = \frac{z_{12} - \bar{z}}{(z_2 - z_1)/2}$	$-\infty \text{ --- } \frac{z_{12} = z_1}{-1} \text{ --- } \frac{z_{12} = \bar{z}}{0} \text{ --- } \frac{z_{12} = z_2}{+1} \text{ --- } +\infty$ <p>Underdominance Recessivity Additivity Dominance Overdominance</p>
Mid-parent	$H_{mp} = z_{12} - \bar{z}$	$-\infty \text{ --- } \frac{z_{12} = \bar{z}}{0} \text{ --- } +\infty$ <p>Negative heterosis Additivity Mid- or best-parent heterosis</p>
	$H_{MP} = \frac{z_{12} - \bar{z}}{\bar{z}}$	$-\infty \text{ --- } \frac{z_{12} = \bar{z}}{0} \text{ --- } +\infty$ <p>Negative heterosis Additivity Mid- or best-parent heterosis</p>
	$H_{PR} = \frac{z_{12} - \bar{z}}{(z_2 - z_1)/2}$	$-\infty \text{ --- } \frac{z_{12} = z_1}{-1} \text{ --- } \frac{z_{12} = \bar{z}}{0} \text{ --- } \frac{z_{12} = z_2}{+1} \text{ --- } +\infty$ <p>Worst-parent heterosis Negative mid-parent heterosis Additivity Positive mid-parent heterosis Best-parent heterosis</p>
Best-parent	$H_{bp} = z_{12} - z_2$	$-\infty \text{ --- } \frac{z_{12} = z_2}{0} \text{ --- } +\infty$ <p>Non-additivity or additivity Best-parent heterosis</p>
	$H_{BP} = \frac{z_{12} - z_2}{z_2}$	$-\infty \text{ --- } \frac{z_{12} = z_2}{0} \text{ --- } +\infty$ <p>Non-additivity or additivity Best-parent heterosis</p>

Figure legends

Figure 1 Relationship between the potence ratio h_P and the two heterosis indices H_{MP} and H_{BP} . (A) & (B) Six traits were measured in maize (FLO: flowering time [days between 50 % flowering and August, 12th], PH: plant height, EH: ear height, GY: grain yield, TKW: thousand-kernel weight, KM: kernel moisture) in four crosses (H1: B73×F252, H2: F2×EP1, H3: F252×EP1, H4: F2×F252) grown in three environments in France (E1: Saint-Martin-de-Hinx, E2: Jargeau, E3: Rhodon). (A) Relationship between h_P and H_{MP} . (B) Relationship between h_P and H_{BP} . (For clarity, four of the 72 trait-cross-environment combinations are not represented because they have high h_P values.) (C) & (D) Five traits were measured in cotton (SY: seed yield, LY: lint yield, BNP: bolls per plant, BW: boll weight, LP: lint percent) in two crosses (H1: X1135×GX100-2 and H2: GX1135×VGX100-2) grown in three environments in China (E1: Handan, E2: Cangzhou, E3: Xiangyang) (Data from Shang *et al.*, 2016). (C) Relationship between h_P and H_{MP} . (D) Relationship between h_P and H_{BP} .

Figure 2 Heterosis values calculated using different indices. (A) Heterosis indices for six traits measured in the F252×EP1 cross grown in Saint-Martin-de-Hinx (France) in 2014. (B) Heterosis indices for ear height in four crosses grown in Saint-Martin-de-Hinx (France) in 2014. (C) Heterosis indices for plant height in the F2×F252 cross grown in the three environments. The six traits and the three environments are the same as in Fig. 1A. The scales of the heterosis indices are normalized by the maximum value in each dataset (figures at the top right of the vertical lines).

272 **Figure 3 Heterosis for flowering in two maize hybrids.** (A) Per-
 273 centage of flowering over time (number of days since January, 1st) for
 274 parents W117 and F192 and their hybrid, adjusted with a Hill function.
 275 (B) Percentage of flowering over time for parents W117 and F252 and their
 276 hybrid. (C) Variations in the heterosis index values for the W117×F192
 277 cross. (D) Variations in the heterosis index values for the W117×F252
 278 CROSS.

Figure 1. Relationship between the potency ratio h_P and the two heterosis indices H_{MP} and H_{BP} . (A) & (B) Six traits were measured in maize (FLO: flowering time [days between 50 % flowering and August, 12th], PH: plant height, EH: ear height, GY: grain yield, TKW: thousand-kernel weight, KM: kernel moisture) in four crosses (H1: B73×F252, H2: F2×EP1, H3: F252×EP1, H4: F2×F252) grown in three environments in France (E1: Saint-Martin-de-Hinx, E2: Jargeau, E3: Rhodon). (A) Relationship between h_P and H_{MP} . (B) Relationship between h_P and H_{BP} . (For clarity, four of the 72 trait-cross-environment combinations are not represented because they have high h_P values.) (C) & (D) Five traits were measured in cotton (SY: seed yield, LY: lint yield, BNP: bolls per plant, BW: boll weight, LP: lint percent) in two crosses (H1: X1135×GX100-2 and H2: GX1135×VGX100-2) grown in three environments in China (E1: Handan, E2: Cangzhou, E3: Xiangyang) (Data from Shang *et al.*, 2016). (C) Relationship between h_P and H_{MP} . (D) Relationship between h_P and H_{BP} .

Figure 2. Heterosis values calculated using different indices. (A) Heterosis indices for six traits measured in the F252xEP1 cross grown in Saint-Martin-de-Hinx (France) in 2014. (B) Heterosis indices for ear height in four crosses grown in Saint-Martin-de-Hinx (France) in 2014. (C) Heterosis indices for plant height in the F2xEP1 cross grown in the three environments. The six traits and the three environments are the same as in Fig. 1A. The scales of the heterosis indices are normalized by the maximum value in each dataset (figures at the top right of the vertical lines).

Figure 3. Heterosis for flowering in two maize hybrids. (A) Percentage of flowering over time (number of days since January, 1st) for parents W117 and F192 and their hybrid, adjusted with a Hill function. (B) Percentage of flowering over time for parents W117 and F252 and their hybrid. (C) Variations in the heterosis index values for the W117×F192 cross. (D) Variations in the heterosis index values for the W117×F252 cross.

279 **Supplementary data**

280 Heterosis indices: What do they really measure?

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282 **Table S1 Heterosis indices expressed as functions of genetic ef-**
 283 **fects.** Subscripts: same as in Table 1. μ , mean of the multilocus homozy-
 284 gous genotypes; $\sum a$, sum of the additive effects; $\sum d$, sum of the dom-
 285 inance effects; $\sum e_{\text{dom}}$, sum of the dominance-by-dominance epistatic ef-
 286 fects; $\sum e_{\text{add}}$, sum of the additive-by-additive epistatic effects; $\sum e_{\text{add even}}$,
 287 sum of the additive-by-additive epistatic effects involving an even num-
 288 ber of genes; $\sum e_{\text{add odd}}$, sum of the additive-by-additive epistatic effects
 289 involving an odd number of genes (from Fiévet *et al.*, 2010).

Reference	Index	Index as function of genetic effects
Mid-parent	$H_{\text{mp}} = z_{12} - \bar{z}$	$\sum d + \sum e_{\text{dom}} - \sum e_{\text{add even}}$
	$H_{\text{MP}} = \frac{z_{12} - \bar{z}}{\bar{z}}$	$\frac{\sum d + \sum e_{\text{dom}} - \sum e_{\text{add even}}}{\mu + \sum e_{\text{add even}}}$
	$H_{\text{PR}} = \frac{z_{12} - \bar{z}}{(z_2 - z_1)/2}$	$\frac{\sum d + \sum e_{\text{dom}} - \sum e_{\text{add even}}}{\sum a + \sum e_{\text{add odd}}}$
Best-parent	$H_{\text{bp}} = z_{12} - z_2$	$\sum d + \sum e_{\text{dom}} - \sum a - \sum e_{\text{add}}$
	$H_{\text{BP}} = \frac{z_{12} - z_2}{z_2}$	$\frac{\sum d + \sum e_{\text{dom}} - \sum a - \sum e_{\text{add}}}{\mu + \sum a + \sum e_{\text{add}}}$

290

291 **Fig. S1** Influence of the scale of the parental values on H_{MP} and
 292 H_{BP} for different values of the potency ratio h_P . (A) to (I) h_P values
 293 from -2 to 2 . $z_m = \frac{z_2 - z_1}{z_1 + z_2}$ and $z_b = \frac{z_2 - x_1}{z_2}$, with $z_1 = 1$ and z_2 varying from
 294 1 to 10 (see equations 1 and 2 in the text). Green line: relationship between
 295 z_m and H_{MP} . Orange line: relationship between z_b and H_{BP} . Dotted line:
 296 H_{MP} or $H_{BP} = 0$. The dark green points show that a given H_{MP} value
 297 (≈ 0.4) can be observed for very different h_P values, and the same is true
 298 for H_{BP} .

299 **Fig. S2 Heterosis for population size (simulations).** Population
300 sizes (dotted curves) follow over time a logistic function with $K = 1$ and
301 $a = 100$ (see text). Parents P1 and P2 and hybrid F1 have respectively
302 growth rates $r = 0.8$, $r = 1.2$ and $r = 1$ (*i.e.* this parameter is considered
303 to be additive). Solid curves: profiles of heterosis indices (right scale).