

1 **Title: Adaptive introgression: an untapped evolutionary mechanism for**
2 **crop adaptation**

3 **Authors:**

4 Concetta Burgarella^{1,2,3,4*}, Adeline Barnaud^{1,2}, Ndjido Ardo Kane^{5,6}, Frédérique Jankowsky^{7,8,9}, Nora
5 Scarcelli^{1,2}, Claire Billot^{3,4}, Yves Vigouroux^{1,2}, Cécile Berthouly-Salazar^{1,2,6*}

6 ¹IRD, UMR DIADE, Montpellier, France

7 ²Université de Montpellier, Montpellier, France

8 ³CIRAD, UMR AGAP, F-34398 Montpellier, France

9 ⁴AGAP, Univ Montpellier, CIRAD, INRA, Montpellier SupAgro, Montpellier, France

10 ⁵Institut Sénégalais de Recherches Agricoles (ISRA), LNRPV, Dakar, Senegal

11 ⁶Laboratoire Mixte International LAPSE, Dakar, Senegal

12 ⁷CIRAD, UPR GREEN, F-34398, Montpellier, France

13 ⁸GREEN, CIRAD, Univ Montpellier, Montpellier, France.

14 ⁹Institut Sénégalais de Recherches Agricoles (ISRA), BAME, Dakar, Senegal

15

16

17 **Corresponding authors:**

18 * Concetta Burgarella: concetta.burgarella@gmail.com

19 * Cécile Berthouly-Salazar: cecile.berthouly@ird.fr

20

21 **Running title:** Adaptive introgression: an untapped evolutionary mechanism for crop adaptation

22

23 **Number of words:** 5900

24 **Number of Figures:** 4

25

26 **Keywords:** crops, wild relatives, domestication, selection, gene flow, adaptive introgression, farmer's
27 practices.

28

29 **ABSTRACT**

30 Global environmental changes strongly impact wild and domesticated species biology and their
31 associated ecosystem services. For crops, global warming has led to significant changes in terms of
32 phenology and/or yield. To respond to the agricultural challenges of this century, there is a strong
33 need for harnessing the genetic variability of crops and adapting them to new conditions. Gene
34 flow, from either the same species or a different species, may be an immediate primary source to
35 widen genetic diversity and adaptations to various environments. When the incorporation of a foreign
36 variant leads to an increase of the fitness of the recipient pool, it is referred to as “adaptive
37 introgression”. Crop species are excellent case studies of this phenomenon since their genetic
38 variability has been considerably reduced over space and time but most of them continue
39 exchanging genetic material with their wild relatives. In this paper, we review studies of adaptive
40 introgression, presenting methodological approaches and challenges to detecting it. We pay
41 particular attention to the potential of this evolutionary mechanism for the adaptation of crops.
42 Furthermore, we discuss the importance of farmers’ knowledge and practices in shaping wild-to-
43 crop gene flow. Finally, we argue that screening the wild introgression already existing in the
44 cultivated gene pool may be an effective strategy for uncovering wild diversity relevant for crop
45 adaptation to current environmental changes and for informing new breeding directions.

46

47 1. Introduction

48 The fate of wild and domesticated species and their associated ecosystem services is increasingly
49 depending on global environmental changes, as climate warming, nitrogen cycle alteration or land
50 use (Perring et al., 2015; Shibata et al., 2015; Walther et al., 2002). For instance, modifications of
51 temperature and rainfall regimes have been shown to directly impact on plant phenology or
52 distribution within these past decades. A meta-analysis including nearly 1600 species showed that
53 41% of them had experienced phenological advancement and northward range movement
54 (Parmesan and Yohe, 2003). In a mountain area, Crimmins et al. (2011) documented downward
55 elevation shifts driven by water deficits in 64 plant species. Forest inventories across the eastern
56 USA revealed direct effects of climate on forest biomass, through changes in tree species
57 composition towards species more drought-tolerant, but slower growing. Climate effects have also
58 been reported on major crop species. Global maize and wheat yield has declined by 4-6% since the
59 early 1980s (Lobell et al., 2011). Earlier flowering and changes in genetic composition have been
60 recorded in the staple African cereal pearl millet (Vigouroux et al., 2011). Reduced flowering time
61 and loss of genetic diversity in response to increasing temperatures have also been observed in wild
62 wheat and barley over less than 30 years (Nevo, 2012). Future climate scenarios foresee an
63 acceleration of the rise in temperature and an increase in hydrological variability (IPCC, 2014),
64 which are probably the prelude to further dramatic consequences for species biology.

65
66 Phenotypic plasticity and dispersal (through seeds and pollen) can be very rapid responses to
67 change, but it is less clear whether adaptation, the evolution of genetic traits making organisms
68 better fitted to survive and reproduce in their environment, could also play a significant role in this
69 process. The ability to adapt to new conditions depends on the rate of environmental change (Loarie
70 et al., 2009) and on the genetic variability available (Doi et al., 2010; Hoffmann et al., 2017). The
71 genetic diversity of a population relies either on standing genetic variation or on new genetic
72 variants. On short time scales, the mutation rate may be too low. Moreover, standing genetic
73 variation may be limited, especially for populations whose genetic diversity has been reduced by
74 demographic bottlenecks, as many domesticated species (Glémin and Bataillon, 2009). However,
75 new variants could arise from gene flow, in numbers up to two or three orders of magnitude more
76 than that introduced by mutation (Grant and Grant, 1994). Thus, gene flow, either from the same
77 species or a different species, may amount to an immediate primary source of functional alleles
78 (Ellstrand, 2014). If a foreign functional variant increases the fitness of the recipient pool, it
79 increases in frequency across generations, a phenomenon referred to as “adaptive introgression”
80 (Anderson, 1949; Rieseberg and Wendel, 1993).

81
82 Prior to any possible “adaptive introgression”, hybridization/gene flow events need to take place.
83 However, the fate of hybrids is uncertain. Hybrids are usually selected against in parental habitats
84 (Baack et al., 2015) because they show reduced fertility and viability (Lowry et al., 2008). This
85 process might be due to genetic incompatibilities and/or the break-up of epistatic co-adapted gene
86 complexes (Barton and Hewitt, 1985; Hewitt, 1988). Yet, when species are not too divergent and
87 isolating barriers are incomplete (Coyne and Orr, 2004), hybridization can lead to the introgression
88 of advantageous alleles (Barton and Bengtsson, 1986). Compared to neutral introgression, which
89 could be lost by drift across generations, adaptive introgression would be maintained and may
90 eventually give rise to fixation (Figure 1). Interestingly, hybridization has the potential to introduce
91 large sets of new alleles simultaneously at multiple unlinked loci, allowing adaptation even for
92 polygenic traits (Abbott et al., 2013; Mallet, 2007), thus playing a key role in species evolution (e.g.
93 Arnold and Kunte, 2017; Arnold and Martin, 2009; Hedrick, 2013).

94
95 In the context of species conservation and management a large body of literature discuss how gene
96 flow could also be associated with negative effects. Undesirable consequences of gene flow are

97 associated with the risks of invasiveness (Ellstrand and Schierenbeck, 2000; Whitney et al., 2006),
98 transgene escape (Ellstrand et al., 2013 and references therein), or genetic erosion of native
99 populations (Wolf et al., 2001). Little attention has been paid to the potential of managed gene flow
100 to increase genetic variation for species rescue (Hedrick, 2009) and adaptation (Aitken and
101 Whitlock, 2013). Up to now, the potential of adaptive introgression as a source of adaptation to on-
102 going global changes for domesticated species has been overlooked.

103
104 In this paper, we review studies of adaptive introgression, paying particular attention to the potential
105 of this evolutionary mechanism for the adaptation of crops. By the term ‘introgression’ we mean the
106 consequence of gene flow, at both the interspecific and the intraspecific level, i.e. independently of
107 the taxonomic classification of the gene pools exchanging genetic material. We focus on sexually
108 reproductive organisms; and we did not directly discuss horizontal gene transfer (reviewed in
109 Arnold and Kunte, 2017). Within this framework, we report on 34 case studies addressing adaptive
110 introgression (Table 1). After discussing methodological approaches and challenges to detecting
111 adaptive introgression, we focus on gene flow in crops and the importance of farmer practices in
112 shaping wild-to-crop gene flow.

113 114 **2. Empirical evidence of adaptive introgression**

115
116 Despite the occurrence of hybridization in nature, involving 25% of plants and 11% of animals
117 (Mallet, 2005), relatively little evidence supports the fact that gene flow leads to enhanced fitness,
118 i.e. adaptive introgression. This may be because investigating the fitness of adaptive introgression
119 is intrinsically difficult. For example, demonstrations of adaptive introgression in *Helianthus* were
120 based on crossing and backcrossing to experimentally reproduce introgression and demonstrate
121 enhanced fitness in the recipient taxon (Whitney et al., 2006, 2010). With high-throughput
122 sequencing technologies, we can instead search for selection signatures on the introgressed variant
123 in the recipient genomes (e.g. Arnold et al., 2016; Racimo et al., 2015). An increasing number of
124 publications involving large-scale genetic data are accumulating in this field (Table 1). Those
125 studies reveal or confirm instances of adaptive introgression in many kinds of organisms, including
126 domesticated species (e.g. Anderson et al., 2009; Hufford et al., 2013; Kovach et al., 2009; Miao
127 et al., 2016; Rochus et al., 2017). It also appears that different abiotic and biotic selective pressures
128 drive the introgression of adaptive traits, with evolutionary consequences spanning different spatial
129 and temporal scales.

130
131 Recent striking studies report ancient adaptive introgression events in animals or humans. Up to 5%
132 of the modern human genome might be of introgressed origin from archaic hominins (e.g. Green et
133 al., 2010; Hsieh et al., 2016; Reich et al., 2009; Sankararaman et al., 2014). Introgressed loci from
134 Neanderthals or Denisovans appear to be linked to skin colour phenotypes (Vernot and Akey,
135 2014), immune responses (Abi-Rached et al., 2011) and hypoxia adaptation to high altitudes
136 (Huerta-Sánchez et al., 2014). In animals, Tibetan Mastiff dogs were also found to have received a
137 genomic region encompassing two genes linked to hypoxia adaptation (the *EPAS1* and the *HBB*
138 genes) from the local populations of grey wolf (Miao et al., 2016; Zhang et al., 2014). On the other
139 hand, the American grey wolf inherited an adaptive allele for coat pigmentation from past
140 hybridization with domestic dogs (Anderson et al., 2009). In Chinese and European pigs, gene flow
141 would seem to date from the Pleistocene era, when northern Chinese and European breeds would
142 appear to have acquired a large adaptive genomic region from a *Sus* species that is now extinct (Ai
143 et al., 2015).

144
145 Adaptive introgression can also take place on a much shorter evolutionary time scale. For instance,
146 the acquisition of pesticide resistance through genetic exchange can be achieved in a few decades,

147 as observed in insects (Lynd et al., 2010; Weetman et al., 2010) and rodents (Liu et al., 2015; Song
148 et al., 2011). A mutation in the voltage-gated sodium channel gene (*kdr*) provides strong resistance
149 to pyrethroid and dichlorodiphenyltrichloroethane (DDT) in the mosquito *Anopheles gambiae*, one
150 of the vectors of malaria in sub-Saharan Africa. The resistance allele was transferred from *A.*
151 *gambiae sensu stricto* (S form) to a conspecific *A. coluzzi* (M form) (Weill et al., 2000) and its
152 frequency has greatly increased in *A. coluzzi* populations over the past two decades (Lynd et al.,
153 2010; Norris et al., 2015). Selection tests and demographic simulations suggest this increase has
154 been driven by selection (Lynd et al., 2010; Weetman et al., 2010). Another recent example of
155 adaptive introgression in plants has been discovered in a population of *Arabidopsis arenosa* (Arnold
156 et al., 2016) using genome scans. Several genomic signatures of selection associated with
157 adaptation to serpentine soils were found to be of introgressed origin from a different species, *A.*
158 *lyrata*. The uncontrolled escape of agricultural adaptations (e.g. resistance to biotic and abiotic
159 stressors, often achieved with transgenes) from fields to wild populations, through weedy forms, is
160 another well-known case of rapid adaptive introgression. This causes substantial yield losses and
161 requires strong economic efforts in managing cultivated and wild species (e.g. Ellstrand et al., 2013;
162 Hooftman et al., 2007; Rose et al., 2009; Uwimana et al., 2012).

163

164

165 **3. Characterizing adaptive introgression with genetic data**

166

167 To infer adaptive introgression, it is necessary to demonstrate 1) the introgression, by showing the
168 foreign origin of the genetic variant and its persistence in the recipient pool (i.e. should be found in
169 backcrossed generations), and 2) its adaptive value, by identifying selection footprints on the
170 introgressed fragment and (if possible) its fitness value. Genomic studies of adaptive introgression
171 seek to aim at gathering these three lines of evidence. Because of multiples factors (migration rate,
172 number of generations since introgression, intensity of selection) affecting the introgression process
173 and its interaction with selection, a variety of genomic patterns can be observed in the recipient
174 population (Figure 1). As these are complex patterns, there is no unique approach to detecting
175 signatures of adaptive introgression (Table 1). Below, we detail some of the most common
176 approaches used to detect introgression and to prove the action of selection (cf. Table 1).

177

178 **3.1 Detection of introgression**

179

180 The aim of detecting introgression is to identify populations and individuals of admixed origin and
181 quantify rates of gene flow, but also to find the traits or the genomic regions that have crossed
182 isolation barriers. Availability of whole genome data maximizes the chances of detecting
183 introgression even when it is rare in the genome (Hufford et al., 2013; Racimo et al., 2015; Rochus
184 et al., 2017; Schaefer et al., 2016). In the following sections, we describe approaches used to detect
185 introgression with genetic data, bearing in mind that none of them provides absolute proof of
186 introgression and that the best strategy is to gather evidence in different ways.

187

188 The ability to detect introgression increases with the divergence between the hybridizing taxa. For
189 higher divergent taxa, we have more markers fixed between species or with large allele frequency
190 differences. These “diagnostic alleles” allow easy identification of the ancestry of a genomic
191 fragment in the recipient population (e.g. Gittelman et al., 2016; Kim et al., 2008; Kovach et al.,
192 2009; Norris et al., 2015; Smith et al., 2004). However, even with slight differences in allele
193 frequencies, genetic clustering methods can be used to identify introgression. A variety of
194 approaches are available, such as multivariate analyses (e.g. Frichot et al., 2014; Jombart et al.,
195 2009) or Bayesian algorithms (e.g. Alexander et al., 2009; Anderson and Thompson, 2002;
196 Pritchard et al., 2000) (Figure 2a). The power of these global ancestry methods to detect gene flow

197 comes from the use of multiple independent (i.e. not physically linked) polymorphic markers. These
198 methods can be applied both genome-wide (Gagnaire et al., 2009; e.g. Rochus et al., 2017) and to
199 single genomic regions. Window-based analyses of ancestry along the maize genome were
200 successfully used to identify introgressed fragments from the wild progenitor teosinte (Hufford et
201 al., 2013).

202
203 When higher density molecular markers are available, other recent methods are able to assign an
204 ancestry probability to each polymorphic variant (Racimo et al., 2015; Schaefer et al., 2016). These
205 local ancestry methods use probabilistic approaches, such as Hidden Markov Models (e.g. Reich et
206 al., 2012), or Conditional Random Fields (e.g. Sankararaman et al., 2014) to infer the ancestry state
207 of each site, taking into account the information of physically close positions. As physical linkage
208 disequilibrium patterns dilute with generations, these approaches are less efficient for the detection
209 of ancient introgression, compared to global ancestry methods. While some implementations
210 require phased data (e.g. Song and Hein, 2005) or training data (e.g. Sankararaman et al., 2014),
211 more recent developments have overcome these constraints (e.g. Guan, 2014). So far, such
212 approaches have been mainly applied to model species (e.g. Staubach et al., 2012 on *Mus musculus*;
213 Turissini and Matute, 2017 on *Drosophila*; Zhou et al., 2016 on humans), but the increasing
214 availability of whole genome data will soon make them suitable for other study systems.

215
216 The approaches described above help to quantify the amount of shared diversity between genetic
217 pools. Shared variants between populations may be the result of different processes other than
218 introgression: the retention of ancestral polymorphic alleles by chance (referred to as Incomplete
219 Lineage Sorting, ILS, Figure 3), balancing selection or convergence (see Hedrick, 2013 for a
220 comparison). For lower divergence times (as for wild-crop complexes), the probability that the two
221 related groups have conserved ancestral polymorphism is higher. Thus, in most cases, the main
222 challenge to detecting introgression is to distinguish it from ancestral shared polymorphism.
223 Tracking the absence of the introgressed variants in ancient samples of the recipient pool would be
224 an efficient way of excluding shared ancestral polymorphism. However, historical samples are
225 difficult to obtain for most biological systems, so different methods have been developed to search
226 for specific signatures on the genome that help to differentiate between introgressed fragments and
227 inherited ancestral fragments.

228
229 Coalescent samplers have been widely used to test for gene flow versus ILS using maximum
230 likelihood or Bayesian models (Pinho and Hey, 2010). However, they are not straightforwardly
231 applied to all study systems, because they require a strong computation effort and are not easy to
232 transpose to a genome-wide scale. An alternative, simpler strategy takes advantage of the
233 expectations associated with phylogenetic relationships between individuals or populations (Figure
234 3). Given a genealogical tree describing the history of divergence between taxa or populations, a
235 precise amount of shared variation between branches is expected because of drift and ILS. A
236 significant excess of shared variation instead may be indicative of gene flow (Kulathinal et al.,
237 2009; Patterson et al., 2012; Peter, 2016). A number of statistics have been developed to test for the
238 excess of shared polymorphism. The most used are the D-statistic (or ABBA-BABA test, Durand et
239 al., 2011; Green et al., 2010) and the f_3 and f_4 statistics (globally referred to as f -statistics, Reich et
240 al., 2009, 2012). These statistics were initially applied to human populations and have proven to be
241 useful in other study systems, e.g. to detect the introgression of adaptation to serpentine soils in
242 *Arabidopsis* species (Arnold et al., 2016). In general, the power of these tests to detect admixed
243 genomes or populations is greater when applied to genome-wide data (see Patterson et al., 2012 for
244 a review; Peter, 2016), but most recent statistics can be applied to small genomic regions, e.g. f_D
245 (Martin et al., 2015; Racimo et al., 2017).

246

247 Other approaches take advantage of haplotype characteristics to distinguish between introgression
248 and ILS. As recombination breaks apart haplotypes over generations, introgressed haplotypes
249 should be longer than haplotypes due to ILS and should exhibit higher levels of linkage
250 disequilibrium (see figure 1 from Racimo et al., 2015). If admixture occurred recently compared to
251 the divergence between populations, these features can be exploited to detect introgressed tracts. A
252 test of significance can be associated by performing coalescent simulations of specific demographic
253 scenarios (setting values of divergence times, recombination rates, population structure or selection
254 adapted to the case in hand) to obtain the expectations for haplotype length statistics in the absence
255 of gene flow. Haplotype length analyses led to the identification of candidate introgressed tracts and
256 estimation of the age of the last introgression event in humans (Racimo et al., 2015) and dogs (Miao
257 et al., 2016). A recently developed statistic, S^* , uses linkage disequilibrium information to detect
258 introgressed haplotypes when no information about the donor is available. S^* is designed to identify
259 divergent haplotypes whose variants are in strong linkage disequilibrium and are not found in a
260 non-admixed reference population. S^* increases as the number of linked SNPs and the distance
261 between them increases (Vernot et al., 2016). This statistic helped to reveal the introgressed origin
262 of the EPAS1 gene in Tibetans, before the identification of the Denisovan donor (Huerta-Sánchez et
263 al., 2014).

264 265 **3.2 Detection of selection**

266
267 To prove adaptive introgression, the action of selection has to be demonstrated on the introgressed
268 variant. A number of reviews address methods and tools for detecting selection with molecular data
269 (e.g. Bank et al., 2014; Pavlidis and Alachiotis, 2017). In practice, most of the available approaches
270 are more sensitive to signatures of strong positive selection (i.e. selective sweeps, Smith and Haigh,
271 1974). For regions under strong positive selection, expectations are lower diversity, higher linkage
272 disequilibrium and specific distortions of the allele frequency spectrum compared to the genome-
273 wide patterns.

274
275 In within-population analyses, local patterns of lower genome diversity (Figure 2b) and shifts of the
276 allele frequency spectrum toward an excess of low frequency alleles are often informative for
277 detecting positive selection. For instance, polymorphism summary statistics, such as π (nucleotide
278 expected heterozygosity) and Tajima's D , have helped to discover and characterize introgressed loci
279 involved in serpentine adaptation of *Arabidopsis arenosa* (Arnold et al., 2016) and in the pesticide
280 resistance of mosquitoes (Norris et al., 2015) and mice (Song et al., 2011). Advanced methods for
281 genomic scans of positive selection are the Composite Likelihood Ratio test approaches (reviewed
282 in Pavlidis and Alachiotis, 2017). These tests compare the probability of the observed local site
283 frequency spectrum under a model of selection with the probability of observing the data under the
284 standard neutral model. The neutral expectations can be inferred by genome-wide observed patterns
285 or by specific simulated demographic scenarios (e.g. Liu et al., 2015; Quach et al., 2016; Staubach
286 et al., 2012).

287
288 Haplotypic information is also extremely useful for identifying almost fixed or very recently fixed
289 selective sweeps. The frequency of the introgressed haplotype in the recipient population can serve
290 for identifying selection. This interpretation is based on the assumption that introgressed regions
291 under selection should be at higher frequencies in the population relatively to the rest of the genome
292 (e.g. Vernot et al., 2016). The extent of linkage disequilibrium generated on the sides of a beneficial
293 mutation (or the haplotype size) is another signature captured by a number of tests for selection
294 (Crisci et al., 2012). The BADH2 gene, responsible for the much-appreciated characteristic
295 fragrance of some Asian rice varieties, provides a nice example of adaptive introgression detected
296 by haplotype analysis. This gene only shows strong signatures of selection in fragrant accessions, as

297 revealed by a dramatic reduction in diversity (π) and a large block of linkage disequilibrium in
298 regions flanking the functional mutation. The selected fragrant allele is likely to have originated
299 after domestication in the genetic background of the *japonica* varietal group and to have been
300 transferred to the *indica* variety by introgression (Kovach et al., 2009).

301
302 Extreme differentiation between populations in specific genomic regions can also be interpreted as
303 a signature of selection subtending local adaptation. For introgressed alleles adaptive in the
304 recipient population, higher differentiation can be expected between the recipient and another non-
305 admixed population (e.g. Ai et al., 2015). In addition, recipient-donor differentiation will be lower
306 for introgressed regions compared to the rest of the genome (Figure 2b). Thus, comparisons of
307 pairwise differentiation values between different populations (i.e. donor, recipient and “reference”
308 non-admixed population) may help to disentangle instances of adaptive introgression (e.g. Arnold et
309 al., 2016; Enciso-Romero et al., 2017; Racimo et al., 2017). A number of differentiation/divergence
310 statistics with different properties are available (e.g. Cruickshank and Hahn, 2014). Among them,
311 estimators of F_{ST} (Wright, 1931) are the most commonly used for detecting selection (e.g. Arnold et
312 al., 2016; Gagnaire et al., 2009; Gittelman et al., 2016).

313
314 It should be noted, however, that inferring separately introgression and selection might not be the
315 best approach to detect adaptive introgression, as expected genetic patterns are not necessarily the
316 same. For example, we do not necessarily expect a reduction of diversity in an introgressed region
317 under positive selection. In fact, it has been shown by simulations that admixture can increase
318 diversity blowing the diversity loss due to selection (Racimo et al., 2017). Recent investigations
319 into the joint dynamics of introgression and positive selection have opened promising avenues for
320 the analysis of genetic data in quest of adaptive introgression instances (Racimo et al., 2017). These
321 authors proposed new statistics informative to identify candidates to adaptive introgression and
322 based to the number and frequency of alleles shared by the donor and the recipient populations (but
323 absent or nearly absent in non-introgressed reference populations). Such “unique shared alleles”
324 should be numerous and at high frequency in genomic regions interested by adaptive introgression
325 (Figure 3c). The proposed statistics resuming these patterns, Q95 and U, have proven successful to
326 retrieve several known regions of archaic adaptive introgression from Neanderthals and Denisovans
327 in modern human genome (Racimo et al., 2017). However, these statistics are not straightforwardly
328 applicable to any study system. Specific demographic simulations are necessary to assess their
329 expected value in absence of adaptive introgression.

330
331 Different types of selection other than selective sweeps may generate genetic patterns that are more
332 difficult to distinguish from non-selective processes with the approaches described above.
333 Balancing selection on an introgressed locus, for instance, might go undetected because it would
334 maintain several variants at intermediate frequency within the recipient population. Such a pattern
335 can be interpreted as the result of migration-drift equilibrium, unless a direct link has been
336 established between the locus and a phenotypic trait. Examples of adaptive introgression driven by
337 balancing selection are the incompatibility locus in *Arabidopsis* (Castric et al., 2008), skin colour
338 change in wolves (Anderson et al., 2009; von Holdt et al., 2016) and the HLA locus in humans
339 (Abi-Rached et al., 2011). Soft-sweeps, fixation of a beneficial allele starting from multiple copies
340 of it in the population (Hermisson and Pennings, 2005), could also interest introgressed regions.
341 Typically, when the migration rate is high, the same beneficial allele can enter the recipient
342 population associated with different genetic backgrounds. This kind of positive selection signature
343 is difficult to detect because diversity and site frequency spectrum patterns do not change
344 dramatically as in hard selective sweeps (Hermisson and Pennings, 2017).

345

346 It should be noted also that inferences of selection based on molecular data only give indirect
347 evidence of the adaptive value of introgressions, particularly when they target genomic regions with
348 an unknown contribution to fitness-related traits (e.g. Gagnaire et al., 2009). However, detecting
349 selection in genic regions linked to specific functions or phenotypes (shown by phenotype-genotype
350 association analysis for instance) greatly helps the interpretation in terms of adaptation (e.g.
351 Hufford et al., 2013; Racimo et al., 2015; Rochus et al., 2017). Ultimately, one direct validation of
352 the adaptive role of introgression is to demonstrate the fitness advantage of the introgressed allele or
353 trait for the recipient population (e.g. Martin et al., 2006; Whitney et al., 2006, 2010, 2015; Figure
354 4). However, field studies involving phenotypic exploration can be time-consuming and difficult to
355 implement for most species.

356

357 **4. Gene flow in crops: challenges and opportunities**

358

359 The domestication process often involves dispersion across long distances and different
360 environmental conditions, combined with intense selection. Under such a process, multiple
361 opportunities arise for gene flow with locally adapted cultivated or wild forms (Allaby et al., 2008;
362 Meyer and Purugganan, 2013). In addition, among domestication characters, genetic divergence
363 between domesticated and wild relatives is often low and the reproductive barriers narrow (e.g.
364 Dempewolf et al., 2012). These characteristics make domesticated species likely carriers of
365 adaptive introgression.

366

367 Thanks to the analysis of genome-wide data, the importance of gene flow in shaping today's
368 diversity of domesticated species is becoming evident, particularly in crops. The evolution of two
369 major cereals, rice and barley, fits a domestication history with frequent gene flow events. In rice,
370 complex introgressive hybridizations have shuffled the genome of Asian rice, leading to the current
371 main groups *O. sativa japonica* and *O. s. indica*. Surveys indicate that *O. s. indica* had acquired
372 major domestication alleles through gene flow from *O. s. japonica* into the wild progenitor *O.*
373 *rufipogon*, or into putative proto-*indica* populations (Choi et al., 2017). White pigmentation,
374 aromatic fragrance and glutinous starch are some of the phenotypic traits involved in allele transfers
375 driven by strong directional selection (Huang et al., 2012; Kovach et al., 2009; Olsen and
376 Purugganan, 2002). In barley, the genome of domesticated forms appears to be a mosaic of
377 fragments originating from different cultivated and wild populations across the Fertile Crescent
378 (Pankin and von Korff, 2017; Poets et al., 2015). Introgression from local wild relatives has also
379 been shown in grapes (Myles et al. 2011), apples (Cornille et al., 2012) and olives (Diez et al.,
380 2015). Similarly, gene flow events have occurred in domesticated animals. For instance, Rochus et
381 al. (2017) analyzed the diversity of French sheep breeds to find that one mutation in a genomic
382 region related to milk production and growth originated in a southern breed and was introgressed
383 and selected for in northern breeds.

384

385 While adaptive introgression of agronomic traits between different breeds or cultivars may occur
386 relatively easily under similar human selective pressures, the transfer of beneficial traits from wild
387 relatives seems more difficult, since selection in natural environments usually goes in the opposite
388 direction from selection in agricultural environments. Crop-wild admixed plants (weeds) may tend
389 to be phenotypically intermediate and thus to have unwanted wild-type traits (e.g. asynchrony of
390 phenology changes, multiple branching, seed shattering, noxious or unpalatable compounds). To
391 understand how wild alleles can enter the crop gene pool by spontaneous gene flow, Jarvis and
392 Hodgkin (1999) point to the necessity of understanding how farmers' taxonomy and practices (i.e.
393 seed management, weeding, etc.) are applied to the new phenotypic variations resulting from
394 hybridization. Barnaud et al. (2009) investigated criteria used by farmers to characterize
395 morphotypes of domesticated and weedy sorghum. While strong counter-selection was performed

396 against weedy types, they found that progenies of weedy types could be misidentified as cultivated
397 forms, thus favoring wild-to-crop introgression. For pearl millet, it has been suggested that
398 incomplete weeding and singling allow hybridization and introgression to occur freely and
399 extensively (Couturon et al., 1997; Robert et al., 2003, Mariac et al. 2006), favoring the
400 maintenance of wild genetic material in the cultivated gene pool. In addition, weedy types can play
401 an important role for food security. In many cases, weedy types are early maturing plants and they
402 are used under harsh conditions or between main harvests. In Sudan, farmers recognize a crop-wild
403 hybrid of sorghum, which is allowed to grow and is selectively harvested in bad years (Ejeta and
404 Grenier, 2005). Hybrids can be harvested during periods of scarcity in the case of pearl millet too
405 (Couturon et al., 2003; Mariac et al., 2006) or in common bean (de la Cruz et al., 2005; Zizumbo-
406 Villarreal et al., 2005). Some studies have also documented farmers practicing conscious directional
407 selection towards evolution and changes of cultivated phenotypes by using the diversity available in
408 the wild relatives. For instance, in Benin, farmers voluntarily grow wild and hybrid yams
409 (*Dioscorea* spp.) in their fields to increase diversity (Scarcelli et al., 2006).

410
411 All in all, this demonstrates how farmer practices can maintain and, in some cases, actively favor
412 wild-to-crop introgression. This can be particularly important for crop adaptation, since the trade-off
413 of strong human selection for certain traits has been the loss of diversity for other important adaptive
414 traits (e.g. Zheng et al., 2008). Notably, traits involved in climate and soil adaptation, or resistance to
415 pests and diseases, display much greater diversity in wild species than in domesticated species
416 (Dempewolf et al., 2017; Guarino and Lobell, 2011; Hajjar and Hodgkin, 2007). Therefore, favoring
417 introgression from wild relatives may be an indirect way for farmers to introduce lost or new
418 adaptations. A compelling example of the potential adaptive outcome of wild-to-crop introgression is
419 the adaptation to altitude acquired by highland maize landraces. Maize was domesticated from low
420 altitude wild populations of teosinte (*Zea mays* ssp. *parviglumis*) and colonized high altitude
421 environments (Matsuoka et al., 2002) where a different wild relative is found (*Z. m. mexicana*).
422 Hufford et al. (2013) performed genomic scans on Mexican sympatric populations of maize and
423 *mexicana* and found nine genomic regions of introgression of *mexicana* into maize landraces. These
424 regions, related to adaptive traits, such as the quantity of leaf macrohairs and pigmentation intensity,
425 could have helped maize to adapt to high altitude (Hufford et al., 2013). Recent study suggested that
426 wild-to-crop gene flow significantly genetic diversity and possibly lead to introgressions of local
427 adaptation in pearl millet, a major staple African crops (Burgarella et al., in press).

428
429 The transferal of wild traits into a cultivated genetic background through classic breeding programs
430 has so far been limited to a narrow range of traits (Warschefsky et al., 2014), e.g. disease resistance in
431 cassava (Bredeson et al., 2016) and tomatoes (Lin et al., 2014). One main difficulty for conventional
432 breeding in introgressing wild genes into cultivated gene pools is that wild diversity is mostly
433 unexplored and desirable characters have still to be identified. Furthermore, wild species have many
434 traits associated with poor agronomic performance (e.g. low yields, seed shattering, small seed or
435 fruit size). Thus, several backcrosses are necessary to dilute the unwanted diversity associated with
436 wild introgression (Dempewolf et al., 2017) or to produce specifically design lines in which small
437 regions of the wild relative are introduced (e.g. Fonceka et al., 2012). We argue that screening the
438 wild introgression already existing in the cultivated gene pool thanks to natural gene flow may be an
439 effective strategy to uncover wild diversity relevant for crop adaptation to environmental changes and
440 to inform new breeding directions. Therefore, research efforts should be devoted to quantifying and
441 characterizing the extent of such spontaneous wild-to-crop introgression. Two main challenges are
442 associated with this approach. First one will need to have access to wild “pure” genetic resources,
443 which highlight the crucial need of wild relative conservation programs. Second, identification of
444 adaptive introgression in crops might be more challenging because of the low genetic divergence
445 usually observed between crop species and their wild relatives (as exposed in paragraph 3). However,

446 interest in the study of adaptive introgression, notably in humans, means the field is moving fast
447 towards new analytical approaches designed to identify specific features in genomes (e.g. Racimo et
448 al., 2017). Of course, the validation of adaptive introgression detected via molecular data should be
449 validated with classic experiments (Figure 4) to measure the strength of selection in the field and to
450 assess the biological function of the introgressed alleles (Suarez-Gonzalez et al., 2018; Whitney et al.,
451 2006). Given their adaptation to human-controlled environments, this step seems easier to accomplish
452 in most crops than in wild species.

453
454 Regarding the introduction or re-introduction of adaptive variation, it might be wondered to what
455 extent introgression from wild relatives can affect the whole crop genome. Recent studies have
456 suggested that introgression can be favored at genome-wide level when it reduces the genetic load
457 of the recipient species (Sankararaman et al., 2014; Wang et al., 2017). Genetic load refers to the
458 genome-wide accumulation of weakly deleterious alleles that reduces its fitness (Crow, 1958).
459 Given the repeated selection rounds associated with the domestication process, crop species
460 experience a reduction in the effective population size and in effective recombination, which in turn
461 reduces the efficacy of purifying selection in removing deleterious alleles and increases the effect of
462 hitchhiking selection (i.e. deleterious variants increase in frequency because they are linked to
463 selected beneficial alleles). Inbreeding, which is commonly practiced to fix traits of interest, also
464 slightly contributes to fixing deleterious alleles. In crops, a reduction in fitness is expected
465 compared to the wild progenitor, the so-called ‘cost of domestication’ (Lu et al., 2006). A greater
466 genetic load than in the wild counterpart was observed in several domesticated species such as rice
467 (Lu et al., 2006), maize (Wang et al., 2017), sunflower (Renaut and Rieseberg, 2015), dogs
468 (Marsden et al., 2016) and horses (Schubert et al., 2014). Since wild species are expected to have a
469 lower genetic load than cultivated species, spontaneous introgression from wild species could be
470 favored, because it alleviates the domestication cost, even in the absence of strong directional
471 selection on the introgressed alleles. Recent findings in maize support this expectation, as negative
472 correlations were observed between wild introgression and genetic load (Wang et al. 2017).

473
474 Despite the potential benefits of wild introgression for crops (i.e. acquisition of specific adaptations
475 and reduction of genetic load), genomic heterogeneity is expected in terms of permeability to gene
476 flow. In particular, regions involved in major domestication characters are expected to be under
477 strong selection, thereby acting as barriers to gene flow (so-called “islands of domestication”, Frantz
478 et al., 2015). Thus, the probability of introgression along the crop genome largely depends on the
479 number and distribution of domestication loci. Loci responsible for domestication traits have been
480 identified in a number of crops (Doebley et al., 2006; Gross and Olsen, 2010; Meyer et al., 2012), but
481 knowledge is far from complete. Up to now, research on the genetic architecture of domestication
482 traits indicates that domestication loci are limited to a few genomic regions in most studied species
483 (Burger et al., 2008; Glémin and Bataillon, 2009) and may not be a major obstacle to introgression in
484 the rest of the genome. The efficiency of counter-selection would thus depend on the genetic distance
485 between the introgressed fragment and the domestication genes, which is determined by the extent of
486 local linkage disequilibrium. According to this expectation, Hufford et al. (2013) identified cold spots
487 and hotspots of wild introgression in the maize genome. Interestingly, cold spots were significantly
488 enriched in domestication genes (Hufford et al., 2013).

489

490 **5. Conclusion and prospects**

491

492 Today’s access to both phenotypic and genomic information provides the opportunity to further
493 investigate the role and mechanism of adaptive introgression in crops. From an applied point of
494 view, it can be a fair source of adaptation to be exploited in breeding programs. Along human

495 migrations, crops had the opportunity to exchange with multiple wild populations. These exchanges
496 might have resulted in the introgression of local adaptations that have already passed the
497 reproductive and the “agronomic” barriers. Identifying such local adaptive introgression, combined
498 with complementary tools (e.g. climatic modeling), could be an efficient way of adapting crops to
499 the predicted new environmental conditions. We therefore think there is a need to emphasize the
500 importance of conserving wild genetic resources and jointly investigating wild and crops relatives.
501 This research will also allow advances on key questions with broader prospects, such as
502 introgression rates and genome permeability (Hufford et al., 2013; Scascitelli et al., 2010). Genomic
503 scan approaches could be complemented by the development of recombinant inbred line (RILs)
504 wild-crop hybrid populations (e.g. Fonceka et al., 2012; Nice et al., 2016). Such pre-breeding
505 material can be exchanged and tested in different environments, which would also help to answer
506 the other side of the coin, the risk of transgene escapes in the case of crop-to-wild gene flow.

507
508

509 **Acknowledgements**

510
511 We thank Peter Biggins for English revision and Miguel Navascués for useful discussions on
512 methodological approaches. This project was supported by Agropolis Fondation under the reference
513 ID 1403-057 through the « *Investissements d'avenir* » programme (Labex Agro:ANR-10-LABX-
514 0001-01) under the frame of I-SITE MUSE (ANR-16-IDEX-0006 and the the NERC/DFID Future
515 Climate For Africa programme under the AMMA-2050 project, grant number NE/M019934/1.

516
517 **Author contribution statement**

518
519 CB, AB and CB-S wrote the first draft, all authors made a substantial, direct and intellectual
520 contribution to this work.

521
522 **Conflict of interest statement**

523
524 The authors declare no conflict of interest.

525

526 **Table legends**

527 **Table 1. Summary of studies reviewed.** Species names for donor and recipient taxa are listed, as
528 well as the type of data and methods used for 1) detection of the introgression and 2) detection of
529 the selection. “Genomic data” term include s whole-genome sequences or candidates genes
530 sequencing. “Genetic data refers to molecular markers such as QTL or SSR.

531

532

533

534

535 **Figure legends**

536

537 **Figure 1. Genomic signature of adaptive introgression.** A genomic fragment is transferred from
538 the donor to the recipient population via gene flow and subsequent backcrosses. If it enhances the
539 fitness of the recipient population, it experiences positive selection and rises in frequency.

540

541 **Figure 2. Approaches to detect introgression (a, b) and adaptive introgression (c).** Regions of
542 donor origin in the recipient genome can be revealed by performing local ancestry analyses (a) and
543 comparisons of donor-recipient differentiation levels (b). Introgressed fragments will show a larger
544 proportion of ancestry in the donor population (a. in black) and lower differentiation (b. arrow) than
545 non-introgressed recipient genomic regions. Positive selection increases the frequency of the donor
546 allele and the neutral variants physically linked to it. The result is a local higher number and
547 frequency of alleles shared by donor and recipient populations and absent in other non-introgressed
548 populations (c. arrow).

549

550 **Figure 3. Hybridization and incomplete lineage sorting (ILS) revealed by molecular**
551 **phylogenetics.** Top: evolutionary process. The species (or population) tree is represented by the
552 grey area. The dotted line represents a single gene genealogy. Bottom: Coalescent tree inferred for
553 the gene. (a) Congruent gene genealogy with species/population tree; (b) ILS: ancestral
554 polymorphism is maintained before the divergence between A and B, so that B shares the allele T
555 with C and not with A; (c) Introgression: B receives the allele T from C by gene flow. In the case of
556 ILS and introgression, the gene genealogy is incongruent with the species/population tree.

557

558 **Figure 4. Direct measure of adaptive introgression.** Direct evidence of the adaptive value of the
559 introgressed fragment (black segment) consists in showing that it confers greater fitness to the
560 recipient genome. This can be achieved by experimental crosses: introgression without positive
561 selection on the introgressed allele (A) vs adaptive introgression (B).

562

563

564

565 **References**

- 566
- 567 Abbott, R., Albach, D., Ansell, S., Arntzen, J. W., Baird, S. J. E., Bierne, N., et al. (2013).
568 Hybridization and speciation. *J. Evol. Biol.* 26, 229–246. doi:10.1111/j.1420-
569 9101.2012.02599.x.
- 570 Abi-Rached, L., Jobin, M. J., Kulkarni, S., McWhinnie, A., Dalva, K., Gragert, L., et al. (2011).
571 The Shaping of Modern Human Immune Systems by Multiregional Admixture with Archaic
572 Humans. *Science* 334, 89–94. doi:10.1126/science.1209202.
- 573 Ai, H., Fang, X., Yang, B., Huang, Z., Chen, H., Mao, L., et al. (2015). Adaptation and possible
574 ancient interspecies introgression in pigs identified by whole-genome sequencing. *Nat.*
575 *Genet.* 47, 217–225. doi:10.1038/ng.3199.
- 576 Aitken, S. N., and Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to
577 climate change. *Annu. Rev. Ecol. Evol. Syst.* 44.
- 578 Alexander, D. H., Novembre, J., and Lange, K. (2009). Fast model-based estimation of ancestry in
579 unrelated individuals. *Genome Res.* 19, 1655–1664. doi:10.1101/gr.094052.109.
- 580 Allaby, R. G., Fuller, D. Q., and Brown, T. A. (2008). The genetic expectations of a protracted
581 model for the origins of domesticated crops. *Proc. Natl. Acad. Sci.* 105, 13982–13986.
582 doi:10.1073/pnas.0803780105.
- 583 Anderson, E. (1949). Introgressive hybridization. ix + 109 pp.
- 584 Anderson, E. C., and Thompson, E. A. (2002). A Model-Based Method for Identifying Species
585 Hybrids Using Multilocus Genetic Data. *Genetics* 160, 1217–1229.
- 586 Anderson, T. M., vonHoldt, B. M., Candille, S. I., Musiani, M., Greco, C., Stahler, D. R., et al.
587 (2009). Molecular and Evolutionary History of Melanism in North American Gray Wolves.
588 *Science* 323, 1339–1343. doi:10.1126/science.1165448.
- 589 Arnold, B. J., Lahner, B., DaCosta, J. M., Weisman, C. M., Hollister, J. D., Salt, D. E., et al. (2016).
590 Borrowed alleles and convergence in serpentine adaptation. *Proc. Natl. Acad. Sci.*,
591 201600405. doi:10.1073/pnas.1600405113.
- 592 Arnold, M. L., and Kunte, K. (2017). Adaptive Genetic Exchange: A Tangled History of Admixture
593 and Evolutionary Innovation. *Trends Ecol. Evol.* 32, 601–611.
594 doi:10.1016/j.tree.2017.05.007.
- 595 Arnold, M. L., and Martin, N. H. (2009). Adaptation by introgression. *J. Biol.* 8, 82.
596 doi:10.1186/jbiol176.
- 597 Baack, E., Melo, M. C., Rieseberg, L. H., and Ortiz-Barrientos, D. (2015). The origins of
598 reproductive isolation in plants. *New Phytol.* 207, 968–984.
- 599 Bank, C., Ewing, G. B., Ferrer-Admettla, A., Foll, M., and Jensen, J. D. (2014). Thinking too
600 positive? Revisiting current methods of population genetic selection inference. *Trends*
601 *Genet.* 30, 540–546. doi:10.1016/j.tig.2014.09.010.

- 602 Barnaud, A., Deu, M., Garine, E., Chantereau, J., Bolteu, J., Kořda, E. O., et al. (2009). A weed–
603 crop complex in sorghum: The dynamics of genetic diversity in a traditional farming system.
604 *Am. J. Bot.* 96, 1869–1879. doi:10.3732/ajb.0800284.
- 605 Barton, N., and Bengtsson, B. O. (1986). The barrier to genetic exchange between hybridising
606 populations. *Heredity* 57, 357–376. doi:10.1038/hdy.1986.135.
- 607 Barton, N. H., and Hewitt, G. M. (1985). Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* 16, 113–
608 148.
- 609 Bredeson, J. V., Lyons, J. B., Prochnik, S. E., Wu, G. A., Ha, C. M., Edsinger-Gonzales, E., et al.
610 (2016). Sequencing wild and cultivated cassava and related species reveals extensive
611 interspecific hybridization and genetic diversity. *Nat. Biotechnol.* 34, 562–570.
612 doi:10.1038/nbt.3535.
- 613 Burgarella, C., Cubry, P., Kane, N. A., Varshney, R. K., Mariac, C., Liu, X., et al. (in press). A
614 western Sahara origin of African agriculture inferred from pearl millet genomes. *Nat. Ecol.*
615 *Evol.*
- 616 Burger, J. C., Chapman, M. A., and Burke, J. M. (2008). Molecular insights into the evolution of
617 crop plants. *Am. J. Bot.* 95, 113–122. doi:10.3732/ajb.95.2.113.
- 618 Castric, V., Bechsgaard, J., Schierup, M. H., and Vekemans, X. (2008). Repeated Adaptive
619 Introgression at a Gene under Multiallelic Balancing Selection. *PLOS Genet.* 4, e1000168.
620 doi:10.1371/journal.pgen.1000168.
- 621 Choi, J. Y., Platts, A. E., Fuller, D. Q., Hsing (邢禹依), Y.-I., Wing, R. A., and Purugganan, M. D.
622 (2017). The Rice Paradox: Multiple Origins but Single Domestication in Asian Rice. *Mol.*
623 *Biol. Evol.* 34, 969–979. doi:10.1093/molbev/msx049.
- 624 Cornille, A., Gladieux, P., Smulders, M. J. M., Roldán-Ruiz, I., Laurens, F., Cam, B. L., et al.
625 (2012). New Insight into the History of Domesticated Apple: Secondary Contribution of the
626 European Wild Apple to the Genome of Cultivated Varieties. *PLOS Genet.* 8, e1002703.
627 doi:10.1371/journal.pgen.1002703.
- 628 Couturon, E., Bezaçon, G., and Renno, J.-F. (1997). Influence des pratiques culturelles sur
629 l'évolution de la fréquence des hybrides chibra dans un champ de mil, *Pennisetum glaucum*
630 (L.) R. Br., au Sahel.
- 631 Couturon, E., Mariac, C., Bezaçon, G., Lauga, J., and Renno, J.-F. (2003). Impact of natural and
632 human selection on the frequency of the F1 hybrid between cultivated and wild pearl millet
633 (*Pennisetum glaucum* (L.) R. Br.). *Euphytica* 133, 329–337.
- 634 Coyne, J. A., and Orr, H. A. (2004). *Speciation*. Sunderland, MA. Sinauer Associates, Inc.
- 635 Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., and Mynsberge, A. R.
636 (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum
637 elevations. *Science* 331, 324–327.
- 638 Crisci, J. L., Poh, Y.-P., Bean, A., Simkin, A., and Jensen, J. D. (2012). Recent Progress in
639 Polymorphism-Based Population Genetic Inference. *J. Hered.* 103, 287–296.
640 doi:10.1093/jhered/esr128.

- 641 Crow, J. F. (1958). SOME POSSIBILITIES FOR MEASURING SELECTION INTENSITIES IN
642 MAN. *Hum. Biol.* 30, 1–13.
- 643 Cruickshank, T. E., and Hahn, M. W. (2014). Reanalysis suggests that genomic islands of
644 speciation are due to reduced diversity, not reduced gene flow. *Mol. Ecol.* 23, 3133–3157.
645 doi:10.1111/mec.12796.
- 646 Dannemann, M., Andrés, A. M., and Kelso, J. (2016). Introgression of Neandertal-and Denisovan-
647 like haplotypes contributes to adaptive variation in human Toll-like receptors. *AJHG*, 98,
648 22-33.
- 649 de la Cruz, E. P., Gepts, P., GarciaMarín, P. C., and Villareal, D. Z. (2005). Spatial Distribution of
650 Genetic Diversity in Wild Populations of *Phaseolus vulgaris*L. from Guanajuato and
651 Michoacán, Méexico. *Genet. Resour. Crop Evol.* 52, 589–599.
- 652 Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., and Guarino, L. (2017). Past and
653 Future Use of Wild Relatives in Crop Breeding. *Crop Sci.* 0.
654 doi:10.2135/cropsci2016.10.0885.
- 655 Dempewolf, H., Hodgins, K. A., Rummell, S. E., Ellstrand, N. C., and Rieseberg, L. H. (2012).
656 Reproductive Isolation during Domestication. *Plant Cell* 24, 2710–2717.
657 doi:10.1105/tpc.112.100115.
- 658 Deschamps, M., Laval, G., Fagny, M., Itan, Y., Abel, L., Casanova, J. L., ... and Quintana-Murci, L.
659 (2016). Genomic signatures of selective pressures and introgression from archaic hominins
660 at human innate immunity genes. *AJHG*, 98, 5-21.
661
- 662 Diez, C. M., Trujillo, I., Martinez-Urdiroz, N., Barranco, D., Rallo, L., Marfil, P., et al. (2015).
663 Olive domestication and diversification in the Mediterranean Basin. *New Phytol.* 206, 436–
664 447. doi:10.1111/nph.13181.
- 665 Doebley, J. F., Gaut, B. S., and Smith, B. D. (2006). The Molecular Genetics of Crop
666 Domestication. *Cell* 127, 1309–1321. doi:10.1016/j.cell.2006.12.006.
- 667 Doi, H., Takahashi, M., and Katano, I. (2010). Genetic diversity increases regional variation in
668 phenological dates in response to climate change. *Glob. Change Biol.* 16, 373–379.
- 669 Durand, E. Y., Patterson, N., Reich, D., and Slatkin, M. (2011). Testing for Ancient Admixture
670 between Closely Related Populations. *Mol. Biol. Evol.* 28, 2239–2252.
671 doi:10.1093/molbev/msr048.
- 672 Ejeta, G., and Grenier, C. (2005). Sorghum and its weedy hybrids. *Crop Feral. Volunt. CRC Press*
673 *Boca Raton FL*, 123–135.
- 674 Ellstrand, N. C. (2014). Is gene flow the most important evolutionary force in plants? *Am. J. Bot.*
675 101, 737–753. doi:10.3732/ajb.1400024.
- 676 Ellstrand, N. C., Meirmans, P., Rong, J., Bartsch, D., Ghosh, A., de Jong, T. J., et al. (2013).
677 Introgression of Crop Alleles into Wild or Weedy Populations. *Annu. Rev. Ecol. Evol. Syst.*
678 44, 325–345. doi:10.1146/annurev-ecolsys-110512-135840.

- 679 Ellstrand, N. C., and Schierenbeck, K. A. (2000). Hybridization as a stimulus for the evolution of
680 invasiveness in plants? *Proc. Natl. Acad. Sci.* 97, 7043–7050. doi:10.1073/pnas.97.13.7043.
- 681 Enciso-Romero, J., Pardo-Díaz, C., Martin, S. H., Arias, C. F., Linares, M., McMillan, W. O., et al.
682 (2017). Evolution of novel mimicry rings facilitated by adaptive introgression in tropical
683 butterflies. *Mol. Ecol.* 26, 5160–5172. doi:10.1111/mec.14277.
- 684 Fitzpatrick, B. M., Johnson, J. R., Kump, D. K., Shaffer, H. B., Smith, J. J., and Voss, S. R. (2009).
685 Rapid fixation of non-native alleles revealed by genome-wide SNP analysis of hybrid tiger
686 salamanders. *BMC Evol. Biol.* 9, 176.
687
- 688 Fonceka, D., Tossim, H.-A., Rivallan, R., Vignes, H., Lacut, E., Bellis, F. de, et al. (2012).
689 Construction of Chromosome Segment Substitution Lines in Peanut (*Arachis hypogaea* L.)
690 Using a Wild Synthetic and QTL Mapping for Plant Morphology. *PLOS ONE* 7, e48642.
691 doi:10.1371/journal.pone.0048642.
- 692 Frantz, L. A. F., Schraiber, J. G., Madsen, O., Megens, H.-J., Cagan, A., Bosse, M., et al. (2015).
693 Evidence of long-term gene flow and selection during domestication from analyses of
694 Eurasian wild and domestic pig genomes. *Nat. Genet.* 47, 1141–1148. doi:10.1038/ng.3394.
- 695 Frichot, E., Mathieu, F., Trouillon, T., Bouchard, G., and François, O. (2014). Fast and Efficient
696 Estimation of Individual Ancestry Coefficients. *Genetics* 196, 973–983.
697 doi:10.1534/genetics.113.160572.
- 698 Gagnaire, Albert V., Jónsson B., and Bernatchez L. (2009). Natural selection influences AFLP
699 intraspecific genetic variability and introgression patterns in Atlantic eels. *Mol. Ecol.* 18,
700 1678–1691. doi:10.1111/j.1365-294X.2009.04142.x.
- 701 Gittelman, R. M., Schraiber, J. G., Vernot, B., Mikacenic, C., Wurfel, M. M., and Akey, J. M.
702 (2016). Archaic Hominin Admixture Facilitated Adaptation to Out-of-Africa Environments.
703 *Curr. Biol.* doi:10.1016/j.cub.2016.10.041.
- 704 Glémin, S., and Bataillon, T. (2009). A comparative view of the evolution of grasses under
705 domestication. *New Phytol.* 183, 273–290. doi:10.1111/j.1469-8137.2009.02884.x.
- 706 Grant, P. R., and Grant, B. R. (1994). Phenotypic and genetic effects of hybridization in Darwin’s
707 finches. *Evolution* 48, 297–316.
- 708 Green, R. E., Krause, J., Briggs, A. W., Maricic, T., Stenzel, U., Kircher, M., et al. (2010). A Draft
709 Sequence of the Neandertal Genome. *Science* 328, 710–722. doi:10.1126/science.1188021.
- 710 Gross, B. L., and Olsen, K. M. (2010). Genetic perspectives on crop domestication. *Trends Plant*
711 *Sci.* 15, 529–537. doi:10.1016/j.tplants.2010.05.008.
- 712 Guan, Y. (2014). Detecting Structure of Haplotypes and Local Ancestry. *Genetics* 196, 625–642.
713 doi:10.1534/genetics.113.160697.
- 714 Guarino, L., and Lobell, D. B. (2011). A walk on the wild side. *Nat. Clim. Change* 1, 374–375.
715 doi:10.1038/nclimate1272.

- 716 Hajjar, R., and Hodgkin, T. (2007). The use of wild relatives in crop improvement: a survey of
717 developments over the last 20 years. *Euphytica* 156, 1–13. doi:10.1007/s10681-007-9363-0.
- 718 Hedrick, P. W. (2009). Conservation Genetics and North American Bison (*Bison bison*). *J. Hered.*
719 100, 411–420. doi:10.1093/jhered/esp024.
- 720 Hedrick, P. W. (2013). Adaptive introgression in animals: examples and comparison to new
721 mutation and standing variation as sources of adaptive variation. *Mol. Ecol.* 22, 4606–4618.
722 doi:10.1111/mec.12415.
- 723 Hermisson, J., and Pennings, P. S. (2005). Soft sweeps: molecular population genetics of adaptation
724 from standing genetic variation. *Genetics* 169, 2335–2352.
725 doi:10.1534/genetics.104.036947.
- 726 Hermisson, J., and Pennings, P. S. (2017). Soft sweeps and beyond: understanding the patterns and
727 probabilities of selection footprints under rapid adaptation. *Methods Ecol. Evol.* 8, 700–716.
728 doi:10.1111/2041-210X.12808.
- 729 Hewitt, G. M. (1988). Hybrid zones-natural laboratories for evolutionary studies. *Trends Ecol. Evol.*
730 3, 158–167. doi:10.1016/0169-5347(88)90033-X.
- 731 Hoffmann, A. A., Sgrò, C. M., and Kristensen, T. N. (2017). Revisiting Adaptive Potential,
732 Population Size, and Conservation. *Trends Ecol. Evol.* 0. doi:10.1016/j.tree.2017.03.012.
- 733 Hooftman, Jong Maaïke, J. De, Oostermeijer, J. Gerard B, and Den Nijs, Hans (j.) C. M (2007).
734 Modelling the long-term consequences of crop–wild relative hybridization: a case study
735 using four generations of hybrids. *J. Appl. Ecol.* 44, 1035–1045. doi:10.1111/j.1365-
736 2664.2007.01341.x.
- 737 Hohenlohe, P. A., Day, M. D., Amish, S. J., Miller, M. R., Kamps-Hughes, N., Boyer, M. C., ... and
738 Luikart, G. (2013). Genomic patterns of introgression in rainbow and westslope cutthroat
739 trout illuminated by overlapping paired-end RAD sequencing. *Mol. Ecol.* 22, 3002-3013.
740
- 741 Hsieh, P., Woerner, A. E., Wall, J. D., Lachance, J., Tishkoff, S. A., Gutenkunst, R. N., et al.
742 (2016). Model-based analyses of whole-genome data reveal a complex evolutionary history
743 involving archaic introgression in Central African Pygmies. *Genome Res.* 26, 291–300.
744 doi:10.1101/gr.196634.115.
- 745 Huang, X., Kurata, N., Wei, X., Wang, Z.-X., Wang, A., Zhao, Q., et al. (2012). A map of rice
746 genome variation reveals the origin of cultivated rice. *Nature* 490, 497–501.
747 doi:10.1038/nature11532.
- 748 Huerta-Sánchez, E., Jin, X., Asan, Bianba, Z., Peter, B. M., Vinckenbosch, N., et al. (2014).
749 Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. *Nature*
750 512, 194–197. doi:10.1038/nature13408.
- 751 Hufford, M. B., Lubinsky, P., Pyhäjärvi, T., Devengenzo, M. T., Ellstrand, N. C., and Ross-Ibarra,
752 J. (2013). The Genomic Signature of Crop-Wild Introgression in Maize. *PLoS Genet* 9,
753 e1003477. doi:10.1371/journal.pgen.1003477.

- 754 IPCC (2014). “Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and
755 Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the
756 Intergovernmental Panel on Climate Change.” in (Cambridge, United Kingdom and New
757 York, NY, USA: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D.,
758 Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S.,
759 Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.)), 1132.
- 760 Jarvis, D. I., and Hodgkin, T. (1999). Wild relatives and crop cultivars: detecting natural
761 introgression and farmer selection of new genetic combinations in agroecosystems. *Mol.*
762 *Ecol.* 8.
- 763 Jeong, C., and Di Rienzo, A. (2014). Adaptations to local environments in modern human
764 populations. *Curr. Opin. Genet. Dev.*, 29, 1-8.
765
- 766 Jombart, T., Pontier, D., and Dufour, A.-B. (2009). Genetic markers in the playground of
767 multivariate analysis. *Heredity* 102, 330–341.
- 768 Kim, M., Cui, M.-L., Cubas, P., Gillies, A., Lee, K., Chapman, M. A., et al. (2008). Regulatory
769 Genes Control a Key Morphological and Ecological Trait Transferred Between Species.
770 *Science* 322, 1116–1119. doi:10.1126/science.1164371.
- 771 Kovach, M. J., Calingacion, M. N., Fitzgerald, M. A., and McCouch, S. R. (2009). The origin and
772 evolution of fragrance in rice (*Oryza sativa* L.). *Proc. Natl. Acad. Sci.* 106, 14444–14449.
773 doi:10.1073/pnas.0904077106.
- 774 Kulathinal, R. J., Stevison, L. S., and Noor, M. A. F. (2009). The Genomics of Speciation in
775 *Drosophila*: Diversity, Divergence, and Introgression Estimated Using Low-Coverage
776 Genome Sequencing. *PLOS Genet.* 5, e1000550. doi:10.1371/journal.pgen.1000550.
- 777 Lin, T., Zhu, G., Zhang, J., Xu, X., Yu, Q., Zheng, Z., et al. (2014). Genomic analyses provide
778 insights into the history of tomato breeding. *Nat. Genet.* 46, 1220–1226.
779 doi:10.1038/ng.3117.
- 780 Liu, K. J., Steinberg, E., Yozzo, A., Song, Y., Kohn, M. H., and Nakhleh, L. (2015). Interspecific
781 introgressive origin of genomic diversity in the house mouse. *Proc. Natl. Acad. Sci.* 112,
782 196–201. doi:10.1073/pnas.1406298111.
- 783 Llopart, A., Herrig, D., Brud, E., and Stecklein, Z. (2014). Sequential adaptive introgression of the
784 mitochondrial genome in *Drosophila yakuba* and *Drosophila santomea*. *Mol. Ecol.* 23, 1124-
785 1136.
786
- 787 Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., and Ackerly, D. D. (2009). The
788 velocity of climate change. *Nature* 462, 1052–1055. doi:10.1038/nature08649.
- 789 Lobell, D. B., Schlenker, W., and Costa-Roberts, J. (2011). Climate trends and global crop
790 production since 1980. *Science* 333, 616–620.
- 791 Lowry, D. B., Modliszewski, J. L., Wright, K. M., Wu, C. A., and Willis, J. H. (2008). The strength
792 and genetic basis of reproductive isolating barriers in flowering plants. *Philos. Trans. R.*
793 *Soc. B Biol. Sci.* 363, 3009–3021.

- 794 Lu, J., Tang, T., Tang, H., Huang, J., Shi, S., and Wu, C.-I. (2006). The accumulation of deleterious
795 mutations in rice genomes: a hypothesis on the cost of domestication. *Trends Genet.* 22,
796 126–131. doi:10.1016/j.tig.2006.01.004.
- 797 Lynd, A., Weetman, D., Barbosa, S., Egyir Yawson, A., Mitchell, S., Pinto, J., et al. (2010). Field,
798 Genetic, and Modeling Approaches Show Strong Positive Selection Acting upon an
799 Insecticide Resistance Mutation in *Anopheles gambiae* s.s. *Mol. Biol. Evol.* 27, 1117–1125.
800 doi:10.1093/molbev/msq002.
- 801 Mallet, J. (2005). Hybridization as an invasion of the genome. *Trends Ecol. Evol.* 20, 229–237.
802 doi:10.1016/j.tree.2005.02.010.
- 803 Mallet, J. (2007). Hybrid speciation. *Nature* 446, 279–283. doi:10.1038/nature05706.
- 804 Mariac, C., Robert, T., Allinne, C., Remigereau, M. S., Luxereau, A., Tidjani, M., et al. (2006).
805 Genetic diversity and gene flow among pearl millet crop/weed complex: a case study.
806 *Theor. Appl. Genet.* 113, 1003–1014. doi:10.1007/s00122-006-0360-9.
- 807 Marsden, C. D., Vecchyo, D. O.-D., O'Brien, D. P., Taylor, J. F., Ramirez, O., Vilà, C., et al.
808 (2016). Bottlenecks and selective sweeps during domestication have increased deleterious
809 genetic variation in dogs. *Proc. Natl. Acad. Sci.* 113, 152–157.
810 doi:10.1073/pnas.1512501113.
- 811 Martin, N. H., Bouck, A. C., and Arnold, M. L. (2006). Detecting Adaptive Trait Introgression
812 Between *Iris fulva* and *I. brevicaulis* in Highly Selective Field Conditions. *Genetics* 172,
813 2481–2489. doi:10.1534/genetics.105.053538.
- 814 Martin, S. H., Davey, J. W., and Jiggins, C. D. (2015). Evaluating the Use of ABBA–BABA
815 Statistics to Locate Introgressed Loci. *Mol. Biol. Evol.* 32, 244–257.
816 doi:10.1093/molbev/msu269.
- 817 Matsuoka, Y., Vigouroux, Y., Goodman, M. M., Sanchez G., J., Buckler, E., and Doebley, J.
818 (2002). A single domestication for maize shown by multilocus microsatellite genotyping.
819 *Proc. Natl. Acad. Sci.* 99, 6080–6084. doi:10.1073/pnas.052125199.
- 820 Meyer, R. S., DuVal, A. E., and Jensen, H. R. (2012). Patterns and processes in crop domestication:
821 an historical review and quantitative analysis of 203 global food crops. *New Phytol.* 196,
822 29–48. doi:10.1111/j.1469-8137.2012.04253.x.
- 823 Meyer, R. S., and Purugganan, M. D. (2013). Evolution of crop species: genetics of domestication
824 and diversification. *Nat. Rev. Genet.* 14, 840–852. doi:10.1038/nrg3605.
- 825 Miao, B., Wang, Z., and Li, Y. (2016). Genomic Analysis Reveals Hypoxia Adaptation in the
826 Tibetan Mastiff by Introgression of the Grey Wolf from the Tibetan Plateau. *Mol. Biol.*
827 *Evol.*, msw274. doi:10.1093/molbev/msw274.
- 828 Nevo, E. (2012). “Evolution Canyon,” a potential microscale monitor of global warming across life.
829 *Proc. Natl. Acad. Sci.* 109, 2960–2965. doi:10.1073/pnas.1120633109.
- 830 Nice, L. M., Steffenson, B. J., Brown-Guedira, G. L., Akhunov, E. D., Liu, C., Kono, T. J. Y., et al.
831 (2016). Development and Genetic Characterization of an Advanced Backcross-Nested

- 832 Association Mapping (AB-NAM) Population of Wild × Cultivated Barley. *Genetics* 203,
833 1453–1467. doi:10.1534/genetics.116.190736.
- 834 Norris, L. C., Main, B. J., Lee, Y., Collier, T. C., Fofana, A., Cornel, A. J., et al. (2015). Adaptive
835 introgression in an African malaria mosquito coincident with the increased usage of
836 insecticide-treated bed nets. *Proc. Natl. Acad. Sci.* 112, 815–820.
837 doi:10.1073/pnas.1418892112.
- 838 Olsen, K. M., and Purugganan, M. D. (2002). Molecular Evidence on the Origin and Evolution of
839 Glutinous Rice. *Genetics* 162, 941–950.
- 840 Pankin, A., and von Korff, M. (2017). Co-evolution of methods and thoughts in cereal
841 domestication studies: a tale of barley (*Hordeum vulgare*). *Curr. Opin. Plant Biol.* 36, 15–
842 21. doi:10.1016/j.pbi.2016.12.001.
- 843 Pardo-Diaz, C., Salazar, C., Baxter, S. W., Merot, C., Figueiredo-Ready, W., Joron, M., ... and
844 Jiggins, C. D. (2012). Adaptive introgression across species boundaries in *Heliconius*
845 butterflies. *PLoS Genet.* 8, e1002752.
846
- 847 Parmesan, C., and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts
848 across natural systems. *Nature* 421, 37–42. doi:10.1038/nature01286.
- 849 Patterson, N., Moorjani, P., Luo, Y., Mallick, S., Rohland, N., Zhan, Y., et al. (2012). Ancient
850 admixture in human history., Ancient Admixture in Human History. *Genet. Genet.* 192, 192,
851 1065, 1065–1093. doi:10.1534/genetics.112.145037, 10.1534/genetics.112.145037.
- 852 Pavlidis, P., and Alachiotis, N. (2017). A survey of methods and tools to detect recent and strong
853 positive selection. *J. Biol. Res.-Thessalon.* 24, 7. doi:10.1186/s40709-017-0064-0.
- 854 Perring, M. P., Frenne, P. D., Baeten, L., Maes, S. L., Depauw, L., Blondeel, H., et al. (2015).
855 Global environmental change effects on ecosystems: the importance of land-use legacies.
856 *Glob. Change Biol.* 22, 1361–1371. doi:10.1111/gcb.13146.
- 857 Peter, B. M. (2016). Admixture, Population Structure, and F-Statistics. *Genetics* 202, 1485–1501.
858 doi:10.1534/genetics.115.183913.
- 859 Pinho, C., and Hey, J. (2010). Divergence with Gene Flow: Models and Data. *Annu. Rev. Ecol.*
860 *Evol. Syst.* 41, 215–230. doi:10.1146/annurev-ecolsys-102209-144644.
- 861 Poets, A. M., Fang, Z., Clegg, M. T., and Morrell, P. L. (2015). Barley landraces are characterized
862 by geographically heterogeneous genomic origins. *Genome Biol.* 16, 173.
863 doi:10.1186/s13059-015-0712-3.
- 864 Pritchard, J. K., Stephens, M., and Donnelly, P. (2000). Inference of population structure using
865 multilocus genotype data. *Genetics* 155, 945–959.
- 866 Quach, H., Rotival, M., Pothlichet, J., Loh, Y.-H. E., Dannemann, M., Zidane, N., et al. (2016).
867 Genetic Adaptation and Neandertal Admixture Shaped the Immune System of Human
868 Populations. *Cell* 167, 643-656.e17. doi:10.1016/j.cell.2016.09.024.

- 869 Racimo, F., Marnetto, D., and Huerta-Sánchez, E. (2017). Signatures of Archaic Adaptive
870 Introgression in Present-Day Human Populations. *Mol. Biol. Evol.* 34, 296–317.
871 doi:10.1093/molbev/msw216.
- 872 Racimo, F., Sankararaman, S., Nielsen, R., and Huerta-Sánchez, E. (2015). Evidence for archaic
873 adaptive introgression in humans. *Nat. Rev. Genet.* 16, 359–371. doi:10.1038/nrg3936.
- 874 Reich, D., Patterson, N., Campbell, D., Tandon, A., Mazieres, S., Ray, N., et al. (2012).
875 Reconstructing Native American population history. *Nature* 488, 370–374.
876 doi:10.1038/nature11258.
- 877 Reich, D., Thangaraj, K., Patterson, N., Price, A. L., and Singh, L. (2009). Reconstructing Indian
878 population history. *Nature* 461, 489–494. doi:10.1038/nature08365.
- 879 Renaut, S., and Rieseberg, L. H. (2015). The Accumulation of Deleterious Mutations as a
880 Consequence of Domestication and Improvement in Sunflowers and Other Compositae
881 Crops. *Mol. Biol. Evol.* 32, 2273–2283. doi:10.1093/molbev/msv106.
- 882 Rieseberg, L. H., and Wendel, J. F. (1993). Introgression and its consequences in plants. *Hybrid
883 Zones Evol. Process*, 70–109.
- 884 Robert, T., Luxereau, A., Mariac, C., Ali, K., Allinne, C., Beidari, Y., et al. (2003). Gestion de la
885 diversité en milieu paysan: influence de facteurs anthropiques et des flux de gènes sur la
886 variabilité génétique des formes cultivées et spontanées du mil (*Pennisetum glaucum* ssp.
887 *glaucum* et ssp. *monodii* dans deux localités du Niger.
- 888 Rochus, C. M., Tortereau, F., Plisson-Petit, F., Restoux, G., Moreno-Romieux, C., Tosser-Klopp,
889 G., et al. (2017). High density genome scan for selection signatures in French sheep reveals
890 allelic heterogeneity and introgression at adaptive loci. *bioRxiv*, 103010.
891 doi:10.1101/103010.
- 892 Rose, C. W., Millwood, R. J., Moon, H. S., Rao, M. R., Halfhill, M. D., Raymer, P. L., et al. (2009).
893 Genetic load and transgenic mitigating genes in transgenic *Brassica rapa* (field mustard) ×
894 *Brassica napus* (oilseed rape) hybrid populations. *BMC Biotechnol.* 9, 93. doi:10.1186/1472-
895 6750-9-93.
- 896 Sams, A. J., Dumaine, A., Nédélec, Y., Yotova, V., Alfieri, C., Tanner, J. E., ... and Barreiro, L. B.
897 (2016). Adaptively introgressed Neandertal haplotype at the OAS locus functionally impacts
898 innate immune responses in humans. *Genome Biol.* 17, 246.
- 899 Sankararaman, S., Mallick, S., Dannemann, M., Prüfer, K., Kelso, J., Pääbo, S., et al. (2014). The
900 genomic landscape of Neanderthal ancestry in present-day humans. *Nature* 507, 354–357.
901 doi:10.1038/nature12961.
- 902 Scarcelli, N., Tostain, S., Vigouroux, Y., Agbangla, C., Daïnou, O., and Pham, J.-L. (2006).
903 Farmers' use of wild relative and sexual reproduction in a vegetatively propagated crop. The
904 case of yam in Benin. *Mol. Ecol.* 15, 2421–2431. doi:10.1111/j.1365-294X.2006.02958.x.
- 905 Scascitelli, M., Whitney, K. D., Randell, R. A., King, M., Buerkle, C. A., and Rieseberg, L. H.
906 (2010). Genome scan of hybridizing sunflowers from Texas (*Helianthus annuus* and *H.*
907 *debilis*) reveals asymmetric patterns of introgression and small islands of genomic
908 differentiation. *Mol. Ecol.* 19, 521–541. doi:10.1111/j.1365-294X.2009.04504.x.

- 909 Schaefer, N. K., Shapiro, B., and Green, R. E. (2016). Detecting hybridization using ancient DNA.
910 *Mol. Ecol.*, n/a-n/a. doi:10.1111/mec.13556.
- 911 Schubert, M., Jónsson, H., Chang, D., Sarkissian, C. D., Ermini, L., Ginolhac, A., et al. (2014).
912 Prehistoric genomes reveal the genetic foundation and cost of horse domestication. *Proc.*
913 *Natl. Acad. Sci.* 111, E5661–E5669. doi:10.1073/pnas.1416991111.
- 914 Shibata, H., Branquinho, C., McDowell, W. H., Mitchell, M. J., Monteith, D. T., Tang, J., et al.
915 (2015). Consequence of altered nitrogen cycles in the coupled human and ecological system
916 under changing climate: The need for long-term and site-based research. *AMBIO* 44, 178–
917 193. doi:10.1007/s13280-014-0545-4.
- 918 Smith, J. M., and Haigh, J. (1974). The hitch-hiking effect of a favourable gene. *Genet. Res.* 23, 23–
919 35. doi:10.1017/S0016672300014634.
- 920 Smith, M. W., Patterson, N., Lautenberger, J. A., Truelove, A. L., McDonald, G. J., Waliszewska,
921 A., et al. (2004). A High-Density Admixture Map for Disease Gene Discovery in African
922 Americans. *Am. J. Hum. Genet.* 74, 1001–1013. doi:10.1086/420856.
- 923 Song, Y., Endepols, S., Klemann, N., Richter, D., Matuschka, F.-R., Shih, C.-H., et al. (2011).
924 Adaptive Introgression of Anticoagulant Rodent Poison Resistance by Hybridization
925 between Old World Mice. *Curr. Biol.* 21, 1296–1301. doi:10.1016/j.cub.2011.06.043.
- 926 Song, Y. S., and Hein, J. (2005). Constructing Minimal Ancestral Recombination Graphs. *J.*
927 *Comput. Biol.* 12, 147–169. doi:10.1089/cmb.2005.12.147.
- 928 Staubach, F., Lorenc, A., Messer, P. W., Tang, K., Petrov, D. A., and Tautz, D. (2012). Genome
929 Patterns of Selection and Introgression of Haplotypes in Natural Populations of the House
930 Mouse (*Mus musculus*). *PLoS Genet.* 8, e1002891. doi:10.1371/journal.pgen.1002891.
- 931 Suarez-Gonzalez, A., Lexer, C., and Cronk, Q. C. B. (2018). Adaptive introgression: a plant
932 perspective. *Biol. Lett.* 14, 20170688. doi:10.1098/rsbl.2017.0688.
- 933 Turissini, D. A., and Matute, D. R. (2017). Fine scale mapping of genomic introgressions within the
934 *Drosophila yakuba* clade. *PLOS Genet.* 13, e1006971. doi:10.1371/journal.pgen.1006971.
- 935 Uwimana, B., D'andrea, L., Felber, F., Hooftman, D. a. P., Nijs, H. C. M. D., Smulders, M. J. M., et
936 al. (2012). A Bayesian analysis of gene flow from crops to their wild relatives: cultivated
937 (*Lactuca sativa* L.) and prickly lettuce (*L. serriola* L.) and the recent expansion of *L. serriola*
938 in Europe. *Mol. Ecol.* 21, 2640–2654. doi:10.1111/j.1365-294X.2012.05489.x.
- 939 Vernot, B., and Akey, J. M. (2014). Human Evolution: Genomic Gifts from Archaic Hominins.
940 *Curr. Biol.* 24, R845–R848. doi:10.1016/j.cub.2014.07.079.
- 941 Vernot, B., Tucci, S., Kelso, J., Schraiber, J. G., Wolf, A. B., Gittelman, R. M., et al. (2016).
942 Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals.
943 *Science*, aad9416. doi:10.1126/science.aad9416.
- 944 Vigouroux, Y., Mariac, C., Mita, S. D., Pham, J.-L., Gérard, B., Kapran, I., et al. (2011). Selection
945 for Earlier Flowering Crop Associated with Climatic Variations in the Sahel. *PLOS ONE* 6,
946 e19563. doi:10.1371/journal.pone.0019563.

- 947 von Holdt, B. M., Kays, R. W., Pollinger, J. P., and Wayne, R. K. (2016). Admixture mapping
948 identifies introgressed genomic regions in North American canids. *Mol. Ecol.*, n/a-n/a.
949 doi:10.1111/mec.13667.
- 950 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., et al. (2002).
951 Ecological responses to recent climate change. *Nature* 416, 389–395. doi:10.1038/416389a.
- 952 Wang, L., Beissinger, T. M., Lorant, A., Ross-Ibarra, C., Ross-Ibarra, J., and Hufford, M. (2017).
953 The interplay of demography and selection during maize domestication and expansion.
954 *bioRxiv*, 114579. doi:10.1101/114579.
- 955 Warschefsky, E., Penmetsa, R. V., Cook, D. R., and Wettberg, E. J. B. von (2014). Back to the
956 wilds: Tapping evolutionary adaptations for resilient crops through systematic hybridization
957 with crop wild relatives. *Am. J. Bot.* 101, 1791–1800. doi:10.3732/ajb.1400116.
- 958 Weetman, D., Wilding, C. S., Steen, K., Morgan, J. C., Simard, F., and Donnelly, M. J. (2010).
959 Association Mapping of Insecticide Resistance in Wild *Anopheles gambiae* Populations:
960 Major Variants Identified in a Low-Linkage Disequilibrium Genome. *PLOS ONE* 5, e13140.
961 doi:10.1371/journal.pone.0013140.
- 962 Weill, M., Chandre, F., Brengues, C., Manguin, S., Akogbeto, M., Pasteur, N., et al. (2000). The *kdr*
963 mutation occurs in the Mopti form of *Anopheles gambiae* s. through introgression. *Insect*
964 *Mol. Biol.* 9, 451–455.
- 965 Whitney, K. D., Broman, K. W., Kane, N. C., Hovick, S. M., Randell, R. A., and Rieseberg, L. H.
966 (2015). Quantitative trait locus mapping identifies candidate alleles involved in adaptive
967 introgression and range expansion in a wild sunflower. *Mol. Ecol.* 24, 2194–2211.
968 doi:10.1111/mec.13044.
- 969 Whitney, K. D., Randell, R. A., and Rieseberg, L. H. (2010). Adaptive introgression of abiotic
970 tolerance traits in the sunflower *Helianthus annuus*. *New Phytol.* 187, 230–239.
971 doi:10.1111/j.1469-8137.2010.03234.x.
- 972 Whitney, K. D., Randell, R. A., Rieseberg, L. H., Elle, A. E. E., and Whitlock, E. M. C. (2006).
973 Adaptive Introgression of Herbivore Resistance Traits in the Weedy Sunflower *Helianthus*
974 *annuus*. *Am. Nat.* 167, 794–807. doi:10.1086/504606.
- 975 Wolf, D. E., Takebayashi, N., and Rieseberg, L. H. (2001). Predicting the Risk of Extinction
976 through Hybridization. *Conserv. Biol.* 15, 1039–1053. doi:10.1046/j.1523-
977 1739.2001.0150041039.x.
- 978 Wright, S. (1931). Evolution in Mendelian Populations. *Genetics* 16, 97–159.
- 979 Zhang, W., Fan, Z., Han, E., Hou, R., Zhang, L., Galaverni, M., et al. (2014). Hypoxia Adaptations
980 in the Grey Wolf (*Canis lupus chanco*) from Qinghai-Tibet Plateau. *PLOS Genet.* 10,
981 e1004466. doi:10.1371/journal.pgen.1004466.
- 982 Zheng, P., Allen, W. B., Roesler, K., Williams, M. E., Zhang, S., Li, J., et al. (2008). A
983 phenylalanine in DGAT is a key determinant of oil content and composition in maize. *Nat.*
984 *Genet.* 40, 367–372. doi:10.1038/ng.85.

- 985 Zhou, Q., Zhao, L., and Guan, Y. (2016). Strong Selection at MHC in Mexicans since Admixture.
986 *PLoS Genet* 12, e1005847. doi:10.1371/journal.pgen.1005847.
- 987 Zhu, Y., Li, W., Yang, B., Zhang, Z., Ai, H., Ren, J., and Huang, L. (2017). Signatures of selection
988 and interspecies introgression in the genome of Chinese domestic pigs. *GBE* 9, 2592-2603.
989
- 990 Zizumbo-Villarreal, D., Colunga-GarcíaMarín, P., de la Cruz, E. P., Delgado-Valerio, P., and
991 Gepts, P. (2005). Population structure and evolutionary dynamics of wild–weedy–
992 domesticated complexes of common bean in a Mesoamerican region. *Crop Sci.* 45, 1073–
993 1083.
- 994
995

96
97
98
99
00

Table 1. Summary of studies reviewed. Species names for donor and recipient taxa are listed, as well as the type of data and methods used for 1) detection of the introgression and 2) detection of the selection. “Genomic data” term include s whole-genome sequences or candidates genes sequencing. “Genetic data” refers to molecular markers such as QTL or SSR.

Group	Donor	Recipient	Data	Method for detection of Introgression	Method for detection of Selection	Adaptive trait	Publication
Animal	<i>Anopheles gambiae</i>	<i>A. coluzzi</i>	Genomic data	Diagnostic alleles	Haplotype based test; Test for temporal evolution of allele frequencies	Pesticide resistance	Lynd et al. (2010)
Animal	<i>Anopheles gambiae</i>	<i>A. coluzzi</i>	Genomic data	Diagnostic alleles	Differentiation approach; Diversity statistics	Pesticide resistance	Norris et al. (2014)
Animal	<i>Drosophila yakuba</i>	<i>D. santomea</i>	Genomic data (mtDNA)	Genes genealogy; Isolation with Migration model	Coalescent simulations	na	Llopart et al. (2014)
Animal	<i>Mus spretus</i>	<i>M. m. domesticus</i>	Genomic and phenotypic data	Genes genealogy; Hudson-Kreitman-Aguade test	Differentiation approach; Fitness measures	Pesticide resistance	Song et al. (2011)
Animal	<i>Mus spretus</i>	<i>M. m. domesticus</i>	Genomic data	Genes genealogy	XP-CLR	Pesticide resistance	Liu et al. (2015)
Animal	<i>Mus musculus musculus</i>	<i>M. m. domesticus</i>	Genomic data	Local ancestry inference	XP-CLR; Differentiation approach; Coalescent simulations	Genetic disease, alpha-amylase genes	Staubach et al. (2012)
Animal	<i>Onchorhynchus mykiss</i>	<i>O. clarkii lewisi</i>	Genomic data	Diagnostic alleles	Heterogeneity test of Long (1991)	Fecondity	Hohenlohe et al. (2013)
Animal	<i>Ambystoma tigrinum mavortium</i>	<i>A. californiense</i>	Genomic data	Diagnostic alleles	Heterogeneity test of Long (1991)	na	Fitzpatrick et al. (2009)
Animal	<i>Sus sp.</i>	<i>Sus scrofa domesticus</i>	Genomic data	Genes genealogy	Differentiation approach	Highland adaptation	Ai et al. (2015)
Animal	<i>Sus celebensis</i>	<i>Sus scrofa domesticus</i>	Genomic data	Genes genealogy; Differentiation statistics	Differentiation approach	Aggressive behaviour	Zhu et al. (2017)
Animal	<i>Canis lupus familiaris</i>	<i>C. lupus lupus</i>	Genomic data	Genes genealogy	Haplotype based test	Concealment during predation	Anderson et al. (2009)
Animal	<i>C. lupus lupus</i>	<i>C. l. familiaris</i>	Genomic data	D statistic	Haplotype based test; Differentiation outlier approach	Highland adaptation	Miao et al. (2016)
Animal	<i>Ovis aries</i>	<i>Ovis aries</i> \$	Genomic data	Local ancestry inference; Populations genealogy	Differentiation outlier approach	na	Rochus et al. (2017)
Animal	<i>Anguilla rostrata</i>	<i>A. anguilla</i>	Genomic data	Local ancestry inference	Differentiation outlier approach; Allele frequencies outlier test	na	Gagnaire et al. (2009)

Animal	<i>Heliconious melpomene</i>	<i>H. cydno clade</i>	Genomic data	Genes genealogy; Isolation with Migration model, Linkage Disequilibrium analysis	Not addressed, but trait previously tested as under natural selection	Wing pattern	Pardo-Diaz et al. (2017)
Animal	<i>Heliconious melpomene</i>	<i>H. beskei</i>	Genomic data	Gene genealogy; D-statistic and <i>f</i> -statistics	Not addressed, but trait previously tested as under natural selection	Wing pattern	Zhang et al. (2016)
Human	<i>Homo s. denisovans</i>	<i>H. s. sapiens</i>	Genomic data	D statistic, S* statistic	Differentiation outlier approach	Highland adaptation	Huerta Sanchez et al. (2014)
Human	<i>Homo s. neandertalensis, H. s. denisovans</i>	<i>H. s. sapiens</i>	Genomic and expression data	Diagnostic alleles	McDonald-Kreitman test; Haplotype based test; Differentiation outlier approach	Immune response	Deschamp et al. (2016)
Human	<i>Homo neandertalensis, H. s. denisovans</i>	<i>H. s. sapiens</i>	Genomic and expression data	Differentiation comparisons; Haplotype length vs. ILS (Incomplete Lineage Sorting)	Differentiation outlier approach; Gene expression; Genotype-Phenotype association	Immune response	Danneman et al. (2016)
Human	<i>Homo neandertalensis, H. s. denisovans</i>	<i>H. s. sapiens</i>	Genomic data	<i>f</i> statistics, S* statistic	Coalescent simulations	Immune response and metabolism	Vernot et al. (2016)
Human	<i>Homo neandertalensis, H. s. denisovans</i>	<i>H. s. sapiens</i>	Genomic data	Diagnostic alleles	Coalescent simulations	Immune response, defense, regulatory regions, pigmentation	Gittelman et al. (2016)
Human	<i>Homo s. neandertalensis</i>	<i>H. s. sapiens</i>	Genomic data	Genes genealogy	Allele frequencies outlier test	Immune response	Mendez et al. (2012)
Human	<i>Homo s. neandertalensis</i>	<i>H. s. sapiens</i>	Genomic data	Diagnostic alleles	Coalescent simulations; Haplotype based test	Immune response	Sams et al. (2016)
Human	<i>Homo s. neandertalensis</i>	<i>H. s. sapiens</i>	Genomic data	Diagnostic alleles	Differentiation outlier approach; Haplotype based test; XP-CLR; Coalescent simulations	Immune response	Quach et al. (2016)
Human	<i>H. s. sapiens</i>	<i>H. s. sapiens</i>	Genomic data	Population genealogy; D statistic and <i>f</i> statistics	Allele frequencies outlier test	Highland adaptation	Jeong et al. (2014)
Plant	<i>Arabidopsis lyrata</i>	<i>A. arenosa</i>	Genomic data	<i>f</i> statistics	Differentiation outlier approach	Serpentine syndrome	Arnold et al. (2016)
Plant	<i>Helianthus debilis</i>	<i>H. annuus</i>	Phenotypic data	Experimental hybrid populations	Common garden experiments - Fitness measures	Herbivory, drought	Whitney et al. (2006, 2010)
Plant	<i>Helianthus debilis</i>	<i>H. annuus</i>	Genomic and phenotypic	Experimental hybrid populations	Genotype-Phenotype association -	Number of seeds and pollen export	Whitney et al. (2015)

			data		Fitness measures		
Plant	<i>Iris fulva</i>	<i>I. brevicaulis</i>	Genomic and phenotypic data	Experimental hybrid populations	Genotype-Phenotype association - Fitness measures	Flood tolerance	Martin et al. (2006)
Plant	<i>Populus balsamifera</i>	<i>P. trichocarpa</i>	Genomic, expression and phenotypic data	Local ancestry inference	Diversity statistics; Genotype-Phenotype association	Light response	Suarez-Gonzalez et al. (2016)
Plant	<i>Zea mays mexicana</i>	<i>Z. m. mays</i>	Genomic data	Local ancestry inference	Genotype-Environment association	Highland adaptation	Hufford et al. (2013)
Plant	<i>Oryza sativa japonica</i>	<i>Oryza sativa indica</i>	Genomic data	Diagnostic alleles	Haplotype based test	Fragrance	Kovach et al. (2009)
Plant	<i>Senecio squalidus</i>	<i>S. vulgaris</i>	Genomic data	Diagnostic alleles	not adressed but strongly suggested	Flower asymmetry	Kim et al. (2008)
Plant	<i>Arabidopsis halleri</i>	<i>A. lyrata</i>	Genomic data	Differentiation comparisons; Isolation with Migration model	not adressed but strongly suggested	Pistil self-incompatibility	Castric et al. (2008)

01
02
03
04

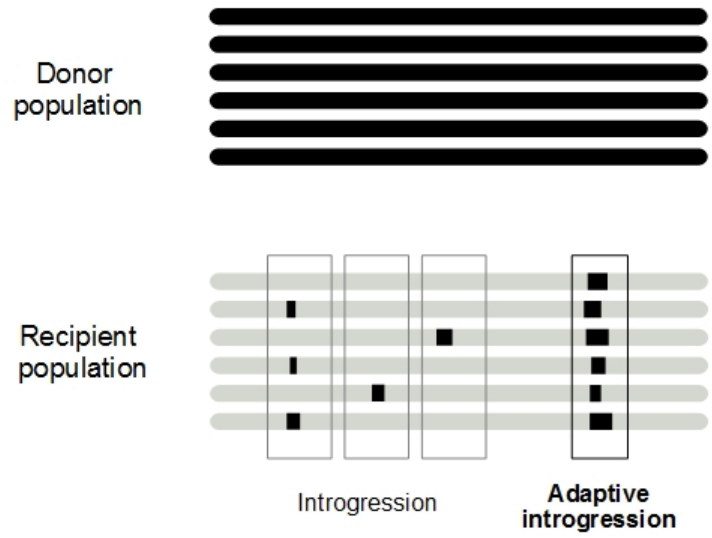


Figure 1

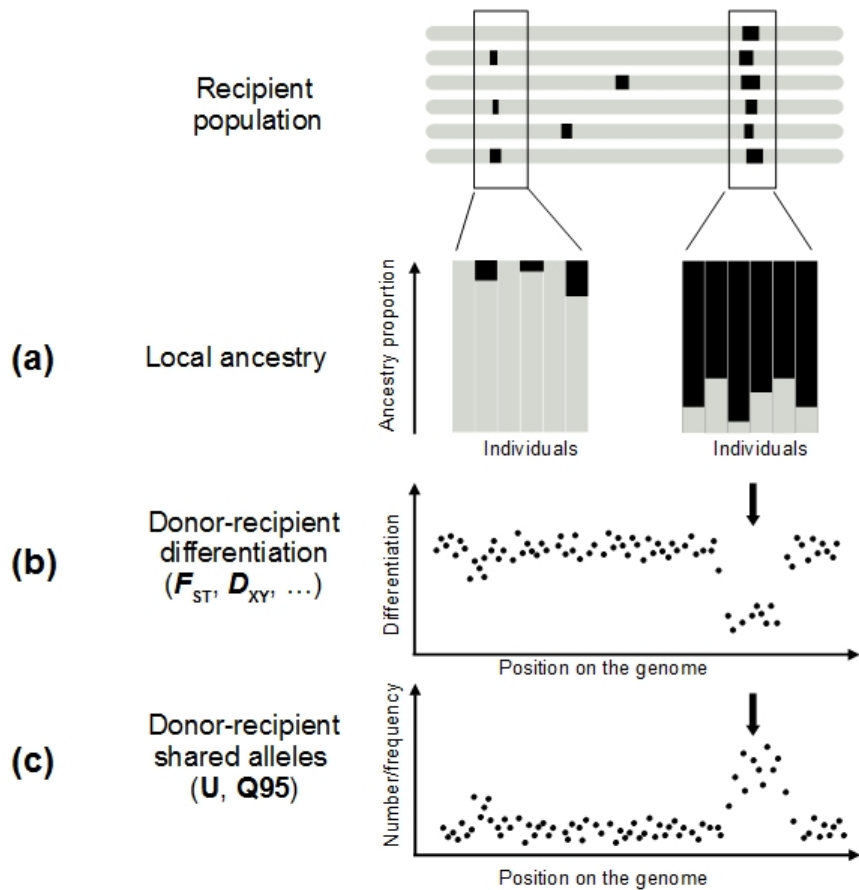


Figure 2

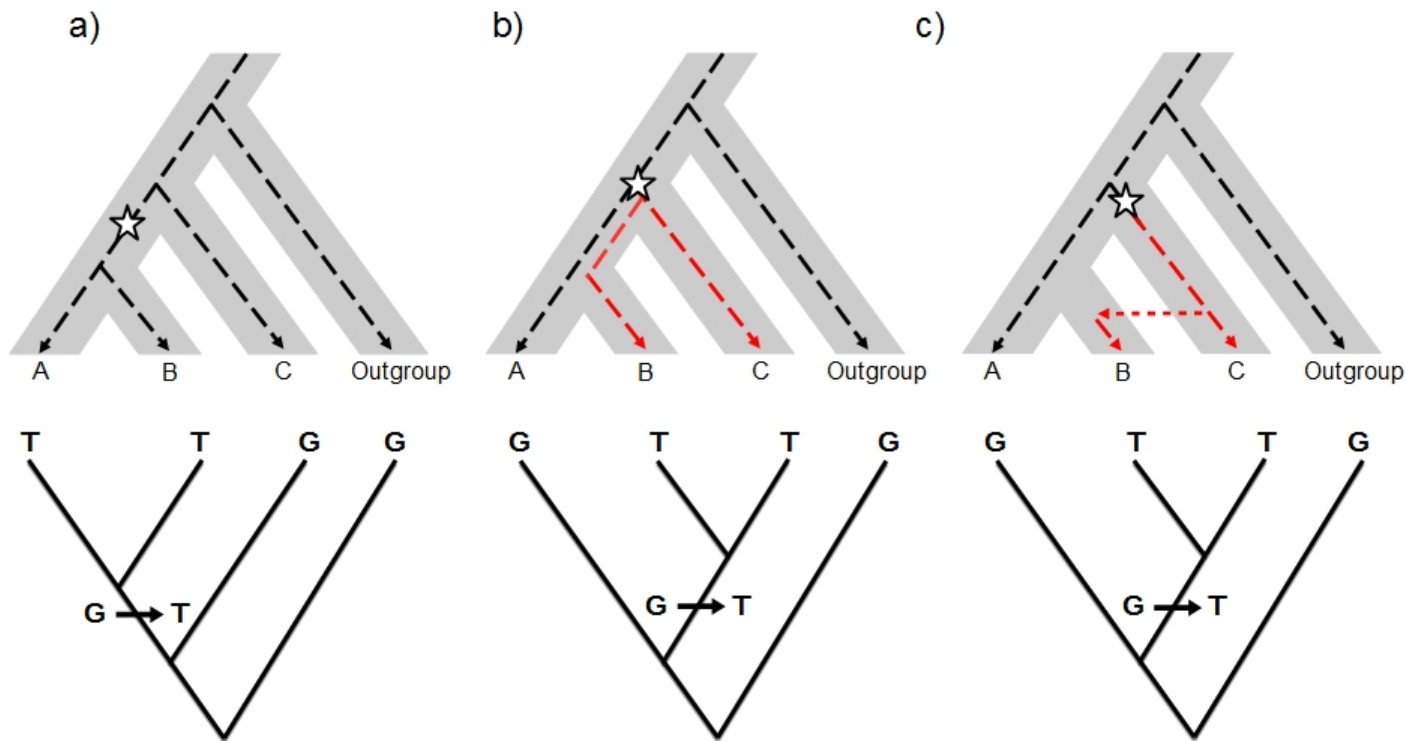


Figure 3

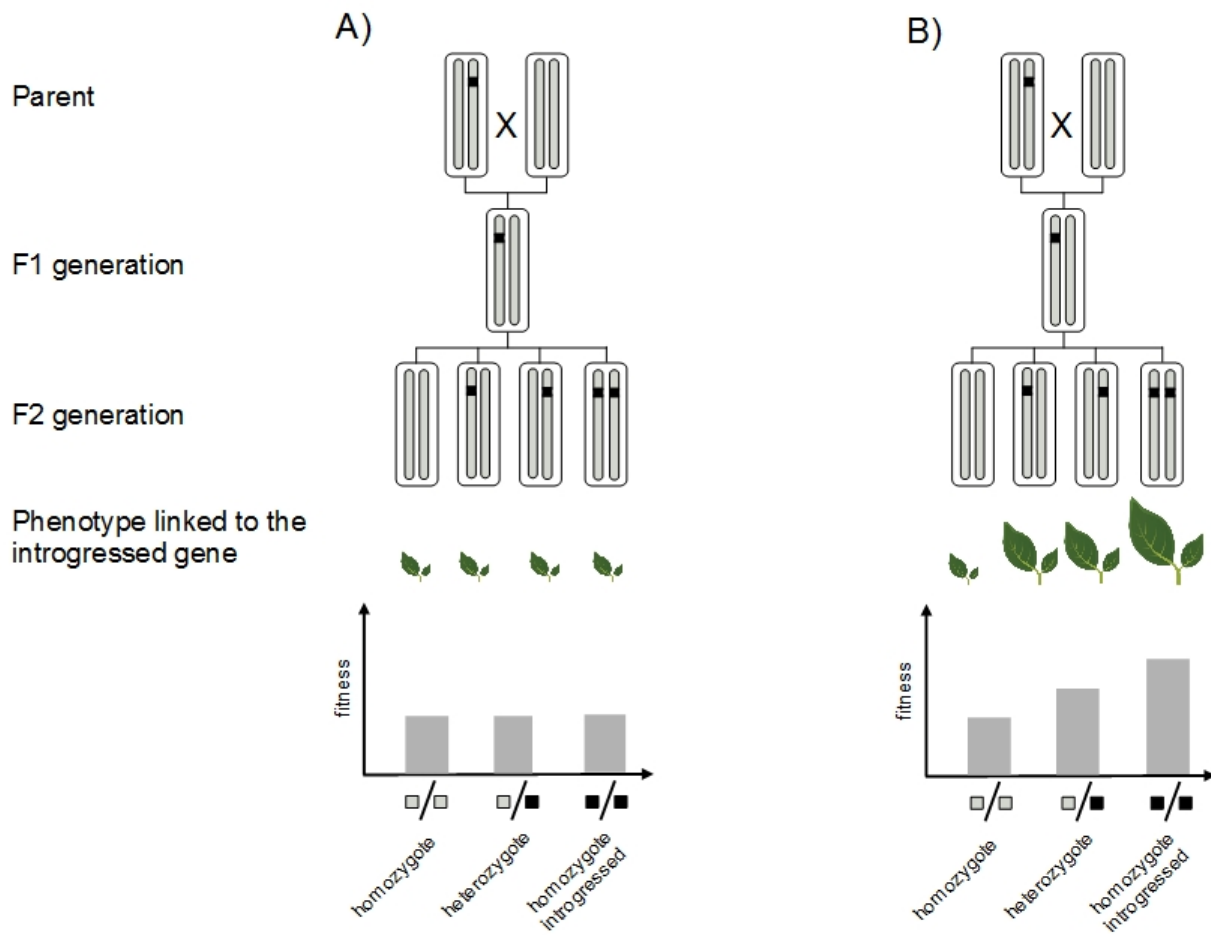


Figure 4.