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1 **Adaptation to novel environments during crop diversification**

2

3 Gaia Cortinovis, Valerio Di Vittori, Elisa Bellucci, Elena Bitocchi*, and Roberto Papa*

4

5 Dipartimento di Scienze Agrarie, Alimentari ed Ambientali, Università Politecnica delle
6 Marche, via Brecce Bianche, 60131 Ancona, Italy

7

8 Gaia Cortinovis, g.cortinovis@pm.univpm.it

9 Valerio Di Vittori, v.divittori@staff.univpm.it

10 Elisa Bellucci, e.bellucci@univpm.it

11

12 ***Corresponding authors**

13 Roberto Papa, r.papa@univpm.it

14 Elena Bitocchi, e.bitocchi@univpm.it

15

16 **Key words:** Crop diversification, crop adaptation, population genomics, adaptive
17 introgression, Columbian Exchange

18 **Abstract**

19 In the context of the global challenge of climate change, mitigation strategies are needed to
20 adapt crops to novel environments. The main goal to address this is an understanding of
21 the genetic basis of crop adaptation to different agro-ecological conditions. The movement
22 of crops during the Colombian Exchange that started with the travels of Columbus in 1492
23 is an example of rapid adaptation to novel environments. Many diversification-related traits
24 have been characterised in multiple crop species, and association-mapping analyses have
25 identified loci involved in these. Here, we present an overview of current knowledge
26 regarding the molecular basis related to the complex patterns of crop adaptation and
27 dissemination, particularly outside their centres of origin. Investigation of the genomic basis
28 of crop expansion offers a powerful contribution to the development of tools to identify and
29 exploit valuable genetic diversity and to improve and design novel resilient crop varieties.

30

31 Introduction

32 Environmental change will result in strong ecological and genetic effects on gene and allele
33 frequencies in many plant populations, as well as altering several aspects of agricultural
34 systems, such as plant physiology and phenology, water availability, soil fertility, pathogen
35 spread and host susceptibility. Many crops have evolved in response to climate change
36 under increasingly stressful conditions in which their extinction is highly possible. However,
37 there is more evidence for climate-driven range expansion than for range contraction [1].
38 This suggests that plants can cope with climate change through adaptive mechanisms, such
39 as phenotypic plasticity and microevolution [2].

40 Genetic diversity represents the raw material on which adaptive selection acts, and
41 as such, it has a fundamental role in both evolutionary history and future evolutionary
42 pathways of a species [3]. Thus, persistent fluctuations in biotic and abiotic environmental
43 factors provide a background of changing selection pressures to which species must
44 respond, and in this way, genetic diversity is maintained within populations. Identification of
45 the molecular basis of plant adaptation is needed to drive plant breeding into the
46 development of novel varieties that can adapt to climate changes. Analysis of genetic
47 diversity through population genomics and genotype–phenotype association approaches
48 can be very useful tools to reach this aim [4], especially with the novel opportunities offered
49 by the more recent advances in genomics and DNA sequencing technologies. The success
50 of such studies critically depends on the type of plant material adopted. Moreover, if the
51 search for the signature of selection is the objective, the populations must have an ancient
52 and strong link with their growing environments, which must have variable agro-ecological
53 conditions.

54 Populations of wild plants and wild crop relatives can easily meet these prerequisites.
55 There are several examples in the literature that have focused on wild germplasm to detect
56 adaptive genetic control, along with studies on model species such as *Arabidopsis thaliana*
57 [5•], with other examples available for crop species. Fustier et al. [6] investigated adaptation
58 in 11 populations of teosinte, the wild progenitor of maize, along two elevation gradients in
59 Mexico that showed continuous environmental changes over a short geographic scale. They
60 evaluated 1,664 individuals for 18 phenotypic traits and genotyped them for 38 microsatellite
61 markers and 171 outlier single nucleotide polymorphisms (SNPs). These significantly
62 differentiated between lowland and highland populations and/or correlated with
63 environmental variables. They showed that >50% of the traits were differentiated due to
64 local selection. A recent landscape genomics study of Rodriguez et al. [7•] reported on an

analysis of correlations between molecular markers and ecological variables at a continental scale. They analysed a sample of 310 wild common bean georeferenced accessions that they genetically characterised at 131 SNPs. Geographic and environmental data were combined with genetic diversity data to separate the effects of geography from those of ecology, and they reported a total of 26 loci (19.9%) that were putatively under selection for adaptation. Among these, different loci were shown to have compatible functions with adaptation features, such as chilling susceptibility, cold acclimation, and mechanisms related to drought stress [7•]. Recently, Mier y Teran et al. [8] characterised 112 wild common bean accessions that were representative of the geographic distribution of the Mesoamerican gene pool. This was applied at the molecular level (11,447 SNP markers) and the phenotypic level (root trait evaluation, comparison of control and drought stress), and considered environmental variables from the geographic coordinates of the origin of each accession. They defined genomic regions that were associated with productivity and drought adaptation in the wild germplasm.

Within the cultivated gene pools, the above-mentioned prerequisites for such studies are satisfied only by populations of landraces (or, if available, by experimental populations, as composite crosses specifically developed over multiple generations of experimental evolution). Landraces offer unique opportunities for integration of association mapping and signatures of selection analyses. Indeed, landraces are the product of an evolutionary interaction with the agro-ecosystem, and consequently, their genetic composition is determined by both stochastic and human-mediated or natural selection over decades of evolution, which means that they have maintained a considerable amount of genetic variability. Moreover, when multiple landrace populations grown in contrasting agroecological environments are compared, it is possible to tag the signatures of divergent selection [9-12]. This makes it possible to investigate the genes that are responsible for the 'genomic architecture' of the local adaptation of plants. After domestication, food crops spread widely between different geographic and cultural areas at different levels and to different extents, and this process ultimately contributes to the diversification of local agricultural subsistence.

Among cereals, barley and maize are examples of crops that have achieved adaptive success worldwide (**Figure 1**). Barley is one of the primary plants that originated and was domesticated in the 'Fertile Crescent' about 11,000 years ago, and was later disseminated worldwide over a wide range of agro-climatic conditions [13]. Some of these conditions were particularly extreme, such as in Tibet, Nepal, Ethiopia and the Andes, where farmers

99 cultivated barley on mountain slopes at altitudes higher than those for any other cereals [14].
100 Maize also has one of the broadest worldwide dissemination ranges. It was domesticated
101 once in the Balsas region in the valley of Mexico about 9,000 years ago, and it subsequently
102 spread to geographically and ecologically diverse environments, from Canada to Chile [15].
103 Similarly, among legumes, the common bean can be considered as a crop that is now
104 successfully widespread [16]. The post-domestication phase of crops outside their centres
105 of origin (i.e., at regional, continental, worldwide levels) towards a wide range of agro-
106 ecosystems has led to phenotypic and genetic divergence between domesticated forms.
107 This process can be considered a fascinating model for the study of the adaptive evolution
108 of crops, and it offers the possibility to discover new interesting genetic variants that have
109 potential use in a climate alarm context, like that which we are currently in.

110

111 **Diversification traits**

112 Meyer and Purugganan [17•] reported on several observed traits in crops that accompanied
113 their domestication and diversification, and their improvement phase. It is not particularly
114 easy to clearly distinguish between genes that underlie domestication and those that control
115 diversification traits. This is the case even if the genetic basis of adaptation might be more
116 related to diversification traits that are related to post-domestication stages, such as for
117 pigments, variations in size and chemical composition of edible parts, changes to the mating
118 system (promoting allogamy or autogamy), resistance or tolerance to abiotic and biotic
119 stresses, reduced vernalisation and photoperiod sensitivity, and changes to flowering time,
120 the life cycle and dwarfism [17•]. It is important to consider that these traits can vary among
121 crop species, considering also that they relate to crops that have adapted to specific agro-
122 ecological conditions and cultures. In this regard, several examples can be found in the
123 literature where the function of genes defined as putatively under selection during
124 domestication of crops can be ascribed to diversification traits, thus traits upon which both
125 natural and human selection have acted during crop expansion.

126 In common bean (*Phaseolus vulgaris*), Bitocchi et al. [18] compared selection
127 analysis data obtained for the same genes in different studies of varying sizes, data types
128 and methodologies. To study the effects of domestication at the genome level, they analysed
129 nucleotide diversity at 49 gene fragments on a sample of 39 wild and domesticated
130 Mesoamerican accessions of *P. vulgaris*. By applying population genomics approaches,
131 they identified several genes that showed footprints of selection. At the same time, they
132 used the SNP data of Rodriguez et al. [7•] to perform selection tests on a wider sample,
133 which included 417 and 160 wild and domesticated accessions, respectively, of common
134 bean. Finally, data were included from two further studies that focused on investigation of
135 the domestication process in common bean [19,20•]. The final comparison of the data from
136 these four studies provided independent evidence of selection for four genes: *AN-Pv33*, *AN-*
137 *DNAJ*, *Leg223*, *AN-Pv69*. Gene-function investigations revealed that all of these genes are
138 involved in plant resistance/ tolerance to abiotic stresses, such as heat, drought and salinity.
139 In this regard, adaptation of plants to abiotic stresses is of crucial importance, because they
140 are among the major environmental factors that affect plant productivity. By accessing the
141 *Arabidopsis thaliana* stress-responsive gene database (<http://srgdb.bicpu.edu.in/>) [21], we
142 have identified a list of genes that were detected as functionally involved in abiotic stress
143 responses in *Arabidopsis*. The OrthoFinder algorithm [22] and the 2.1 version of the *P.*
144 *vulgaris* reference genome (<https://phytozome.jgi.doe.gov/pz/portal.html>) were then used to

145 identify orthologous genes in common bean. A total of 770 common bean genes were found
146 to be orthologous to *Arabidopsis* genes involved in abiotic stress responses (**Table S1**), 126
147 of which showed signature of selection during domestication in Bellucci et al. [20] and/or
148 Schmutz et al. [19] (**Figure 2; Table S1**). Among these genes, a very interesting candidate
149 is a homologue of *K⁺ uptake transporter6 (KUP6)*. The *KUP6* gene has been shown to be a
150 key factor in osmotic adjustment, through the balancing of potassium homeostasis in cell
151 growth and drought stress responses in *A. thaliana* [23]. Its function is directly mediated by
152 abscisic acid signalling, and under water-deficit stress this involves inhibition of cell
153 expansion in both roots and guard cells, which is driven by decreased turgor. In Bellucci et
154 al. [20], *KUP6* was also among the small fraction of outlier genes for which selection has
155 increased the nucleotide diversity in the domesticated pool compared to the wild pool, which
156 suggests selection due to crop expansion into the new environments with unexpected biotic
157 and abiotic stresses (i.e., diversifying selection).

158 Meyer et al. [24] reported an example of geographic and environmental divergent
159 adaptation between four populations of African rice (*Oryza glaberrima* Steud.). They
160 sequenced the genomes of 93 landraces that spanned from west to central sub-Saharan
161 Africa, to investigate the African rice post-domestication spread, its subsequent adaptation
162 to local environments, and the genes that were involved in these processes. They focused
163 on salinity tolerance, as one of the major traits associated with geographic adaptation of
164 African rice. The accessions were phenotyped for various salinity-associated fitness traits,
165 and they found a significant loss of salinity tolerance in the southwest inland population.
166 This adaptive phenotype was thus suggested to arise from the costs of maintaining tolerance
167 in a geographic area associated with greater precipitation and decreased soil salinity. In
168 contrast, no significant differences were seen for the northwest, northeast and southeast
169 subpopulations. Genome-wide association studies allowed them to identify 11 loci that
170 contained several genes that were putatively involved in salt-stress tolerance. Among the
171 most significant of these was an orthologue of the *O. sativa* *HAK5* gene. *HAK5* has been
172 shown to be a key component in the acquisition and transport of potassium, to improve salt
173 resistance in potassium-deficient rice plants [25], and it might have had a crucial role in *O.*
174 *glaberrima* adaptation along the western Atlantic coast.

175 The timing of important developmental stages (e.g., flowering time) is another main
176 diversification trait that defines adaptation of plant populations to different environments. In
177 maize, numerous studies have focused on identification of the genetic control of flowering
178 time and on genetic variations at identified genes in different materials from diverse

179 environments. Buckler et al. [26•] used a nested association mapping population of 200
180 recombinant inbred lines from 25 crosses, which resulted in a total of 5,000 lines for
181 identification of genes or genomic regions associated with flowering time. These lines were
182 phenotyped in four locations over 2 years. Quantitative trait locus (QTL) mapping showed
183 that the differences in flowering time were not caused by a few genes that had large effects,
184 but rather by the cumulative effects of numerous QTLs (i.e., <100), each of which had only
185 a small impact on this trait [26•]. However, to date, although a large body of mapping
186 information on the QTLs that control maize flowering time is available [27,28], the molecular
187 basis of these QTLs remains almost totally unknown, with the exception of four genes that
188 have been demonstrated to be involved in flowering time: *Dwarf8* [29]; *ZmCCT* [30-32]; *Vgt1*
189 [33]; and *ZCN8* [34].

190 The *Dwarf8* gene has been shown to be an orthologue of the gibberellic acid
191 insensitive (*GAI*) gene, which is a transcription factor that negatively regulates gibberellin
192 responses in *A. thaliana*. Association analysis has identified several interesting
193 polymorphisms in maize *Dwarf8*. One of these is a 6-bp deletion in the C-terminal region of
194 the open reading frame, and this showed strong association with flowering time [29]. With
195 the aim to evaluate the contribution of *Dwarf8* to maize adaptation to temperate climates,
196 Camus-Kulandaivelu et al. [35] analysed a wide collection of traditional landraces (144 from
197 America, 131 from Europe) for indel polymorphisms in the *Dwarf8* gene. They reported a
198 variation in the frequency of the *Dwarf8* deletion associated with altitude and latitude, which
199 demonstrated that these features have an important role in driving local maize adaptation
200 [15,35]. In particular, for American landraces, they showed that the frequency of the *Dwarf8*
201 deletion was higher in northern Flint maize (83%) compared to maize groups from the
202 tropical Caribbean (2%) and Mexican (4%). Instead, the Andean group that was represented
203 by populations that originated from high altitudes (on average, 2,200 m a.s.l.) showed a
204 frequency of *Dwarf8* deletion of 58%. Similarly, in Europe, *Dwarf8* deletion has prevailed in
205 landraces from northern Europe.

206 *Vgt1* is also one of the major maize flowering-time QTLs, and a miniature transposon
207 that is located ~70 kb upstream of *ZMRap2.7* was shown to be the causative variant of *Vgt1*
208 that contributes to maize adaptation to temperate regions [33,36,37]. Ducrocq et al. [36]
209 carried out an association mapping study on 375 maize inbred lines, which included inbred
210 lines representative of the American and European diversity, with a wide range of flowering
211 times. They reported that the *Vgt1* early allele showed higher frequency in the tropical
212 materials. Moreover, the frequency of *Vgt1* alleles among the tropical populations varied

213 with the altitude of the collection site, while the early allele was rare at low altitudes. These
214 data support the hypothesis that adaptive selection followed domestication of maize, with
215 early and late materials adapted to high altitude and low altitude cultivation systems,
216 respectively.

217 Yang et al. [31] showed that a CACTA-like transposon insertion within the *ZmCCT10*
218 promoter repressed *ZmCCT10* expression, which makes maize insensitive to long days.
219 Likewise, Huang et al. [32] identified a Harbinger-like transposable element at ~57 kb
220 upstream of *ZmCCT9* that functions as a *cis*-acting repressor of *ZmCCT9*, to enhance maize
221 adaptation to higher latitudes. Comparisons of the gene sequence from teosinte and tropical
222 and temperate maize revealed that both the adaptive insertions were completely absent in
223 teosinte, and so they are likely to be *de-novo* mutations that occurred after the initial maize
224 domestication [30-32].

225 Recently, Guo et al. [34] reported that two natural *cis*-variants in the promoter of
226 *ZCN8* were gradually targeted by selection during the spread of maize from its tropical origin
227 to northern North America, which led to earlier flowering plants that were adapted to the
228 temperate growing regions. In more detail, *ZCN8* was proposed to be homologous to *A.*
229 *thaliana* FLOWERING LOCUS (FT), and they considered it to be the maize florigen gene
230 [38,39].

231 Another interesting example was the study of Vigouroux et al. [40••] on pearl millet.
232 They analysed a total of 192 landraces that had been collected during two different periods
233 (i.e., 1976, 2003) throughout Niger, in the Sahel, which is one of the driest agro-ecosystems
234 in Africa. This geographic area had undergone recurrent drought during this interval of 25
235 years. Along with the analysis of the phenological and morphological changes in the two
236 samples evaluated in field experiments, they also investigated the genetic diversity across
237 these two samples. In particular, they analysed the change in allele frequency at the *PHYC*
238 flowering time locus [41], and showed that the allele that conferred earliness increased from
239 9.9% to 18.3% over this time frame. This study is an example of the strong adaptation of
240 plants to changing environmental conditions even over relatively short evolutionary
241 timescales. It also suggested that exploitation of genetic variability within landrace
242 populations represents a strategy in response to future climate changes. However, they
243 recommended the consideration of the mating system of the crop species, as they indicated
244 that this strategy might be successful for allogamous species, such as pearl millet, but that
245 further studies would be needed for autogamous species [40••].

246 SNPs are the markers of choice in different population genomics studies because
247 they are the most abundant bi-allelic and co-dominant markers that are characterised by
248 simple mutational patterns and by high-throughput and low-cost detection. Despite this,
249 many other examples exist in literature that are based on structural variations, which refers
250 to genomic changes in DNA segments of >1 kbp, such as insertions, deletions, inversions,
251 or copy-number variations. It is highly possible that genes responsible for acclimatizing and
252 adaptation to different agro-ecological conditions and stress resistances will be identified in
253 such genomic changes [42••]. As an example, Zhou et al. [43] reported the duplication and
254 evolutionary history of the *COR15* gene that is involved in cold-stress defence, which was
255 previously detected in two copies in several species of *Brassicaceae*. They cloned the
256 homologous *COR15* sequences of 10 species of *Brassicaceae*, and when they performed
257 evolutionary analyses they found significant inter-lineage differences in the evolutionary
258 rates between the original and the duplicated genes. The most interesting data were
259 perhaps observed for the analysis of the *COR15* genes of the *Draba* species, which contrary
260 to the other lineages, is mainly present in cold-temperature, highly arid regions. Three
261 important lines of evidence were observed: (i) the estimated non-synonymous and
262 synonymous substitution ratio appeared to be higher among the duplicated genes; (ii)
263 positive selection was detected for the duplicate *COR15* gene; and (iii) functional divergence
264 was shown between the two groups of the proteins. Overall, these observations indicated
265 that the functional differences in the *Draba* lineage between *COR15a*, as the original gene,
266 and *COR15b*, as the duplicated gene, have been driven by adaptive evolution. This allowed
267 its spread to cold locations during the Quaternary climatic oscillations, and subsequently its
268 expansion to arid alpine and arctic regions. Similarly, De Bolt [44] examined whether
269 *Arabidopsis* plants grown under different temperatures for several generations showed any
270 differences in copy number variations relative to the control situation of growth under normal
271 conditions. They showed that high temperatures promoted chromosomal segmental
272 duplications.

273 Recent studies have also suggested that polyploids might have greater phenotypic
274 flexibility for gene expression in response to environmental differences [45]. Ceccarelli et al.
275 [46] showed that chromosome endoreduplication in *Sorghum bicolor* is a fundamental part
276 of the adaptive response of plant genomes to salt stress. Their results showed that when
277 exposed to salt-induced treatments, only competent genotypes underwent endopolyploidy
278 of the root cortex cells, which allowed them to grow under sublethal salinity concentrations.
279 The wide variability obtained as a result of polyploidy events was thus directly correlated

280 with the tolerance increase of *S. bicolor* to salinity, which highlighted the important role of
281 this mechanism in adaptive responses to different abiotic conditions. Similarly, Saleh et al.
282 [47] reported that citrus tetraploid rootstock is more tolerant to salt stress than their
283 corresponding diploid.

284

285 **Selection for adaptation**

286 Local adaptation occurs when populations that grow under heterogeneous environmental
287 conditions evolve different phenotypic traits that provide a fitness advantage in their specific
288 environment [48]. Selection acts on sequence variation, which can derive from the standing
289 variation that has a long history of segregation within a crop before the advent of selection,
290 or *de-novo* mutations that originate in populations (i.e., wild forms or landraces), or from
291 hybridisation. Knowing the sources of variation on which selection for adaptation can act is
292 important for several reasons, such as, for example, to understand how rapidly populations
293 can adapt [3]. Exhaustive evidence that shows the relative role of standing variation or *de-*
294 *novo* mutations after changes in the environment is still lacking. Adaptation is likely to be
295 slower if selection acts on *de-novo* mutations, compared to what would be expected when
296 it acts on standing variation, where beneficial alleles might already be available at higher
297 frequencies [49]. Moreover, on average, adaptation from standing variation appears to occur
298 through the fixing of more alleles with small effects [3,50], and can have greater potential for
299 adaptation if the rate of environmental change is fast, rather than slow, by traversing larger
300 distances in the phenotype space.

301 Along with useful standing variation and *de-novo* mutations, selection for adaptation
302 can also act on new genotypic variations due to recombination after hybridisation [51,52]. In
303 common bean, Bellucci et al. [20•] analysed RNA sequencing data from a set of
304 Mesoamerican wild and domesticated accessions, and they showed that most of the genes
305 detected as under selection during domestication showed reduced diversity in their
306 domesticated compared to their wild forms, as expected under positive selection from
307 standing variation. However, 2.8% of the outlier genes showed no diversity in the wild form,
308 and polymorphism in the domesticated form. This thus suggested that in some cases the
309 selection increased the nucleotide diversity of domesticated materials at target loci, the
310 function of which was associated with adaptation traits, such as abiotic stress responses
311 and flowering time [20•]. Interestingly, in the same species, Bitocchi et al. [18] analysed
312 nucleotide data of 49 gene fragments in a sample of Mesoamerican wild and domesticated
313 accessions, and they detected an excess of nonsynonymous mutations in the domesticated
314 forms, particularly in the coding regions, compared to the non-coding regions. These
315 mutations appeared to be recently derived mutations, and the investigations into the
316 functions of their relative genes (responses to biotic and abiotic stresses) support a scenario
317 where new functional mutations were selected for adaptation during diversification.

318 In maize, Guo et al. [34] asked whether the *ZCN8* gene can affect natural variations
319 in flowering time. They performed association analysis by sequencing *ZCN8* and its
320 upstream and downstream regions in segregant populations derived from a cross between
321 W22, a temperate *Zea mays* ssp. *mays* inbred line, and 8759, a *Z. mays* ssp. *parviglumis*
322 accession. They found a SNP in the promoter region of *ZCN8* (i.e., SNP-1245) that
323 coincided precisely with the allelic differences in flowering time between all of the parents of
324 the teosinte–maize populations used in their study. They also sequenced the *ZCN8* gene in
325 a panel of 513 maize inbred lines and 45 teosinte lines (including lines of *Z. mays* ssp.
326 *parviglumis*, the maize progenitor, and lines of its close relative species *Z. mays* ssp.
327 *mexicana*). These data revealed that the early flowering allele of SNP-1245 was present in
328 ~24% of the teosinte accessions, which suggested that this polymorphism was a standing
329 variant in the maize wild progenitor selected during the early domestication of maize. Guo
330 et al. [34] also detected a three-base-pair deletion variant (i.e., Indel-2339) about 1,000
331 bases from SNP-1245 that was associated with flowering time and showed higher
332 expression of *ZCN8*. Moreover, they did not find this allelic variant in the maize progenitor,
333 although it was present in *Z. mays* ssp. *mexicana*, from which gene flow resulted in its
334 introgression into maize [53]. Furthermore, low frequency of Indel-2339 (5%) was shown for
335 South America germplasm (i.e., tropical maize), while it was selected at a higher frequency
336 in northern United States accessions (30%; temperate maize). Overall, these data
337 suggested that two independent associated mutations (i.e., *cis*-regulatory variants) in the
338 promoter region of *ZCN8* arose in a stepwise manner: SNP-1245 during the early
339 domestication of maize, and subsequently Indel-2339 during maize diversification into the
340 Mexican highlands. The discovery that *ZCN8* has more than one functional mutation that
341 segregates indicated that genes associated with crop domestication and diversification are
342 subject to recurrent mutations that might be selective targets at different times during
343 evolution.

344 Identification of adaptive introgression can be relatively easy when materials
345 collected at different times are available, such as with historical collections. A recent
346 example was seen by the study of Bitocchi et al. [11], where the effects were evaluated for
347 hybridisation of modern maize and landraces over a relatively short period of 50 years.
348 Bitocchi et al. [11] analysed and compared the genetic diversity of two samples of maize
349 landraces from central Italy that were collected at two different times: an old collection that
350 was carried out before the introduction of hybrid varieties, and a recent collection that had
351 evolved in co-existence with modern maize. Population structure analysis allowed the

352 detection of introgression from modern maize. Coupled to the data of selection analyses
353 (i.e., detection of outlier loci in comparisons between historical and recent maize collections),
354 these data indicated that selection pressures for adaptation have favoured new alleles that
355 were introduced by migration from hybrids over the last 50 years. These data showed the
356 crucial role of migration in the evolution of landrace populations grown on farms.
357

358 **The Columbian Exchange: adaptation of crops from American homelands into Europe**

359 The introduction of New World crops into Europe after the Columbus 1492 voyage was one
360 of the most important evolutionary events related to agriculture, adaptation and biological
361 changes, and more generally, to human society. In 1972, the historian Alfred Crosby coined
362 the term ‘Columbian Exchange’, to designate the process of the biological diffusion triggered
363 by the colonisation of the Americas by Europe. The benefits of the New World crops have
364 resulted in their adoption in all parts of the world, which demonstrated that as the basis of
365 this process, the plants underwent significant adaptation to the various agro-ecological
366 conditions [54]. The growing knowledge about the adaptation of crops to new environments
367 through the study of their introduction and expansion into Europe (i.e., a historically well-
368 defined event of recent introduction and rapid adaptation) will be of great use for future major
369 environmental and socio-economic changes, such as increases in temperature, variability
370 of rainfall, and new consumer preferences. Several crops were introduced into Europe from
371 the Americas (e.g., tomato, maize, beans, squash, potato, tobacco). This dissemination
372 process occurred during the same historical period for several species, and it was
373 characterised by diverse features (e.g., different mating systems and ploidy) that can be
374 exploited to investigate their effects on genome diversity and to highlight the genetic control
375 of adaptation. There are numerous studies in the literature for different crops that have
376 highlighted the changes that occurred in their genomes due to colonisation of new agro-
377 ecosystems. Here, we present some examples for three crops that were involved in the
378 Columbian Exchange, and which have been among the most important: potato, maize and
379 common bean.

380 Following long debate during which most studies have suggested multiple
381 domestications for *Solanum tuberosum* L (potato), Spooner et al. [55] demonstrated the
382 monophyletic origin of cultivated potatoes through phylogenetic analysis and cladistic data.
383 These showed that landraces of potato originated in the Andes of southern Peru, and
384 subsequently became widespread throughout Chile, thus assuming the present-day
385 distributions of the original cultivars. Potato was not brought to Europe by Columbus or
386 others soon after the discovery of the New World in 1492; potato arrived later. The reason
387 for this is that potato is a cool temperate crop of the high Andes of South America and was
388 not discovered by the Spaniards until 1532 [56]. Potato cultivation in Europe spread rapidly,
389 and also reached locations with significative growth and climate differences. For potato, the
390 most important adaptation trait to European conditions – and a key event in its history – was
391 to overcome the short-day dependency for tuberisation, due to the equatorial origin of

392 potatoes [57-59••]. Indeed, when introduced into temperate zones, wild material forms
393 tubers only during the shorter autumnal day lengths. The gradual arrival of winter, which is
394 characterised by freezing temperatures, stops the correct maturation of the tubers,
395 consequently killing the plant. In the *A. thaliana* model system, the pathway that controls
396 flowering time is very complex, and the complexity of this regulation involves four intricate
397 networks of signalling pathways (i.e., photoperiod, vernalisation, autonomous, gibberellins)
398 [60] (**Figure 3A**). Among the proteins involved in this complex pathway, cycling Dof (DNA-
399 binding with one finger) factors (CDFs) are a group of plant-specific transcription factors that
400 repress flowering by down-regulation of the expression of the *CONSTANS* (*CO*) gene, a
401 central regulator of the photoperiod pathway [61]. In potato, the plant maturity phenotype
402 has been reported as a major effect QTL that maps to chromosome 5, and this phenotype
403 is a measure of several important secondary traits. These include development of the
404 canopy, vegetative growth, onset of tuberisation, leaf senescence, life-cycle length and
405 pathogen resistance [62]. Kloosterman et al. [57] used ultra-dense amplified fragment length
406 polymorphism markers and two diploid segregant potato populations derived from crosses
407 between wild and domesticated genotypes. In this way, they narrowed down the locus
408 responsible for the plant maturity phenotype to a region of around 110 kb on chromosome
409 5. Screening for putative candidate genes, they identified the potato homologue of *CDF1* in
410 this QTL region (*StCDF1*, *Solanum tuberosum* CDF gene 1). They sequenced *StCDF1* in
411 the progenies of the mapping populations, which allowed identification of three *StCDF1*
412 allelic variants: *StCDF1.1*, which was characteristic of short-day-dependent tuberisation
413 descendants, and two insertion variants, *StCDF1.2* and *StCDF1.3*, that were typical of the
414 early maturing/ tuberising descendants. Kloosterman et al. [57] established that *StCDF*
415 conserves its repressive function on the two potato *CONSTANS* genes (*StCO1/2*) that
416 repress tuber formation during long days [63]. They also suggested that due to the loss of
417 their C-terminal end, the *StCDF* Andean variants (i.e., *StCDF1.2*, *StCDF1.3*) led to
418 accumulation of *StCO1/2* repressors. This interaction indirectly induced expression of
419 *StSP6A*, the potato homologue of *FLOWERING TIME* (*FT*), which resulted in induction of
420 tuber development under long days (**Figure 3B**). The absence of post-translational
421 regulation of *StCDF1.2* and *StCDF1.3* allowed them to remain constant throughout the day,
422 which formed the basis of potato diversification at different latitudes. A recent investigation
423 explored haplotype diversity at the potato maturity locus *StCDF1* using a panel of 58
424 samples [58]. These included South American wild species, South American landraces, and
425 North American cultivars derived from modern breeding programmes. Here, Hardigan et al.

[58] reported 55 haplotypes for *StCDF1* that encoded 27 peptide variants. Four haplotype groups contained conserved deletions that affected the structure of the *StCDF1* peptide. The DNA phylogeny of haplotypes at the *StCDF1* locus revealed that almost all long-day landraces/ cultivars contained alleles that encoded shortened *StCDF1* proteins that were derived from introgression from wild species. This suggested a key role for the extant natural populations as essential sources of untapped adaptive potential. In the case of potato, *StCDF1* allele introgression from the wild species allowed potato cultivation in North America, and, probably, also subsequently in Europe. A very interesting study that focused on the origins and adaptation of European potatoes was carried out by Gutaker et al. [59••]. The strength of their work was the investigation of historical samples that spanned 350 years of potato evolution in Europe. Their materials included 29 historical herbarium specimens that they obtained from different European museums, which included three Chilean and 26 European historical samples. They also analysed 43 South American modern samples, and 16 European modern samples. An array-based targeted re-sequencing approach was used that allowed them to target the whole chloroplast genome and ~4.3 Mb of the nuclear genome, including *StCDF1* [57]. Analysis of these genetic data initially allowed Gutaker et al. [59••] to highlight the very complex scenario related to the introduction and wide spread of potatoes in Europe. These data indicated that the oldest European materials (i.e., collected between 1650 and 1750) derived from an ancestor of the Andean landraces, while in the subsequent 100 years there was introgression from newly introduced Chilean potatoes. The scenario is more complex considering that twentieth century European potatoes did not descend from their nineteenth century admixed predecessors, but are the result of introgression from wild potato species, as they were used in twentieth-century breeding programmes to introduce pathogen resistance [64]. It is also interesting that Gutaker et al. [59••] highlighted the re-introduction of European potatoes into America, and that this impacted upon the Andean and Chilean potato diversity; indeed, European ancestry was detected in potatoes in the South American modern-day sample. Gutaker et al. [59••] also investigated the origins of the long-day adaptive alleles in the *StCDF1* gene. They reported the appearance of *StCDF1.2* and *StCDF1.3* adaptive alleles in Europe starting from 1810 only, with none of these insertion variants present in the oldest European samples of Andean descent (1650-1750), nor in the Andean landraces. For this reason, they excluded (with high confidence) the possibility that adaptation to long-day tuberisation had arisen from the Andean landraces standing variations. They showed the appearance of the adaptive alleles in Europe in correspondence with admixture with the newly introduced Chilean

460 potatoes. However, there was no evidence of direct correlations between the adaptive
461 variants and the historical samples from the lowlands of Chile. Gutaker et al. [59••] thus
462 hypothesised that the adaptive insertions in the *StCDF1* gene originated *de novo* in Europe,
463 and then became rapidly fixed due to their dominant inheritance and breeding advantage.
464 However, they also stated that this hypothesis needs to be further confirmed, as their
465 sampling of historical Chilean specimens is not particularly representative, and thus it did
466 not allow clear rejection of the possibility of a Chilean origin of these adaptive insertions.

467 Another very important crop that became widespread in Europe during the Columbian
468 exchange was *P. vulgaris* (common bean). This species originated in Mesoamerica, and
469 wild forms became widespread by subsequent migration into South America; domestication
470 took place independently in two geographically distant areas, Mesoamerica and the Andes,
471 which represented the two main gene pools of the species [16]. The Mesoamerican common
472 bean appears to have arrived in Europe through Spain and Portugal in 1506, following the
473 first voyage of Columbus; then in 1528, the exploration of Peru by Pizarro opened the
474 possibility of the introduction of the Andean common bean. *P. vulgaris* spread into the Old
475 World over a very short time, and many common bean landraces rapidly evolved in Europe
476 as a result of its adaptation to new agro-ecological growth conditions. The dissemination of
477 common bean into and across Europe followed very complex pathways, which involved
478 different introductions from the Americas, and at the same time, direct exchanges among
479 countries within Europe, and between European and other Mediterranean countries [16]. To
480 investigate the evolutionary patterns of the common bean far from the Americas, Angioi et
481 al. [54] analysed a wide sample of *P. vulgaris* accessions, as 94 from the Americas, and 307
482 from Europe. They included chloroplast simple sequence repeats (SSRs), and nuclear data
483 (i.e., phaseolins, three indel-spanning markers of the *PvSHATTERPROOF1*, *PvSHP1*,
484 gene) and morphological data (i.e., coat pattern, seed size, colour and shape). In this way,
485 Angioi et al. [65] showed that both the Mesoamerican and Andean gene pools were present
486 in Europe and that the European germplasm was more prevalent as the Andean origin
487 (67%). The trend was maintained at a smaller scale (i.e., a country level), whereby the
488 Mesoamerican proportion was higher in the eastern parts of Europe, with a maximum of
489 46% in Greece, while the Andean type was most frequently found in three European macro
490 areas: the Iberian Peninsula, Italy and central-northern Europe. Interestingly, and contrary
491 to expectations, the European common bean did not show any strong reduction in genetic
492 diversity due to the introduction bottlenecks and selection for adaptation to these new agro
493 ecosystems and consumer preferences; indeed, Angioi et al. [54] and previous studies have

494 shown very low reductions in diversity in common bean from Europe. These findings
495 indicated a high level of gene flow among the different European geographic regions.
496 Furthermore, they highlighted the role of the breakdown of the spatial isolation between the
497 Mesoamerican and Andean accessions in Europe, with promotion of hybridisation, which
498 had a significant impact on the maintenance of genetic diversity. By combining these
499 chloroplast and nuclear data, they were able to identify hybridisation events, and they
500 estimated that 44.2% of the European landraces derived from at least one hybridisation
501 event between the Mesoamerican and Andean forms. Gioia et al. [66] complemented the
502 dataset of Angioi et al. [65] with nuclear SSRs, and analysed a set of 89 American and 256
503 European landraces. Gioia et al. [66] combined the data from the recombination of the gene-
504 pool-specific chloroplast SSRs, phaseolin and *PvSHP1* markers and the Bayesian
505 assignments and admixture analysis based on nuclear SSRs, through which they were able
506 to identify hybrids and distinguish them as 'pure' Mesoamerican and Andean genotypes.
507 Novel combinations of genes/ genomic regions thus arose in Europe after the common bean
508 introduction and during its dissemination, on which adaptive selection acted (i.e., adaptive
509 introgression). The new '-omics' technologies can help to fine-tune the molecular basis of
510 these adaptations of the common bean in Europe, an aspect that is ongoing in the
511 BEAN_ADAPT project (funded through the 2nd ERA-CAPS call, ERA-NET for Coordinating
512 Action in Plant Sciences). This project is based on a multidisciplinary approach (i.e.,
513 genomics, population/ quantitative genetics, biochemistry, plant physiology), with the aim
514 being to dissect out the genetic basis and phenotypic consequences of the adaptation of *P.*
515 *vulgaris* and its sister species *P. coccineus* from their centres of origin in the Americas into
516 Europe and the new European agro-ecological environments.

517 Maize is probably the most important New World crop that was involved in the
518 Columbian Exchange. Rebourg et al. [67] characterised a set of 131 European maize
519 landraces according to morphological and genetic data (i.e., restriction fragment length
520 polymorphism), and classified them into genetic groups that showed clear differentiation
521 according to latitude. Six main European races were detected based on morphological and
522 genetic differences: 'German flint', which included landraces mainly grown in Germany or
523 the Alsace; 'north-eastern European flint', which included landraces mainly from France,
524 and also Spain, Portugal and several eastern European countries; 'southern European flint',
525 which was characterised by landraces from various countries which were mainly in southern
526 Europe; 'Italian orange flint', as Italian landraces, with some others from southern Spain;
527 'Czechoslovakian type'; and 'Pyrenees-Galicia flint', which was characterised by two

homogeneous subgroups, as the landraces from Galicia, and those from the Pyrenees and other regions of France. Then Rebourg et al. [68] included genetic data of 88 American landraces that were representative of the main American races in their previous dataset [56], to infer the genetic relationships among American and European maize populations. They showed signatures for the introduction of a bottleneck (European landraces retained overall 75% of the genetic diversity of those from America), and identified various types of American maize that were introduced into Europe at different times or in different places, which gave rise to distinctive European races [69]. Beyond confirming the importance of Caribbean germplasm, which was the first maize type to be introduced into Europe, they highlighted the close relationship between southern Spain and Caribbean populations, whereby the data revealed that introductions of North American flint populations had a key role in the adaptation of maize to the European climate. In particular, the data supported the hypothesis that present-day northern and eastern European flint germplasm was directly derived from North American flint populations. Northern flint populations were relatively insensitive to day length, and they had low temperature requirements for flowering. Earliness was a key factor for adaptation to the more temperate climates. Brandenburg et al. [70•] sequenced 67 genomes from both continents that covered 11 major groups, as representative of all of the American and European diversity. They used several population genomics and association mapping approaches to trace the origins of the European maize, and to investigate its demographic and selective history. One of the main outcomes of this study was the detection of admixture in the European maize materials. In particular, they reported the admixed origins of the Italian flints from two contributions, the European flint and the southern European populations. This excluded the possibility of a third independent introduction, as had previously been suggested by Rebourg et al. [68], and instead emphasised the pivotal role of admixture in environmental maize adaptation. Moreover, the data of Brandenburg et al. [70•] highlighted the admixed origins of the European flints from the northern European flints and the tropical landraces. Interestingly, they also investigated the footprints of selection for adaptation to a wide range of climatic and ecological conditions, and they showed that numerous genes/ gene networks were involved in flowering time, drought and cold tolerance, and in plant defence and starch properties. An example of the candidate genes for adaptation that were detected by associations between latitude and allele frequency was defined at GRMZM2G095955, a gene that is located in the vicinity of the maize floral activator, *ZCN8* [39]. They reported that in the *ZCN8* region there was a haplotype that was common to all temperate materials, and they showed segregation of this

562 'temperate' haplotype with a 'tropical' haplotype within the tropics, and to a lesser extent
563 within the corn belt dents. Along with the previously characterised genes, they also revealed
564 new candidates, including *ZCN5* (also known as *zen1* and *pebp5*), a gene from the same
565 family as *ZCN8* that was recently reported to be associated with flowering time variations
566 [71]. They also defined genes associated with plant responses to biotic and abiotic stresses,
567 such as the *ZmASR2* gene (abscisic acid-, stress-, and ripening induced protein 2), which
568 was shown to have increased expression at the transcript and protein level under water-
569 deficit conditions [72], and the *TPS23* gene that is involved in the control of the synthesis of
570 a volatile sesquiterpene that attracts natural enemies of herbivores upon release [73].
571

572 **Conclusions**

573 Deeper understanding of the evolutionary processes and complex genetics mechanisms
574 that form the basis of adaptation of plants to different environmental conditions is a very
575 ambitious goal for evolutionary biologists, breeders and geneticists. It also has strong
576 implications for overcoming the current challenges that agriculture has to face, such as to
577 guarantee food security and quality, to adapt crops to marked variations in climate, and to
578 protect and improve the environment. In this context, the identification of the genetic
579 architecture both at genotype and population level, that contribute to adaptive changes, can
580 strongly influence breeding targets and strategies. The potential applications are nearly
581 infinite for the constitution of novel varieties in breeding programmes, but it will be crucial
582 also for biodiversity conservation, to provide help in the implementation of the appropriate
583 strategies. We have now in-hand novel tools and approaches that allow us to face this
584 challenge through exploiting the unprecedented experimental power available. These
585 include:

586 (i) Particularly advanced techniques that offer unique opportunities to scan a genome, not
587 only to obtain genotypic information, but also to analyse the molecular phenotype of the
588 whole genome, through analysis of the transcriptome, the metabolome, and the proteome
589 [20, 74-76].

590 (ii) We can count on improvements to the tools and approaches to analyse these data, which
591 have also evolved to catch the complexity of these biological processes. Population
592 genomics approaches allow the identification of candidate loci for adaptation using
593 genotypic data without any prior information about phenotypes. Along with classical
594 approaches aimed at detection of 'selective sweeps' [77], new methods and integrated
595 approaches can be applied that take into account the concept that genes do not often
596 actually operate as sole effectors, as they have roles in complex interactive systems, or
597 gene networks, that ultimately lead to a phenotype [78]. As an example of the impact that
598 gene interactions can have on the determination of the phenotype, an *A. thaliana* genome-
599 wide association analysis reported that for root length, epistatic effects can be so strong that
600 they overcome the additive genetic variance [79•]. In soybean, Fang et al. [80] carried out a
601 comprehensive genome-wide association studies that enabled identification of the
602 underlying genetic loci, loci interaction, and genetic networks across important traits.

603 (iii) Multidisciplinary approaches can be applied and integrated to decipher the complexity
604 of the genetic basis of adaptation. These can combine evidence from the signatures of
605 selection analyses with association mapping to increase the power for the detection of
606 regions that influence complex traits, while also reducing the number of false-positive signals
607 [81,82]. Moreover, recently, different approaches have been developed based on the use of
608 environmental variables that are treated as quantitative traits, and their association with
609 molecular traits can be exploited as a tool to identify the loci that underlie local adaptation
610 [12,83]. Similarly, network analyses can be used to investigate the roles of interactions
611 between genes in local adaptation [84], using information on linkage disequilibrium shared
612 between genome-wide multiple loci to perform linkage disequilibrium network analyses.

613 (iv) Landrace populations of crops are the 'perfect' model to apply all of these approaches
614 to investigate adaptation features in the plant genome. They also allow the possibility to
615 compare the effects of the same evolutionary process on the genome when this occurs as
616 the following: independently on different populations of the same species (e.g.,
617 domestication in common bean occurred independently in Mesoamerica and the Andes)
618 [18,19]; among different crop species within the same genus (e.g., different domesticated
619 *Phaseolus* species) [16]; and/ or among species of different genera (i.e., shattering trait in
620 cereals) [85] that are characterised by different features (e.g., diverse mating systems,
621 diverse ploidy levels). These aspects offer great opportunities to go deeply into the
622 molecular and developmental mechanisms at the basis of adaptation.

623 In this scenario, the Columbian Exchange represents a pivotal model. It offers a great
624 opportunity to exploit all of these available tools and approaches, along with the plant genetic
625 resources, to finally dissect out the genetic basis and phenotypic consequences of plant
626 adaptation to new environments. This can now come through the study of their introduction
627 from their respective centres of domestication in the Americas, and their expansion through
628 Europe as a recent and historically well-defined event of rapid adaptation. Numerous crop
629 species have been protagonists of these processes and have experienced adaptation in a
630 relatively short period of time in the same geographic range (i.e., with the same
631 environmental changes). What we need to do now is to investigate this process more deeply
632 in different crops, and to compare and integrate the information obtained. A better
633 understanding of variation in landscape structure across species and environments is also
634 necessary to understand and predict how populations will adapt [86]. Moreover, advances
635 in statistics and increased computing power already provide the possibility to develop
636 predictive approaches, as demonstrated by Exposito-Alonso et al. [87••] who were able to

637 build genome-wide environmental selection models to predict how evolutionary pressures
638 on species will work in inaccessible environments, or even under future hypothetical
639 climates.

640

641 **Figure legends**

642 **Figure 1. Geographic distribution of barley (top), maize (middle) and common bean**
643 **(bottom) landraces from their centres of domestication.**

644 The centres of domestication are represented by white dots with black borders. The
645 distributions of the landraces/ traditional cultivar accessions were obtained by plotting the
646 geographic coordinates for where the seeds were collected. Data were extracted from the
647 database of the Genesys platform (<https://www.genesys-pgr.org/>), which includes
648 information from several genebanks.

649

650 **Figure 2. Physical map of the 11 common bean chromosomes and genomic locations**
651 **of genes putatively involved in abiotic stress responses and with selection signatures**
652 **in common bean.**

653 Common bean genes were identified based on orthology with those involved in abiotic stress
654 responses in *Arabidopsis thaliana*, according to *The Arabidopsis Stress Responsive Gene*
655 *Database* [21] and using the OrthoFinder algorithm [22]. The orthologous protein to the *A.*
656 *thaliana* KUP6 is also shown in chromosome Pv03. For the map representation, we selected
657 a subset of 126 common bean orthologues (see **Table S1** for the full list) that show selection
658 signatures according to Schmutz et al. [19] and/or Bellucci et al. [20]. Genes potentially
659 associated to different stress responses based on the orthology with *A. thaliana* genes are
660 highlighted according to the legend. The physical distances in the scale are reported in
661 megabases (Mb).

662

663 **Figure 3. Schematic representation of CDF gene function and interactions in the**
664 **photoperiod pathway.**

665 During long days, in the *A. thaliana* model system (**A**), the interaction between GIGANTEA
666 (*GI*) and FLAVIN-BINDING KELCH REPEAT F-BOX 1 protein (*FKF1*) induces degradation
667 of CYCLING DOF FACTOR (*CDF*), which is a repressor of CONSTANS (*CO*). *CO* promotes
668 flowering by initiating transcription of the FLOWERING TIME (*FT*) gene. In *S. tuberosum* L.
669 (**B**), the *CDF* adaptive variant does not interact with the GI-FKF1 complex, which leads to
670 repression of *CO1/2*. In contrast to *A. thaliana*, *CO1/2* act as repressors of *SP6A*, which is

671 the potato homologue of *FT*. Repression of *CO1/2* allows expression of *SP6A* and promotion
672 of potato tuberisation under long days, which forms the basis of potato diversification at
673 different latitudes. Arrow, promotion of gene expression; truncated arrow, repression of gene
674 expression; truncated dotted arrow, lack of repression due to pathway interruption.

675

676 **Supplementary**

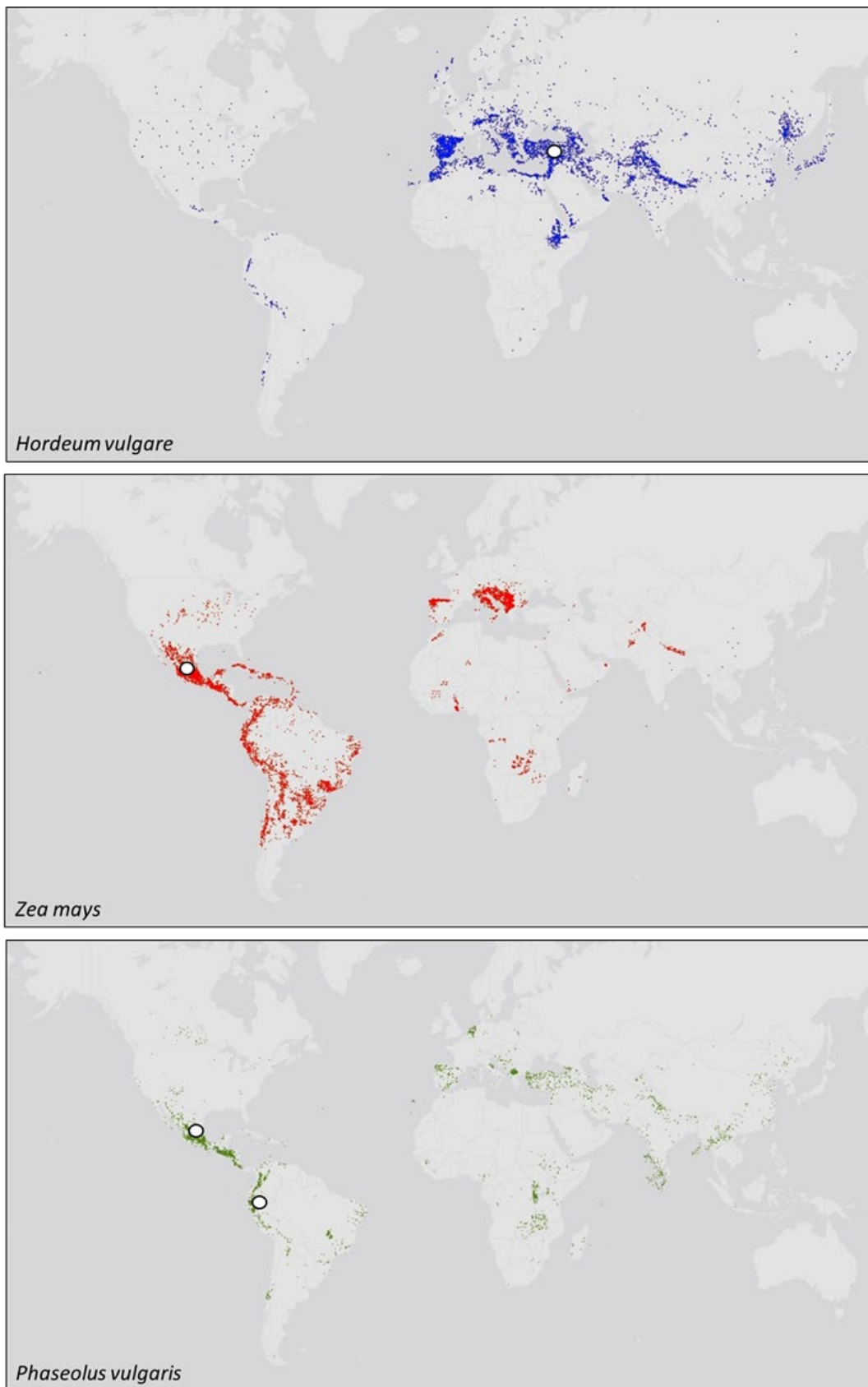
677 **Table S1. Genes putatively involved in abiotic stress responses in common bean.**

678 Genes were identified based on the orthology relationships (OrthoFinder algorithm) [22] with
679 *A. thaliana* genes listed in *The Arabidopsis Stress Responsive Gene Database* [21], and
680 with the KUP6 protein sequence. The orthogroup (i.e., cluster of orthologous genes across
681 *A. thaliana* and common bean), the type of stress response of the orthogroup genes, the
682 common bean gene name, its genomic location and description based on Phytozome, and
683 the presence of selection signatures [19;20] are reported for each common bean gene.

684 PN; putatively neutral gene.

685 n.m; no homologous contigs from Bellucci et al. (2014) have been identified

686 * in the column K, according to the data of Bellucci et al. (2014), the PS (putative under
687 selection) contig that mapped on the gene showed polymorphisms for the nucleotide
688 sequence across domesticated accessions and was fixed monomorphic in the wild pool of
689 genotypes.



690

691 **Figure 1**

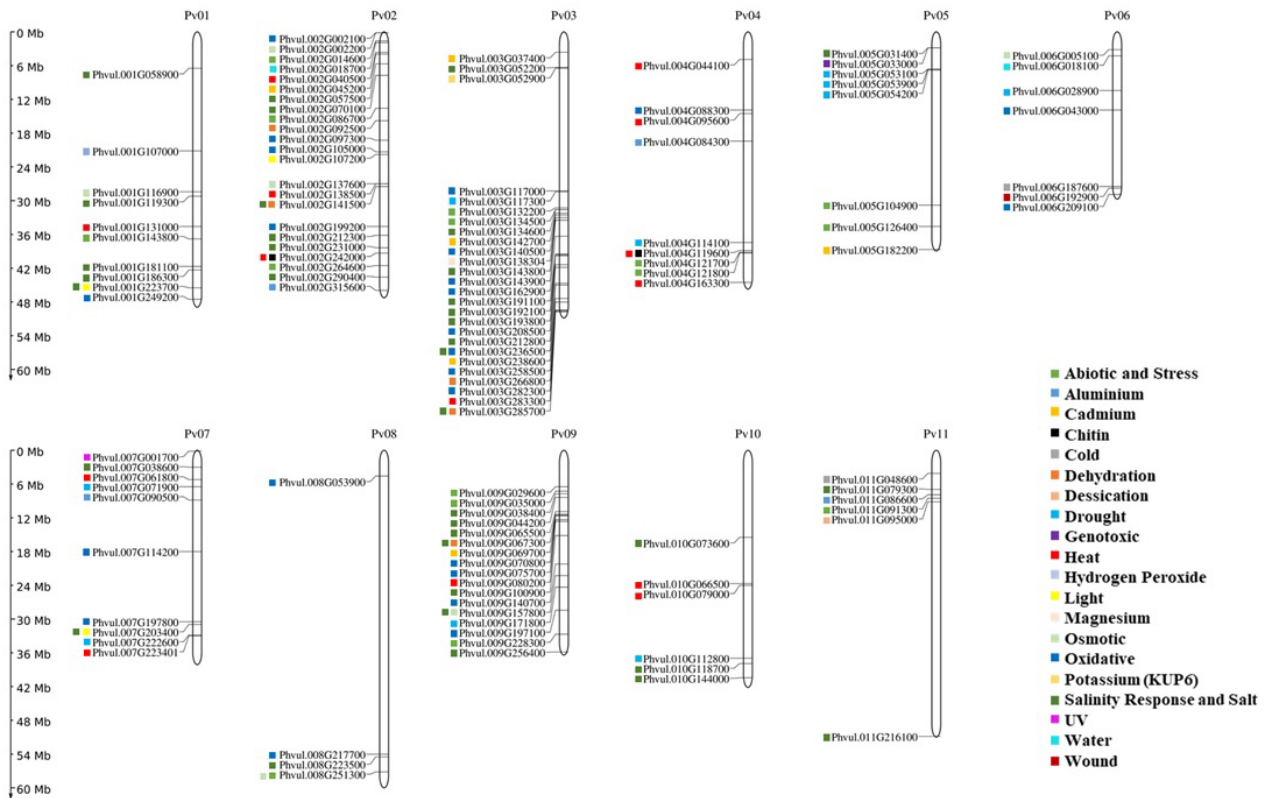
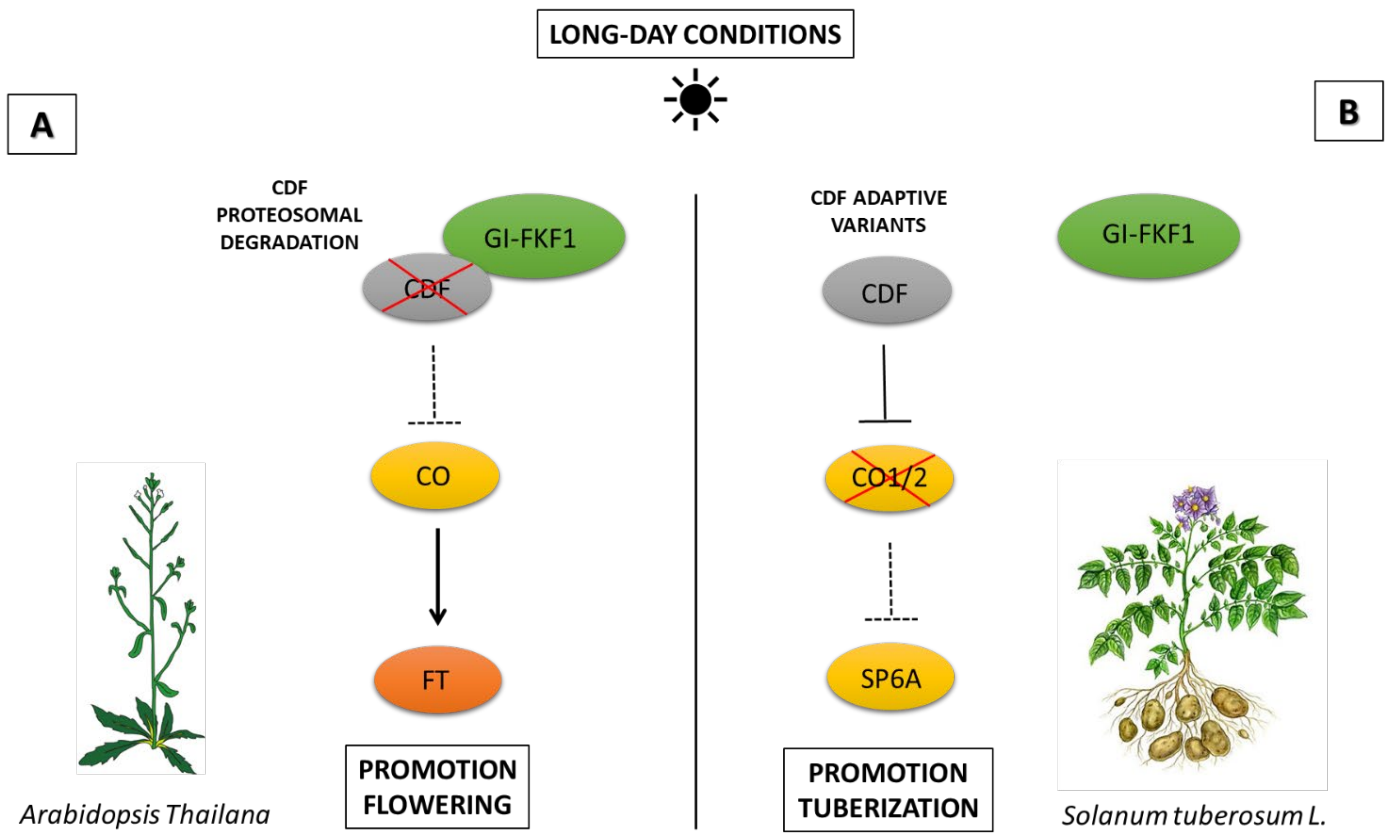


Figure 2



694

695

Figure 3

696 **References**

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1051 *concept for the use of genome-wide environment selection models for evolution-aware*
1052 *predictions of risks for biodiversity that are associated with climate changes.*
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