

# 1 **Evolutionary plant breeding as a response to the complexity of climate** 2 **change**

3 **Salvatore Ceccarelli<sup>1\*</sup>, Stefania Grando<sup>1</sup>**

4 <sup>1</sup>Independent Consultant, Corso Mazzini 256, 63100 Ascoli Piceno (Italy)

## 6 **\* Correspondence:**

7 Corresponding Author

8 ceccarelli.salvatore83@gmail.com

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10 Climate change is one of the processes that have already overstepped the safe planetary  
11 boundaries, together with the rate of biodiversity loss and human interference with the  
12 nitrogen and phosphorus cycles. The three processes are related to agriculture and, as such,  
13 to both food safety and food security, and ultimately to human health. Adaptation to climate  
14 change is a difficult breeding objective because of its complexity, its unpredictability and its  
15 location specificity. However, one strategy exists, which is based on a more dynamic use of  
16 agrobiodiversity in agriculture through the cultivation of evolutionary populations. In this  
17 review, we show how the translation into agricultural practice of nearly 100 years of research  
18 on evolutionary populations and mixtures, is able to address the complexity of climate change  
19 while stabilizing yield, decreasing the use of most agrochemicals, thus reducing emissions and  
20 producing healthy food.

## 22 **The complexity of climate change**

23 The concept of “planetary boundaries” was proposed in 2009 to define a “safe operating  
24 space for humanity” (Rockström et al., 2009). The boundaries include climate change, rate of  
25 biodiversity loss, ozone depletion, acidification of the oceans, human interference with  
26 nitrogen and phosphorus cycle, global freshwater use, change in land use, chemical pollution,  
27 and atmospheric aerosol loading. Three of the nine boundaries, namely climate change, rate  
28 of biodiversity loss and human interference with nitrogen and phosphorus have been already  
29 crossed (Steffen et al., 2015), together with the use of fresh water (Jaramillo and Destouni,  
30 2015).

31  
32 The three processes affect agricultural productivity, and in fact there has been already a  
33 decline in crop resilience as recently shown in the case of wheat in Europe (Kahiluoto et al.,  
34 2019). However, the argument of resilience is still debated as Piepho (2019) disputed the  
35 previous claim and a new methodology to estimate resilience has been recently proposed  
36 (Zampieri et al., 2020).

37  
38 In the case of climate change, it is recognized that projections of future climate change and  
39 its impacts are uncertain (IPCC, 2018), which makes crop adaptation to climate change a  
40 difficult breeding objective. The difficulty is made even greater because changes in  
41 temperature and rainfall influence the spread, growth and survival of crop pathogens  
42 (Rosenzweig et al., 2001). There are several examples of interactions between climate change,

43 crop development and both pests and their natural enemies (Heeb et al., 2019). Zavala et al.  
44 (2008) showed how elevated CO<sub>2</sub> increases the susceptibility of soybean to an invasive insect,  
45 while Deutsch et al. (2018) estimated a 10-25% global yield losses per degree of global mean  
46 surface warming of three staple grains – rice, maize and wheat: this is because individual  
47 insect’s metabolic rate accelerates with the increase of temperature and an insect’s rate of  
48 food consumption must rise accordingly. Furthermore, the number of insects will change  
49 because population growth of insects also vary with temperature. Pollinators such as  
50 bumblebees are also affected by climate change as it is shown by the range shift in bumblebee  
51 species (Kerr et al., 2015). Newton et al. (2011) and Pautasso et al. (2012) reviewed several  
52 studies showing the complexity of the interactions of each component of the host-pathogen  
53 relation, and how these interactions are affected by climate change, thus representing  
54 another area of uncertainty in predicting the effects of climate change. Climate change affects  
55 the adaptation and the spreading of weeds as well as an increased risk for the evolution of  
56 herbicide-resistant weeds (Ziska and Dukes, 2010; Colautti and Barrett, 2013; Matzrafi et al.,  
57 2016). The expansion of the geographical ranges of several important insects, weeds and  
58 pathogens has been documented in the USA (Rosenzweig et al., 2000).

59

60 In addition to affecting diseases, insects and weeds in a largely unpredictable and  
61 continuously evolving way, a further aspects of climate change is represented by the  
62 frequency of extreme climatic events such as spells of very high temperatures, torrential rains  
63 and droughts, which besides affecting crop yields directly, may affect the transmission  
64 dynamics of insect pests and plant diseases (Rosenzweig et al., 2001). Tropical storms are  
65 additional event, which may contribute to the spreading of diseases (Campbell and Madden,  
66 1990; Lehmann et al., 2020).

67

68 The challenge posed by climate change has led terms such as “climate-smart agriculture”  
69 (Lipper et al., 2018), “climate-smart crops” (Kole, 2020) or “climate-resilient crops” (Kole et  
70 al., 2015) to become popular. However, most of the strategies suggested are based on the  
71 identification and incorporation of traits conferring tolerance or resistance to specific biotic  
72 or abiotic stresses, failing to recognize the evolving nature of the challenge. This applies also  
73 to the attempts to stack tolerance to more than one stress, particularly when this is done in  
74 controlled conditions (Menkir et al., 2020). Most of these solutions are “within the capacity  
75 for micro-evolutionary change of the parasite” (Robinson, 2009), and several examples of  
76 accelerated evolutionary changes in disease organisms, agricultural pests and weeds have  
77 been reported (Palumbi, 2001; McDonald and Stukenbrock, 2016; Bøhn and Millstone, 2019).  
78 In contrast, spatial and temporal crop diversity can reduce the need to breed for new  
79 resistance or to discover new pesticides, given that “each defence sows the evolutionary seed  
80 to its own demise” (Tilman and Clark, 2014).

81

82 Setting objectives for a breeding program that aims at adapting a crop to climate change,  
83 becomes therefore a daunting exercise. In fact, it is a case of breeding for multiple objectives.  
84 On one hand we have abiotic stresses such as high temperature and drought, and on the other  
85 we have biotic stresses affected by those abiotic stresses: each of these stresses is a separate  
86 breeding objective, which in the real word have to be tackled together. For a situation like  
87 this, breeders have standard multi-trait breeding schemes such as tandem selection,  
88 independent culling and index selection (Falconer, 1960), but whose efficiency depends on  
89 the correlations between the traits involved, which can change in space and in time. In fact,

90 correlation coefficients have both a genetic and environmental component and their relative  
91 strength affects selection efficiency. Multi-objective optimized breeding strategies are being  
92 considered as a promising alternative although based on unrealistic assumptions such as  
93 constant heritability (Akdemir et al., 2019). In addition, as we have seen, those multiple  
94 objectives are largely unpredictable. By the time one breeding cycle is completed, the  
95 objectives set at its inception, may have already changed.

96  
97 Climate change also affects human health both directly due to the occurrence of heat waves,  
98 floods and fires and indirectly due to its effects on agriculture, food supply and diets  
99 (Springmann et al., 2016; Ceccarelli, 2019). One of the paths connecting climate change with  
100 human health is through biodiversity loss (Watts et al., 2018).

101  
102 Two strategies to cope with climate change are usually discussed in the literature: a mitigation  
103 strategy, which relies on the reduction of greenhouse gas emissions and an adaptation  
104 strategy based on adapting crops to climate change. D’Amato et al. (2010) and IPCC (2014)  
105 suggested ways in which the two strategies can be combined. In this paper we propose that  
106 it is possible to combine the two strategies in crop management by cultivating diversity.

## 107 108 **Biodiversity and Human Health**

109  
110 Biodiversity, and in particular agrobiodiversity is a key to food security making production  
111 systems more resilient (FAO, 2019) and is an essential resource for crop improvement to  
112 adapt agriculture to a changing climate and consumer preferences (Hufford et al., 2019). Yet,  
113 the very same science, which is based on this resource, namely plant breeding, is considered  
114 to be one of the causes of its decline (van der Wouw et al., 2010). The reduction of diversity  
115 associated with plant breeding is somewhat controversial: for example Landjeva et al. (2006)  
116 found that genetic diversity did not decline in Bulgarian winter wheat while Bonnin et al  
117 (2014), using an integrative indicator of genetic diversity developed by Bonneuil et al. (2012),  
118 found a decline in the genetic diversity of wheat during the 20<sup>th</sup> century. Reiss and Drinkwater  
119 (2018) reached similar conclusions.

120  
121 Already in 1950 there was a warning that the “concept of purity has not only been carried to  
122 unnecessary length but that it may be inimical to the attainment of highest production”  
123 (Frankel, 1950).

124  
125 At farm level, agrobiodiversity can be in the form of different crops, of different varieties  
126 within the same crop, and of heterogeneous (genetically not uniform) varieties. Out of 7000  
127 plant species used for food through the millennia, over the past 50 years, only six crops,  
128 wheat, soybeans, maize, rice, barley and rapeseed, have covered 50% of the arable land  
129 (Jacobsen et al., 2015).

130  
131 The decline in agrobiodiversity that contributes to our food is even more striking: rice, wheat  
132 and maize contribute about 60% of our plant-based calories and 56% of our plant-based  
133 proteins (Thrupp, 2000; FAO, 2013) and use nearly 50% of all the water used for irrigation.  
134 The most widely grown varieties of these crops are genetically uniform, being pure lines or  
135 hybrids, making the reduction of agrobiodiversity even greater.

137 The decline of agrobiodiversity has two major consequences. Firstly, it makes our crops more  
138 vulnerable because their genetic uniformity makes them unable to respond to both short and  
139 long terms climate changes (Keneni et al., 2012), and provide an ideal breeding ground for  
140 the rapid emergence of fungicide-resistant variants (Fisher et al., 2018). A recent study shows  
141 that, globally, climate variability accounts for roughly a third (32-39%) of the observed yield  
142 variability (Ray et al., 2015). Secondly, in the last 10 years, medicine has recognized the  
143 association of agrobiodiversity with diet diversity and human health (Heiman and Greenway,  
144 2016; Ceccarelli, 2019). In fact, the composition and diversity of the microbiota affects both  
145 our physical and mental health (Khamsi, 2015; Hoban et al., 2016), and the diet affects the  
146 composition and diversity of the microbiota (Singh et al., 2017). Nutritionists recommend a  
147 diet as diverse as possible for having a healthy microbiota (Heiman and Greenway, 2016), but  
148 a diversified diet remains a challenge, given the decline in agrobiodiversity described earlier.

149  
150 Food production is the largest cause of global environmental change being responsible for up  
151 to 30% of global greenhouse-gas emission and 70% of freshwater use (Willet et al., 2019). Our  
152 present food system leaves almost 1 billion people hungry, on the other side almost 2 billion  
153 are eating too much of the wrong food while unhealthy diets account for up to 11 million  
154 avoidable premature deaths per year (Lucas and Horton, 2019).

155 Despite global efforts and after years of decline, the number of people who suffer from  
156 hunger has been on the rise again since 2015 (FAO, IFAD, UNICEF, WFP and WHO, 2019).

157

### 158 **Cultivating diversity may offer the solution**

159

160 To cope with the complexity of climate change combined with the need to address  
161 heightened demand due to human population increase, food security, food safety and human  
162 health, there is a need to reconsider plant breeding strategies in a way that generates  
163 diversity rather than eroding it. One strategy, which is able to maximize genetic gains and  
164 crop genetic diversity is decentralized selection, defined as selection in the target  
165 environment (TE) (Ceccarelli, 2015). Such a strategy emphasises specific adaptation and  
166 therefore leads to selecting different varieties, each adapted to a specific TE. In terms of  
167 selection theory, this allows to eliminate genotype x location (GL) interactions keeping only  
168 genotype x year within location (GY<sub>L</sub>) interactions (Allard and Hansche, 1964; Singh et al.,  
169 2006). This is important because GY<sub>L</sub> interactions are largely unpredictable, and even more so  
170 because of climate change, while GL interactions can be, to some extent repeatable and  
171 therefore predictable: decentralized selection makes a positive use of GL interactions by  
172 selecting different, locally adapted, varieties. However, while this is the solution to GL  
173 interactions, the solution to GY<sub>L</sub> interactions, namely building the resilience to the  
174 unpredictable year-to-year variations can be achieved by growing heterogeneous  
175 populations. In fact, heterogeneous populations have the advantage of exploiting both  
176 individual and population buffering (Allard and Hansche, 1964). Such a solution responds to  
177 the natural selection theory because the fitness of an individual is the result of the interaction  
178 of the phenotype with the environment, and not an intrinsic feature of either one (Wade and  
179 Kalisz, 1991).

180

181 There are two types of heterogeneous populations: those known as composite crosses (CC)  
182 or evolutionary populations (EP), or bulk populations, are obtained by mixing the F<sub>1</sub> or the F<sub>2</sub>  
183 seed obtained by crossing in all or several combinations a number of varieties. We will use

184 the term EP throughout the paper. Those known as mixtures are obtained by mixing the seed  
185 of different varieties. Mixtures, in turn, can be either static or dynamic (Wolfe and Ceccarelli,  
186 2020). Static mixtures are mixtures that are re-constituted from their original component  
187 varieties at the beginning of each growing season. Some farmers, however, prefer to grow  
188 mixtures from the seed harvested at the end the previous cropping season, thus converting  
189 them to dynamic mixtures. Because of natural inter-crossing within the dynamic mixtures,  
190 within a few seasons, following segregation, recombination and natural selection, they  
191 become populations.

## 192 **The science of evolutionary populations and mixtures**

193  
194 Research on heterogeneous populations started with the original paper of Harlan and Martini  
195 (1929) who proposed the composite cross method of plant breeding that they implemented  
196 by pooling an equal number of F<sub>2</sub> seeds obtained from 378 crosses among 28 superior barley  
197 cultivars representing all the major barley growing areas of the world. They called CCII this  
198 first EP. Harlan and Martini (1938) were also the first to demonstrate evolution by natural  
199 selection in dynamic mixtures, with few varieties becoming dominant in specific locations,  
200 while almost disappearing in others; they also showed how rapidly poorly adapted varieties  
201 disappeared everywhere.

202  
203 It was only in 1956 that the method was called evolutionary plant breeding and was suggested  
204 as a plant breeding method by Suneson (1956).

205  
206 Suneson (1956) suggested a “prolonged subjection [of the population] to competitive natural  
207 selection in the area of intended use”. This is what is represented as path 1 in Figure 1: the  
208 population is planted and harvested year after year using a portion of the seed harvested the  
209 previous year and hence let evolve under the sole force of natural selection. However, as the  
210 population evolves, farmers, alone or in partnership with scientists, can use the population  
211 as a source to impose artificial selection leading to either improved sub-populations or  
212 uniform varieties as shown in the various paths. In the figure we refer to spikes, but the  
213 scheme can be applied to pods (in the case of legumes), or to berries (in the case of tomatoes).

214  
215 One possible drawback is represented by correlations due to genetic linkages that may limit  
216 the development of new genetic combinations. However, as demonstrated by Allard and  
217 Hansche (1964), this can be overcome by the use of large population size. Indeed,  
218 evolutionary plant breeding allows working with much larger population size than  
219 conventional breeding. For example, Raggi et al. (2017) used a population size of 30.000  
220 individuals to propagate a barley EP to rule out genetic drift and sampling effects. However,  
221 EPs often evolve in farmers’ fields while grown as normal crops and therefore, most often as  
222 even larger populations. The issue of population size has been discussed also by Brumlop et  
223 al. (2019) but with regards to the need of avoiding genetic drift.

224  
225 One additional concern is selection for competitive ability which, for example in the case of  
226 cereals, translated into selection for tall plants (Goldringer et al., 2001; Knapp et al., 2020),  
227 thus shifting the population in a direction opposite to the reduction of plant height, which has  
228 been one of the main objectives of modern plant breeding (Denison et al., 2003). Indeed,  
229 under organic no-herbicide conditions, a relatively tall crop may be of advantage (Knapp et

230 al., 2020) because of its ability to suppress the development of weeds as often informally  
231 reported by the several Italian farmers currently growing these EPs as commercial crops.

232  
233 When artificial selection is applied, molecular tools ranging from marker assisted selection to  
234 high-throughput phenotyping and to genomic selection can be incorporated in the process.  
235 Goldringer et al. (2001), Rhoné et al. (2010) and Raggi et al. (2016) are examples of the  
236 potential of EPs to generate interdisciplinary research ranging from climatology, evolutionary  
237 science, plant protection, genetics, seed quality etc.

238  
239 So far there has been a large body of research demonstrating that natural selection in EPs and  
240 mixtures is effective in changing phenology, improving yield, yield stability and host plant  
241 resistance to pathogens.

242  
243 Most of this research has been reviewed during the past 15 years. Phillips and Wolfe (2005)  
244 reviewed the evidence that EPs may provide useful genetic material in agricultural systems  
245 with dynamic selection pressures between and within years, with advantages particularly in  
246 low input systems. Dawson et al. (2008) suggested merging participatory and evolutionary  
247 plant breeding to maximize the efficiency of decentralized selection as a way to address the  
248 need of farmers in heterogeneous environments.

249  
250 A more recent review (Döring et al., 2011) underlines the importance of the resilience of EPs  
251 as one of their most important attributes to cope with the environmental unpredictability.  
252 Interestingly, in this review the authors call for a change in legislation to allow the practical  
253 use of EPs, anticipating the “Commission Implementing Decision” that the EU Commission  
254 issued on March 18 2014 that we will discuss later in the paper.

255  
256 Most research on EPs and mixtures has been conducted on small grains, notably the self-  
257 pollinated wheat and barley and to a less extent rice, likely because these were the crops of  
258 interest to those scientists addressing the issue of diversity in plant breeding. However, there  
259 are good reasons to believe that if a technique relying on recombination and selection works  
260 on a self-pollinated crop, it should work even better on cross-pollinated crops. In fact, in one  
261 of the most recent meta-analysis (Reiss and Drinkwater, 2018), the largest positive effect on  
262 relative yield was found in the 125 studies of corn.

263  
264 *Evolutionary populations and phenology*

265 One of the first demonstrations that EPs can evolve adapting their phenology has been  
266 obtained with rice. A random sample of the F<sub>2</sub> deriving from a cross between a late and an  
267 early heading rice variety was sent to 20 rice research stations scattered all over Japan and  
268 was grown as a bulk from F<sub>2</sub> to F<sub>5</sub> generations. The average heading time of the populations  
269 grown in northern locations shifted gradually towards earliness, while in those grown in more  
270 southern locations shifted gradually towards lateness (Allard and Hansche, 1964).

271  
272 Similar results were obtained with an EP of bread wheat developed by crossing 16 parents.  
273 The population was grown for 10 generations in seven locations all over France. After 10  
274 generations, the population that evolved in northern France was significantly later heading  
275 than the population that evolved in Southern France with a much warmer climate (Goldringer

276 et al., 2006). The response to selection was found associated with genes with a strong effect  
277 on flowering time (Rhoné et al., 2010).

278

### 279 *Evolutionary populations and yield*

280 Suneson (1956) was one of the first to show the ability of EPs (four different barley CCs grown  
281 in California) to evolve to produce higher yields than the widely grown variety Atlas 46 (a  
282 parent of all the CCs). Another interesting feature of this experiment was the demonstration  
283 of the potential of using artificial line-selection within an evolving EP: while after 12  
284 generations, not a single line selected from the EPs yielded more than Atlas 46, after 20  
285 generations a line out-yielded Atlas 46 by 37% and, after 24 generations, three top selections  
286 out-yielded Atlas 46 by 56%.

287

288 One of the classical experiments throwing lights not only on the effects of natural selection  
289 on grain yield but also on how they can vary with environment and type of heterogeneous  
290 populations is the one of Patel et al. (1987). This experiment showed that a) natural selection  
291 reduced the frequency of low yielding genotypes and increased mean yield; b) this effect was  
292 higher in the EPs than in the mixtures; and c) natural selection improved yield when the  
293 method was used within the intended region of adaptation. This fits with the original  
294 description of the core features of evolutionary breeding by Suneson (1956) as “a broadly  
295 diversified germplasm and a prolonged subjection of the mass of the progeny to competitive  
296 natural selection in the area of contemplated use”.

297

298 Experiments showing the evolution of both EPs and mixtures towards higher yields were also  
299 reported by Rasmusson et al. (1967), Soliman and Allard (1991) and more recently by Raggi  
300 et al. (2017) and by Bocci et al. (2020). Murphy et al. (2005) reviewed the yield advantages of  
301 EPs and mixtures underlining that the advantage is evident under drought but tend to  
302 disappear under more favourable conditions. The dynamics of yield evolution in evolutionary  
303 populations has been described in detail by Döring et al. (2011). Brumlop et al. (2017) showed  
304 that EPs are comparable with modern cultivars in yielding ability under organic conditions.

### 305 *Evolutionary populations and yield stability*

306 The buffering ability of heterogeneous populations is expected to be higher than that of  
307 uniform material. One of the most convincing proof that this is indeed the case, comes from  
308 an experiment conducted in 1961 (Allard, 1961), which showed how the stability of EPs is  
309 greater than the stability of mixtures, which in turn is higher than that of pure lines.

310 A meta-analysis of 91 studies and more than 3600 observations concluded that cultivar  
311 mixtures are a viable strategy to increase diversity in agroecosystems, increasing yield and  
312 yield stability as well as disease resistance (Reiss and Drinkwater, 2018).

313

314 The genetic background affects yield stability of EPs: those with a wide genetic basis have a  
315 better dynamic stability while those with a narrow genetic basis tend to have a better static  
316 stability (Weedon and Finckh, 2019). Döring et al. (2015) found an advantage of EPs and  
317 mixtures over the mean of their components in terms of cultivar superiority. Raggi et al.  
318 (2017) identified barley EPs combining high yield and stability across years and locations.

319

320 *Evolutionary populations and pest resistance*

321 Evolution of resistance to pests and in particular to diseases, has been the most widely  
322 documented advantage of EPs and mixtures. Simmonds (1962) reported several cases of  
323 reduced severity and incidence of diseases in mixtures of crops. In a review of mixture  
324 cultivation in both developing and developed countries, Smithson and Lenné (1996)  
325 suggested more durable resistance to insect and diseases as one of the perceived advantages  
326 of mixtures over their components and possibly one of the reasons for larger and more stable  
327 yields. The most important mechanism to explain the reduction in severity of diseases in  
328 mixtures is the dilution of inoculum that occurs due to the distance between plants of the  
329 same genotype (Mundt, 2002). There is also a large variation in the efficacy of mixtures in  
330 reducing disease incidence.

331 A larger than expected number of families resistant to more than one race and a high  
332 proportion of segregating families even after several generations of selfing suggested a higher  
333 than expected outcrossing rate or a larger advantage of heterozygotes (Jackson et al., 1982).  
334 The frequency of resistance alleles that protected against the most damaging pathotypes  
335 increases sharply in the host populations, indicating that the evolutionary processes that take  
336 place in genetically variable populations propagated under conditions of cultivation can be  
337 highly effective in increasing the frequency of desirable alleles and useful multilocus  
338 genotypes (Allard, 1990).

339 The evolution of resistance to powdery mildew in three subpopulations of the same  
340 Composite Cross showed that 1) there have been large directional shifts towards increased  
341 resistance; 2) there are differences between the three populations in the rate of increase of  
342 the frequency of resistant plants and c) there was a strong increase in the frequency of  
343 resistant plants at almost the same time in the three populations (Ibrahim and Barret, 1991).

344 Evolution of resistance to powdery mildew was found in populations of bread wheat with the  
345 highest level of adult resistance developed when the populations evolved in sites where  
346 powdery mildew pressure is known to be high (Paillard et al., 2000).

347 More recently, agricultural diversity measured by the richness in variety diversity has been  
348 shown to be associated with a decrease in the average damage level in banana, plantain and  
349 bean in Uganda (Mulumba et al., 2012).

350

351 The advantage of mixture in reducing the incidence and severity of fungal diseases has been  
352 demonstrated in several studies (McDonald et al., 1988; Finckh and Mundt, 1992; Finckh et  
353 al., 2000; Finckh and Wolfe, 2006).

354

355 *The speed of evolution*

356

357 One of the advantages of EPs is its ability to evolve and adapt to new environments. One  
358 questions frequently asked by farmers interested in starting the cultivation of EPs is how  
359 quickly they adapt to a new environment. In selection theory terms the answer to this  
360 question depends on the magnitude of genetic diversity available in the population for traits  
361 associated with adaptation, the heritability of those traits and the magnitude and consistency  
362 of directional selection (Kingsolver et al., 2001). In bread wheat we found evidence of

363 divergent selection after 5 years of evolution in contrasting locations (Bocci et al., 2020).  
364 Goldringer et al. (2006) found that after 10 years populations diverged significantly for  
365 days to maturity along a north-south gradient in France.  
366

### 367 **The use of evolutionary populations and mixtures**

368

369 Despite this very rich body of research, and until recently, there has been only one example  
370 of large scale use of the advantages of heterogeneous populations, and this refers only to  
371 mixtures and not to populations. During the 1970's in the UK, static mixtures proved highly  
372 successful in slowing development of diseases, particularly powdery mildew. This approach  
373 was taken to the former German Democratic Republic where it was built up to cover an area  
374 of some 350,000 hectares, effectively the whole of the spring barley area, leading to a massive  
375 reduction of the percentage of fields affected by severe mildew epidemics from 50 to 10%  
376 and a threefold reduction of the percentage of fields sprayed with fungicides (Wolfe et al.,  
377 1992).

378

379 One possible explanation for the very limited practical exploitation of the evidence of the  
380 multiple benefits of cultivating heterogeneous material is that such material does not fit with  
381 the requirement for variety registration. Other reasons that make uniformity desirable is the  
382 uniform response of a crop to agronomic treatments and uniform response to processing and  
383 cocking.

384

385 In 2008 and in 2009, while working at the International Center for Agricultural Research in the  
386 Dry Areas (ICARDA), then in Aleppo, Syria, we made three EPs by mixing 2000, 700 and 1600  
387 segregating populations of bread wheat, durum wheat and barley, respectively, derived from  
388 crosses between widely diverse parents from all over the world, including old local varieties  
389 and, in the case of barley, the wild progenitor of the crop. The barley EP was sent to Syria,  
390 Algeria, Eritrea, Jordan and Iran, while the two wheat EPs were sent to Syria, Morocco, Algeria  
391 and Jordan. We will refer to these three EPs as "ICARDA EPs".

392

393 In Iran, the ICARDA barley EPs was used as an inspiration to constitute a bread wheat EP made  
394 with local breeding material. This EP eventually spread in several provinces as farmers and  
395 bakers were pleased with the bread made from the EP, which was marketed in local artisanal  
396 bakeries (Rahmanian et al., 2014).

397

398 By the time it was found that the bread obtained from the bread wheat EP was a commercial  
399 success in Iran, the three ICARDA EPs were already spreading in Italy. In fact, beginning in  
400 2010, there has been in Europe a growing interest in supporting projects with a focus on  
401 diversity, and it was within the framework of one of these European projects, that the three  
402 populations were introduced in Italy in 2010.

403

404 In 2014, perhaps acknowledging that some outputs of the projects the European Union (EU)  
405 was financing could be heterogeneous material, which did not have a legal status, the EU  
406 Commission issued on March 18 2014, a "Commission Implementing Decision". With such a  
407 decision, the EU Commission organized a "temporary experiment at Union level for the  
408 purpose of assessing whether the production, with a view to marketing, and marketing, under  
409 certain conditions, of seed from populations belonging to the species Oats, Wheat, Barley and

410 Corn, may constitute an improved alternative to the exclusion of the marketing of seed not  
411 complying with the requirements.....”, which made it possible, in Europe, to market  
412 experimentally heterogeneous materials of oats, barley, maize and wheat up to 29 February  
413 2021, after their approval by the designated authors (Petitti et al., 2018).

414

415 This had made possible the official certification and authorization to sell and buy seed of the  
416 populations, but most importantly for farmers, to become the producers of their own seed  
417 throughout the years. The possibility of using heterogeneous material, hence populations and  
418 mixtures, has been extended to all crops with the new EU regulations on organic agriculture  
419 effective on January 1<sup>st</sup>, 2022.

420

421 By 2017, the three ICARDA EPs had spread widely in Italy (Figure 2), particularly the bread  
422 wheat EP, as several artisanal bakeries confirmed the quality and the consumer acceptance  
423 of the bread, which had been found earlier in Iran. The two regions where the EP was first  
424 planted (Sicily and Tuscany) are those where the two EPs were cultivated continuously on the  
425 same farms, using part of the seed harvested the previous year.

426

427 After a slow rate of diffusion during the first four years, the diffusion accelerated and the  
428 major increase took place after 2017. In that year the sale of the seed of the two populations  
429 which evolved continuously in Sicily and Tuscany was authorized based on the EU Commission  
430 Implementing Decision mentioned earlier. The possibility of legally sell and buy the seed  
431 boosted the diffusion which reached 16 regions out of 20 by the end of 2018.

432

433 The two farms where the populations evolved continuously since 2010, differed in rainfall and  
434 temperature with Sicily being systematically drier and warmer than the farm in Tuscany  
435 (Petitti et al., 2018). The two populations, which evolved continuously in the two farms  
436 offered therefore the possibility of studying whether there was evidence of any divergent  
437 selection. This was done within the framework of one of the EU project, which started in 2014,  
438 by comparing the two populations together with other genetic material in four contrasting  
439 locations including the two farms during four cropping seasons (from 2014/2015 till  
440 2017/2018). The experiment showed that the EP became specifically adapted to the region  
441 where they were cultivated in which they also exhibited a high temporal stability (Bocci et al.,  
442 2020). One example of divergent evolution is shown in Figure 3 where on the left are two  
443 hectares of the same original population after 10 years of evolution in Sicily (south Italy) and  
444 on the right the same population after 10 years of evolution in Tuscany (Central Italy). A four  
445 years experiment showed that that the same original EP grown continuously in different  
446 locations evolved into locally adapted populations with significant differences in important  
447 quantitative traits such as grain yield and plant height (Bocci et al., 2020).

448

449 The experiment continues by addressing the issue of seed circulation and seed sharing among  
450 farmers to define the area of adaptation of each population. The strategy we follow consists  
451 in recommending the exchange of a sufficient *number* (rather than quantity) of seed to allow  
452 the population to adapt to a new environment. Farmers and Institutions should monitor these  
453 exchanges.

454

455 This is a particularly important issue because free seed circulation can easily cause  
456 uncontrolled spreading of seed borne diseases. This can be avoided not only with training of  
457 farmers but also with the involvement of small seed companies, which assist farmers in  
458 producing and maintain the seed free of seed-borne diseases and of impurities.  
459

## 460 **Conclusions**

461  
462 There are a number of points to be made in relation to using heterogeneous material, either  
463 populations or mixtures, as farmers' main crops. The first is that they represent a dynamic  
464 response to the complexity of climate change not only in its physical characteristics  
465 (temperature and rainfall) but also in its biotic aspects and in its location specificity. EPs and  
466 mixtures, with their capacity to evolve in response to both biotic and abiotic stresses, as long  
467 as they maintain sufficient genetic diversity, appears to be the quickest, cost-effective and  
468 evolving solution to such a complex and evolving problem with the additional advantage of  
469 increasing yield gains resulting from a combination of natural and artificial selection and  
470 genetic recombination.

471  
472 The second is their ability to control pests, which makes them particularly suited to organic  
473 systems, representing an ecological solution to pest control – because they do not create a  
474 selection pressure favouring the evolution of resistance. This will fill an important gap  
475 represented by the scarce availability of varieties specifically adapted to organic conditions.  
476

477 The third, which is a consequence of the first two, is that they represent at the same time a  
478 mitigation and an adaptation strategy. A mitigation strategy because they reduce  
479 considerably the use of chemical inputs, and an adaptation strategy associated with their  
480 ability to continuously evolve to adapt to new combinations of biotic and abiotic stresses.

481  
482 Finally, as they evolve, they generate a continuous flow of novel cultivated agro biodiversity  
483 even within the same crop, which will be beneficial in increasing diet diversity and  
484 ultimately human health.

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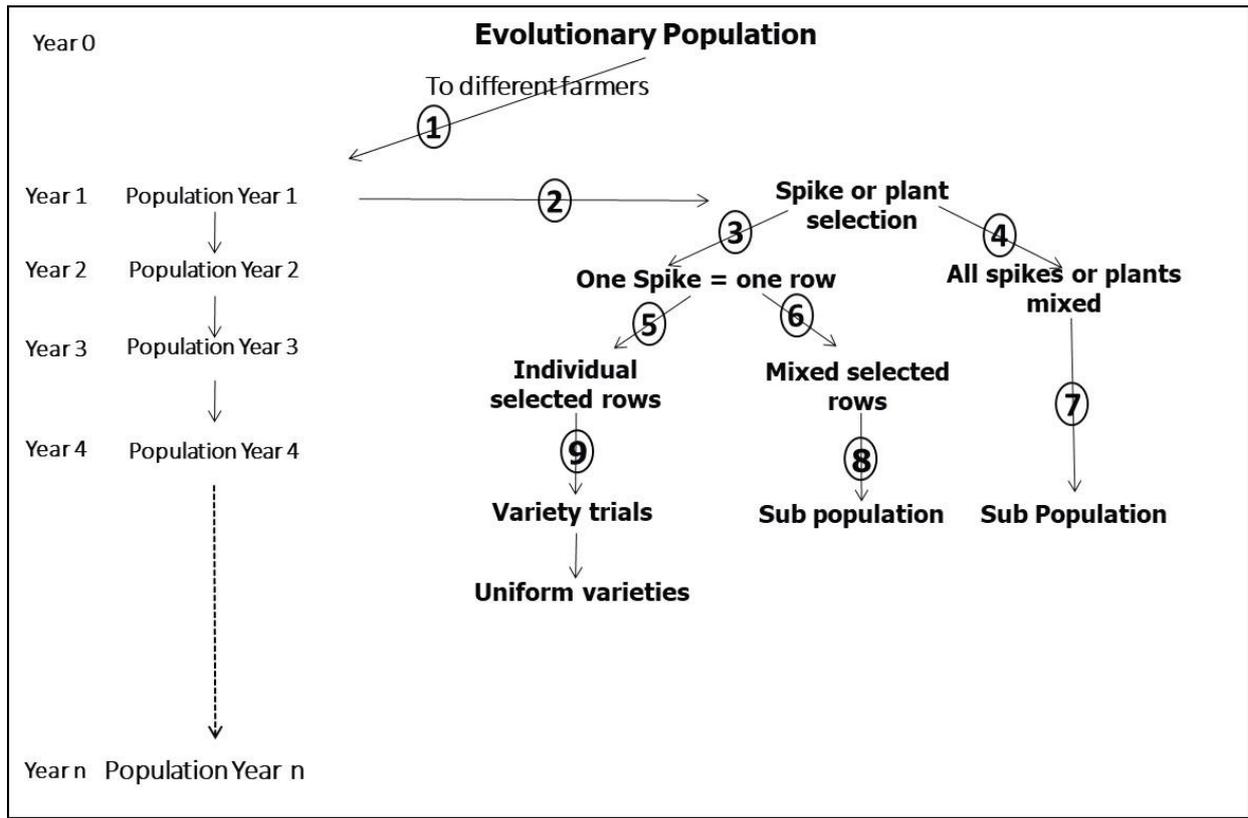
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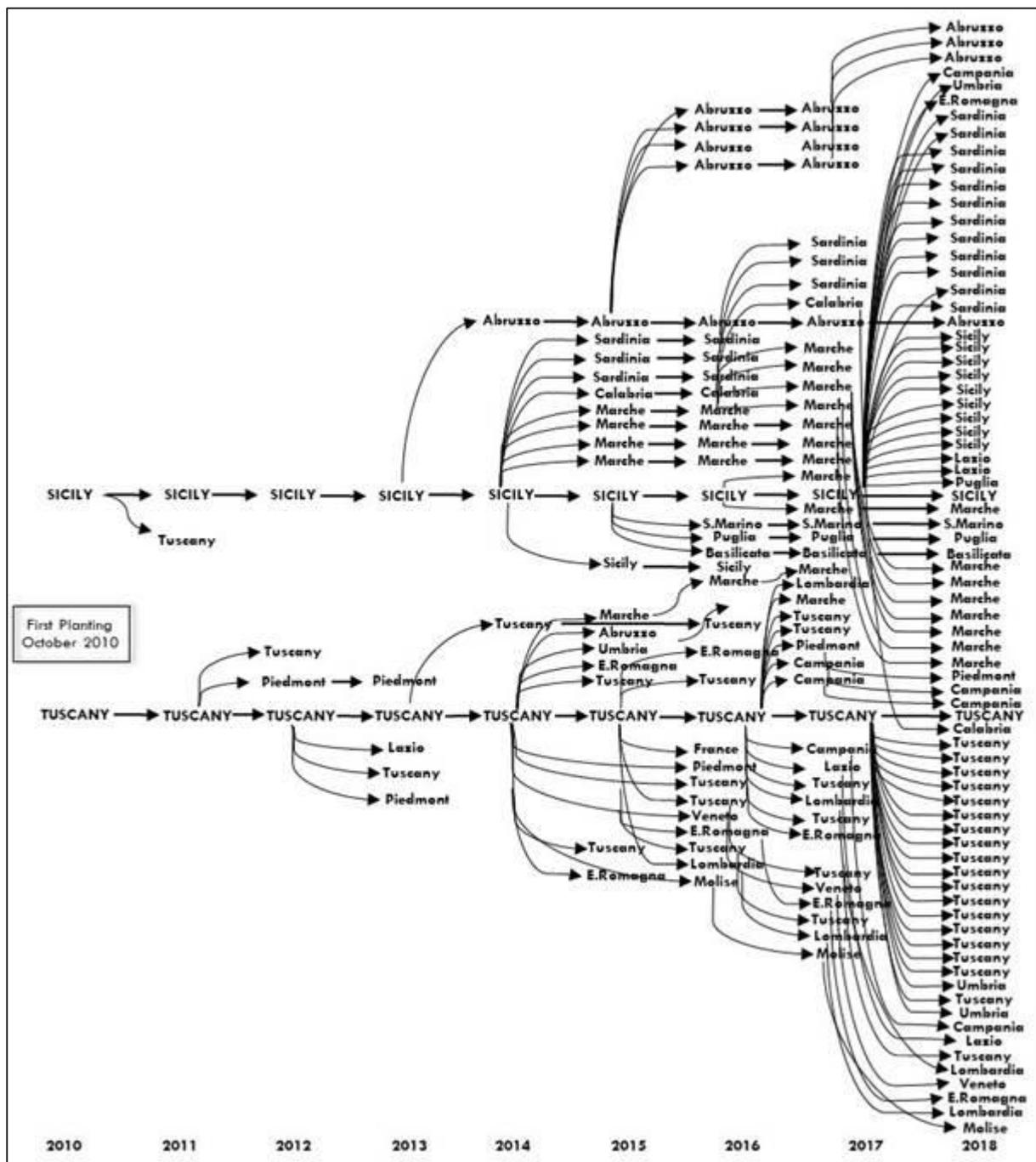
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2

3 Figure 1. An evolutionary population is distributed to different farmers and is left evolving  
 4 independently in each farmer's field (path 1). It can also be subjected to selection (path 2)  
 5 leading to either improved sub-populations (paths 4-7 or 3-6-8) or uniform varieties (path 3-  
 6 5-9).

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Figure 2. Diffusion throughout Italy of the ICARDA bread wheat EP made in Syria and planted in Sicily and Tuscany, for the first time in 2010.



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13 Figure 3. The ICARDA evolutionary bread wheat population after 10 years evolution in Sicily  
14 (left) and the same population after 10 years evolution in Tuscany (right) grown in Marche,  
15 in 2020 (courtesy of Pierluigi Valenti).