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► To cite this version:

Lucie Mahaut, Samuel Pironon, Jean-Yves Barnagaud, François Bretagnolle, Colin K. Khoury, et al.. Matches and mismatches between the global distribution of major food crops and climate suitability.. Proceedings of the Royal Society B: Biological Sciences, 2022, 289 (1983), pp.20221542. 10.1098/rspb.2022.1542 . hal-03833716

HAL Id: hal-03833716

<https://u-bourgogne.hal.science/hal-03833716v1>

Submitted on 21 Nov 2023

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1 **Matches and mismatches between the global distribution of major food crops and**
2 **climate suitability**

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23

24 **Abstract**

25 Over the course of history, humans have moved crops from their regions of origin to new
26 locations across the world. The social, cultural, and economic drivers of these movements
27 have generated differences not only between current distributions of crops and their climatic
28 origins, but also between crop distributions and climate suitability for their production.
29 Although these mismatches are particularly important to inform agricultural strategies on
30 climate change adaptation, they have, to date, not been quantified consistently at the global
31 level. Here, we show that the relationships between the distributions of twelve major food
32 crops and climate suitability for their yields display strong variation globally. After
33 investigating the role of biophysical, socio-economic and historical factors, we report that
34 high-income world regions display a better match between crop distribution and climate
35 suitability. In addition, although crops are farmed predominantly in the same climatic range as
36 their wild progenitors, climate suitability is not necessarily higher there, a pattern that reflects
37 the legacy of domestication history on current crop distribution. Our results reveal how far the
38 global distribution of major crops diverges from their climatic optima and call for greater
39 consideration of the multiple dimensions of the crop socio-ecological niche in climate change
40 adaptive strategies.

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48 Introduction

49 Ensuring food security while adapting to climate change and preserving the environment is a
50 central challenge for humanity [1,2]. Adaptive strategies in agriculture notably include the
51 migration of cropland to areas that will be more suitable for agricultural production according
52 to different scenarios of climate change (e.g. [3–6] and the selection of new species and
53 varieties better adapted to future climatic regimes (e.g., [7–9]). These strategies should lead to
54 a better adjustment of the distribution and identity of crops to climatic conditions which could
55 in turn reduce the need for agricultural inputs [10] and improve the resilience of agricultural
56 systems to climate change [11]. However, apart from limited evidence of crop presence in
57 areas of low climatic suitability (e.g., [12]), the relationships between the current distribution
58 of crops and the suitability of climate for their growth have been largely overlooked, leaving
59 unknown the potential for improving matches between crop distribution and climate.

60 Recent shifts in where crops are grown at both global and regional scales suggest that human
61 societies modulate the distribution of cropland areas to buffer the adverse effects of climate
62 change on crop yields [13,14]. Conversely, environmental and agricultural factors that
63 directly affect crop yields, such as soil characteristics (e.g., [3]), crop pests (e.g. [15]) or the
64 use of agricultural inputs (e.g. irrigation and fertilisation, [16,17]) can decouple the
65 distribution of crops from the suitability of climate for their growth. The fact that farmers
66 adapt the crops they grow according to complex socioeconomic factors can also lead to strong
67 inconsistencies in the distribution of crops with respect to climate [18]. Deciphering the role
68 of multiple biophysical, agricultural and socio-economic factors in shaping the relationships
69 between crop distribution and climate suitability is therefore a crucial step in assessing the
70 potential levers that human societies have to reduce crop distribution-climate suitability
71 mismatches.

72 In addition, crops have undergone substantial geographical expansion over millennia, from
73 their respective centres of origin to the rest of the world [19]. Such historical changes in the
74 geographical distributions of crops are well documented globally (e.g. [20]). However, the
75 extent to which climatic conditions in areas where crops have been introduced (i.e. the
76 introduced range) differs from that in the crop's centres of origin (i.e. the native range)
77 remains largely unknown. This is particularly problematic given that sites of crop origin host
78 much of the associated agrobiodiversity, including numerous crop wild progenitors and
79 relatives as well as traditional farmer varieties [21,22]. As such, these centres are perceived as
80 reservoirs from which to draw new genetic resources to improve crop resilience and
81 adaptation to future climatic conditions [23,24]. However, if historical globalization, together
82 with innovations in agricultural practices, have shifted the climatic niche of crops (i.e. the
83 range of climates where a crop is grown) from the one of their wild progenitors, domesticated
84 plants may no longer share the same climatic optima as their wild progenitors.

85 In this study, we use a global dataset of the geographic distribution of crop areas and yields
86 [25] to characterise the current climatic niche of twelve major food crops and investigate how
87 the distribution of their harvested areas co-vary with climate suitability for their yields (Figure
88 1). Using multiple regressions, we quantify the marginal effects of climate on crop yields
89 while controlling for the role of multiple soil, topography, agricultural inputs and socio-
90 economic factors to determine climate suitability for the yield of each crop. Then, we build a
91 mismatch index to analyse the relationship between harvested areas and climate suitability
92 and to examine the role of non-climatic factors in producing these (mis)matches. Finally, we
93 quantify shifts between the native and the introduced climatic range of crops and test whether
94 harvested areas, climate suitability and crop areas-climate suitability mismatch differ across
95 the two ranges.

97 **Material and Methods**

98 *Crop data set*

99 We tested the relationship between the distribution of harvested areas and climate suitability
100 for barley, cassava, groundnut, maize, potato, rapeseed, rice, sorghum, soybean, sugarbeet,
101 sunflower and wheat (Supplementary Table S1). The 12 crops were chosen because they are
102 widely cultivated worldwide, providing more than 70% of calorie intake globally [16], and
103 because agronomic and wild progenitor data are available. For each of these crops, the global
104 distribution of harvested area and yield was extracted from public data sources that have been
105 created by combining national-, state-, and county-level census statistics with a global data set
106 of croplands for the 1997-2003 period at a 5 arc-minute (~10km) resolution [25]. We
107 controlled for the influence of the availability of agricultural land [26] by computing the
108 fraction of available cropland allocated to each crop's growth in each grid cell. For each crop,
109 harvested areas is therefore expressed in terms of percentage of available cropland.

110 *Crop progenitors data set*

111 We used native occurrences of each crop's wild progenitors to delineate the climatic range of
112 the centre of origin of each crop (i.e. native climatic range). We identified 23 progenitors of
113 the 12 crops using published literature (Supplementary Table S1; [27]). Wheat includes
114 *Triticum aestivum* and *Triticum durum*, which are the two main wheat species cultivated
115 worldwide. Therefore, we considered the progenitors of both wheats. There are also two
116 species of cultivated rice, *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice).
117 However, because *O. sativa* is by far the main cultivated species of rice, we only considered
118 the wild progenitor of the Asian rice in our analysis. We extracted progenitor occurrence
119 records from five global and two regional databases. We used the BIEN and rgbif packages in
120 R to download global occurrence records from the Botanical Information and Ecology

121 Network [28] and the Global Biodiversity Information Facility databases, respectively. In
122 addition, we extracted global occurrences of crop wild progenitors from “A global database
123 for the distributions of crop wild relatives”, the BioTIME database [29] and GENESYS
124 (<https://www.genesys-pgr.org/>). We downloaded further regional occurrences using the
125 RAINBIO database, which contains records for Sub-Saharan African vascular plants [30] and
126 speciesLink, a national database for plant and animal occurrences in Brazil
127 (<https://splink.cria.org.br/>). Because occurrence data are often inaccurate [31], we removed
128 records that were documented before 1950. Further, we used the *CoordinateCleaner* package
129 in R [32] to remove occurrence records found within a 1 km radius of country and capital
130 centroids, with equal longitude and latitude coordinates, or assigned to institutional locations
131 such as botanical gardens, herbaria or the GBIF Headquarters. We also removed records with
132 high coordinate uncertainty (over 10 km), cultivated records (e.g. breeding/research material,
133 advanced/improved cultivar, GMO and those found in markets or shops, institutes/research
134 stations and genebanks and from seed companies), and records located in the sea/oceans. For
135 progenitors with the same species name as their crop, we only extracted records confirmed as
136 wild and ignored any record with an unknown cultivation status. We also removed records
137 outside of the wild species native range to ensure no introduced or cultivated records were
138 included. Native ranges were identified at administrative levels according to the USDA
139 Agricultural Research Service, Germplasm Resources Information Network. After filtering,
140 8715 occurrence points remained for 23 wild progenitor species of the 12 crops
141 (Supplementary Table S1).

142 *Climatic, soil, topographic, agronomic and socio-economic data set*

143 We collected eight bioclimatic variables from the CHELSA database [33] at a 30 arc-seconds
144 (~1 kilometre) resolution that corresponded to the mean of annual data for the years 1979–
145 2013 (Supplementary Table S2). This includes mean annual temperature (BIO1), temperature

146 seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum
147 temperature of the coldest month (BIO6), annual sum of precipitation (BIO12), precipitation
148 of the wettest (BIO13) and driest (BIO14) months, and precipitation seasonality (BIO15).
149 These eight variables were selected to capture mean, seasonal and extreme (potentially
150 limiting) temperature and precipitation regimes.

151 We estimated the role of agricultural factors by gathering the amount of nutrients applied on
152 individual crops (hereafter fertilisation in ton/ha) and the percentage of land area equipped for
153 irrigation (hereafter irrigation). We used the Nutrient-Application-For-Major-Crops maps [17]
154 that compiled national and subnational data of mineral fertilizers, manure, and atmospheric
155 deposition with detailed maps of crop areas to produce crop-specific nutrient application rate
156 (tons per ha) at a 5 arc-minute resolution (Supplementary Table S2). These data represent
157 mean annual values for the 1997-2003 period. We downloaded the Global Map of Irrigation
158 Areas from the FAO AquaStat portal that represents the percentage of area equipped for
159 irrigation circa 2005 as a 5 arc-minute raster (Supplementary Table S2). Soil pH, organic
160 content and maximum water holding capacity were used to define soil conditions. These data
161 were collected from the ISRIC World Soil information portal at a 250m resolution
162 (Supplementary Table S2). Topography was characterized by terrain slope from the EarthEnv
163 portal at a 1km resolution (Supplementary Table S2). Finally, socio-economic factors were
164 approximated by the Human Development Index (HDI) and Gross Domestic Product (GDP).
165 HDI is a composite index of average achievement in three key dimensions of human
166 development (a long and healthy life, being knowledgeable and having a decent standard of
167 living [34]). We downloaded these data from the Gridded global datasets for Gross Domestic
168 Product and Human Development Index over 1990-2015 at a 5 arc-min resolution
169 (Supplementary Table S2). For each index, we computed the mean of 1990-2015 annual data.
170 Climate, soil and topography layers were all upscaled to a 5 arc-minutes resolution using the

171 *aggregate* function from the *raster* package [35] in the R software to match the resolution of
172 the crop dataset.

173 *Data analyses*

174 We used a PCA to characterize the main axes of variation of the climatic conditions of the
175 terrestrial surfaces occupied by cropland globally (step 1 in Figure 1). We used the global
176 distribution of cropland areas at a 5 arc-minute resolution [26] and selected pixels with
177 cropland cover >0. We extracted the values of the bioclimatic variables previously described
178 for each of these pixels and summarized their variation according to the two first principal
179 component axes (Dim. 1 and Dim. 2, respectively). Dim.1 explained 51.1% of the variance
180 and principally reflected the variation in temperature with increasing values corresponding to
181 increasing mean annual temperatures and decreasing seasonality in
182 temperature (Supplementary Figure 1). Dim.2 explained 26.8% of the variance. It was related
183 to precipitation, with increasing values corresponding to increasing seasonality in
184 precipitation and decreasing total annual precipitation (Supplementary Figure S1). The PCA
185 was performed using the *factoMineR* R package (Husson et al., 2020). Hereafter we use
186 “climatic niche” to refer to the portion of the climatic space made by Dim.1 and Dim.2 that is
187 occupied by a crop (i.e. the range of climatic conditions where a crop is found). Dim.1 and
188 Dim.2 are identical among crops and thus comparable.

189 We then projected harvested areas (in % of available cropland) and yields within the climatic
190 niche of each crop (step 2 in Figure 1). We used the function *rasterize* from the *raster* R
191 library [35] to build a 150 x 150 pixels grid defined by Dim.1 and Dim.2. For each pixel of
192 this climatic grid, we computed the average values of the fraction of cropland allocated to
193 each crop and average crop yield. This grid size was chosen so that each of these 150x150
194 pixels corresponded on average to 25 pixels of the geographical distribution of crops (and

195 thus to 25 measures of yields and harvested areas). We smoothed harvested areas values using
196 a loess regression to identify hot- and cold-spots of cultivation (Supplementary Figure S2).
197 Furthermore, we assessed climate suitability by computing the marginal effects of climate (i.e.
198 Dim.1 and Dim.2) on the yields of each crop while accounting for soil (i.e. soil organic
199 content, soil pH, soil water capacity), topography (i.e. slope), agricultural inputs (i.e.
200 fertilisation rate and irrigation) and socio-economics (i.e. gross domestic product and human
201 development index) factors. For each 150 x 150 pixel of the climatic grid and each crop, we
202 calculated the average values of these non-climatic factors. We used linear models and the
203 function *predict* from the *stats* R library to quantify the marginal effects of Dim. 1 and Dim. 2
204 (as second order polynomials) while controlling for the effects of non-climatic factors.
205 Climate suitability thus corresponds to the expected yields given the climate, all other things
206 being equal.

207 Third, we quantified the extent to which the distribution of harvested areas matched climate
208 suitability for the yields of each crop (step 3 in Figure 1). We calculated Spearman correlation
209 between smoothed values of harvested areas and climate suitability. For each crop, we
210 randomly sampled 1,000 pixels of the 150 x 150 pixels climatic grid, computed Spearman
211 correlation index and repeated the process 1,000 times to calculate 95% confidence intervals
212 of the correlation index.

213 Then, we analysed variation in the relationships between harvested areas and climate
214 suitability within the climatic niche of each crop by computing a local mismatch index (step 4
215 in Figure 1). We computed for each crop and for each pixel of the climatic niche the centiles
216 of the smoothed values of harvested areas and the centiles of climate suitability. We
217 calculated the log-ratio between climate suitability centiles and crop areas centiles. The
218 resulting mismatch index varied between $\log(0.01)$ (climate suitability value belonging to the
219 1st centile/harvested areas value belonging to the 100th centile) and $\log(100)$ (climate

220 suitability value belonging to the 100th centile/ harvested areas value belonging to the 1st
221 centile). When equal to zero, this index indicates a balanced situation (i.e. absence of
222 mismatch) between harvested areas and climate suitability. Positive values describe situations
223 where climate suitability is disproportionately large with respect to the portion of cropland
224 allocated to a crop while negative values indicate situations where crop harvested areas are
225 disproportionately large with respect to climate suitability.

226 We examined the role of agricultural inputs, soil conditions, topography and socio-economic
227 factors in generating matches and mismatches between harvested areas and climate suitability.
228 We used linear models to quantify the effects of each of these factors on the absolute values
229 of the mismatch index of each crop. Using the absolute value of the crop area-climate
230 suitability mismatch index allowed differentiating factors that are associated with a low
231 mismatch from the ones associated with a high mismatch, whether the mismatch was in the
232 direction of harvested areas or climate suitability. All covariates were scaled before analysis
233 so that estimated coefficients are comparable.

234 Finally, we compared the climatic conditions in areas where crops have been introduced (i.e.
235 introduced range) to those where the wild progenitors live (i.e. native range) to investigate
236 how agricultural expansion could affect the relationships between current crop areas and
237 climate suitability. We defined the native climatic range of each crop by drawing convex
238 polygons around occurrence points of its wild progenitors (see step 2 in Figure 1; [21]).
239 Because species occurrence data is prone to geo-referencing errors and because the use of
240 convex polygons is sensitive to outliers, we removed crop wild relative occurrence points
241 with Mahalanobis distance to the centroid of the native climatic range ≥ 10 . The introduced
242 climatic range of a crop corresponded to the portion of its climatic niche occupied by the crop
243 but outside its native range. For each crop, we compared mismatch index, crop distribution

244 and climate suitability between the two climatic ranges through an analysis of variance. All
245 analyses were conducted using R version 4.0.3.

246 **Results**

247 *Relationships between harvested areas and climate suitability*

248 The models used to quantify climate suitability explained between 35% (groundnut) and 73%
249 (maize) of the variance of crop yields (Supplementary Table S3). We found significant
250 positive correlations between the distribution of harvested areas and climate suitability for
251 eight of the 12 major crops under study (barley, groundnut, maize, rapeseed, soybean,
252 sugarbeet, sunflower and wheat) (Figure 2). The other four crops - cassava, potato, rice and
253 sorghum - displayed significant, negative harvested areas-climate suitability correlations
254 (Figure 2). The magnitude of positive correlations varied between 0.2 (maize) and 0.9 (barley)
255 while negative correlations varied between -0.25 (sorghum) and -0.5 (cassava) (Figure 2).

256 *Local (mis)matches between harvested areas and climate suitability*

257 The analysis of the mismatch index revealed strong variation in the relationships between
258 harvested areas and climate suitability for crop yields (Figure 3). This index allowed the
259 identification of climatic zones where crop areas (in % of available cropland) were
260 disproportionately large with respect to climate suitability (blue zones in Figure 3), zones
261 where climate suitability was disproportionately large with respect to harvested areas (red
262 zones in Figure 3) and zones with balanced harvested areas and climate suitability (beige
263 zones in Figure 3). Imbalanced zones were particularly marked for cassava, potato, rice and
264 sorghum (i.e. crops displaying negative harvested areas - climate suitability correlations). The
265 harvested areas of cassava, rice and sorghum was disproportionally large with respect to
266 climate suitability in the warmest climates with strong precipitation seasonality while zones
267 with lower harvested areas with respect to climate suitability were concentrated in colder

268 climates with strong temperature seasonality (Figure 3). The mismatch index of barley (i.e.
269 the crop showing the strongest positive correlation between harvested areas and climate
270 suitability) showed the lowest variation, situations with balanced harvested areas and climate
271 suitability predominating (Figure 3).

272 *Drivers of harvested areas - climate suitability (mis)matches*

273 Overall, soil conditions, topography, agricultural inputs and socio-economic factors together
274 explained between 16% (groundnut) and 43% (wheat) of the variation in the absolute value of
275 the mismatch index (Figure 4). For all crops except groundnut, cells with higher Human
276 Development Index (HDI) and/or Gross Domestic Product (GDP) showed a higher match
277 between the amount of cropland area devoted to a crop and climate suitability for its yield (i.e.
278 negative effect on the mismatch index; Figure 4 & Supplementary Table S3). Soil conditions
279 and topography were other important drivers of the mismatches but their effects varied among
280 crops (Figure 4 & Supplementary Table S3). For all crops except cassava and sugarbeet, cells
281 with higher soil organic content displayed greater mismatches between harvested areas and
282 climate suitability (Figure 4 & Supplementary Table S3). Higher soil pH was associated to
283 higher mismatches for barley, groundnut, maize, potato, rape, rice, sorghum, soybean and
284 sugarbeet and wheat and to lower mismatches for cassava and sunflower (Figure 4 &
285 Supplementary Table S3). Compared to these biophysical factors, agricultural inputs exerted
286 lower influences on harvested areas - climate suitability mismatches (Figure 4 &
287 Supplementary Table S3). Increasing fertilisation had negative effects on the mismatch index
288 for barley, groundnut, maize, rapeseed, sorghum and wheat (Figure 4 & Supplementary Table
289 S3). Similarly, increasing irrigation had negative effects on the mismatch index for barley,
290 cassava, groundnut, rape, rice, soybean and wheat (Figure 4 & Supplementary Table S3).

291 *Native vs introduced climatic ranges*

292 Native and introduced climatic ranges always fully overlapped, with native ranges
293 corresponding approximately to the centre of the climatic niche of each crop (Figure 3). The
294 average mismatch between harvested areas and climate suitability in the native climatic
295 ranges was negative for all crops except barley, indicating relatively large harvested areas
296 with respect to climate suitability for crop yields (Figure 5). By contrast, the average
297 mismatches in the introduced climatic ranges was null or slightly positive, with the highest
298 values observed for rice and sorghum (Figure 5). In addition, the harvested areas of all crops
299 were larger in native climatic ranges (Figure 5 & Supplementary Figure 2) while the average
300 climate suitability for crop yields was worse in introduced ranges (Figure 5 & Supplementary
301 Figure 3).

302 **Discussion**

303 Here, we report for the first time the relationship between the global distribution of twelve
304 major food crops and climate suitability for their yields. We find that the amount of available
305 cropland allocated to a crop and climate suitability for its yields are positively correlated for
306 eight of these crops, confirming that climate is a determinant element in the choice of
307 cultivation areas [13,14]. However, we report negative correlations between harvested areas
308 and climate suitability for cassava, potato, rice and sorghum. We also reveal strong variation
309 in the relationships between harvested areas and climate suitability for all crops, even for
310 those crops that display positive harvested areas-climate suitability correlations. Together,
311 these results clearly indicate that the global distribution of crop areas is not optimised for
312 climate and that several other factors limit this adjustment.

313 Our results demonstrate the importance of socio-economic factors in regulating the
314 relationships between the distribution of crop harvested areas and climate suitability for
315 yields. Globally, regions with high gross domestic product and high human development

316 index display better adjustments of crop distributions to climate. The richest regions of the
317 world also display the lowest differences between observed yields and those potentially
318 attainable (so-called “yield-gap”, [17,36]). These regions might therefore be best able to
319 optimize the distribution of crop areas in relation to climate and environment, potentially
320 through strong investments in agricultural policies, centralized planning and greater
321 regionalization of production areas in these countries [37]. In addition, we report negative
322 correlations between harvested areas and climate suitability for the yields of three crops that
323 are all commonly found across smallholder and subsistence food systems, namely cassava,
324 sorghum and rice. Cassava is notably a key crop for food security across the African continent
325 and represents a lifeline when other crops fail due to droughts or pest outbreaks, especially
326 during famine period [38]. Sorghum is also staple crops of smallholder farmers in sub-
327 Saharan Africa [12,39], and almost 30% of rice cultivation in South Asia takes place in low-
328 input farming systems [40]. These results suggest that poorer regions may grow staple crops
329 that still produce food under harsh climatic conditions that deviate from crop climatic optima,
330 so that harvested areas are disproportionately large with respect to climate suitability.

331 Soil conditions and farming practices are other important drivers of the relationships between
332 harvested areas and climate suitability, which can either enhance or limit the adjustment of
333 crop distribution to climate. Soil conditions are indeed important drivers of crop yield and
334 modulate crop responses to extreme climatic events such as drought [41]. However, a panel of
335 farming practices can modify edaphic conditions, including liming, mulching and the addition
336 of organic matter [42]. These practices can therefore enhance the potential of crop cultivation
337 in zones with suitable climate but unsuitable soil characteristics. Conversely, irrigation and
338 fertilisation can be used to overcome low climate suitability by allowing crops to be cultivated
339 beyond their biophysical limits. Accordingly, the use of agricultural inputs can generate
340 mismatches between harvested areas and climate suitability. This is notably the case for

341 potato (i.e. the fourth crop that displays negative harvested areas - climate suitability
342 correlation) for which we found positive effects of both irrigation and fertilisation on the
343 mismatch index (Figure 4). However, we also report numerous cases where agricultural inputs
344 have negative effects on the mismatch index, indicating higher rates of fertilization and
345 irrigation where climate suitability and harvested areas are in balance. This result can reflect
346 the fact that agricultural inputs are mostly used to increase the productive capacity of areas
347 that are already (climatically) suitable for crop yield [16,17].

348 Other factors, not directly considered in this study, can further explain the decoupling
349 between the distribution of harvested areas and climate suitability for crop yields. The fact
350 that some crops share the same climatic optima (e.g. wheat and barley, Supplementary Figure
351 3), leading to competition for space, can for example increase the mismatches between
352 harvested areas and climate suitability. These mismatches may also arise because local food
353 systems, and especially smallholder ones, typically cultivate a diversity of crops to serve
354 multiple purposes (livelihood, subsistence, pest control [43]). Management factors such as
355 multiple cropping systems [44] and year-to-year crop rotations [45] can further create patterns
356 of harvested areas that deviate from climate suitability. Interspecific interactions, and notably
357 the presence of natural enemies (pests and pathogens), may be another important driver of
358 these mismatches since farmers may choose to reduce the area allocated to a crop that is
359 exposed too intensely to pests. Although there is no globally available dataset for pests across
360 many crops, we were able to test this hypothesis for sunflower using published occurrence
361 records of *Sclerotinia sclerotiorum* [46], a major sunflower pathogenic fungus worldwide (see
362 Supplementary Figure S4 for details). We found that harvested areas were disproportionately
363 large compared climate suitability in presence of the pest (Supplementary Figure S4). This
364 result shows that the presence of *S. sclerotiorum* and the associated yield damage can hardly
365 be separated from the effects of climate at this scale, probably because the pest share the same

366 climatic niche as its host [46]. Nevertheless, these results, if true for other crops and pests,
367 would suggest a strong ecological anchoring of the harvested areas - climate suitability
368 mismatches.

369 Finally, our results bring novel insights to understand how the geographical expansion of
370 crops from their origin centres to the rest of the world has affected their climatic niche.
371 Despite the global homogenization of cropping patterns [20,47], we show that major crops are
372 still farmed predominantly in their native climatic range. Such differences in the distribution
373 of harvested areas between native and introduced climatic ranges can highlight the biological
374 constraints of crop species to wide climate adaptation. However, we find that native climatic
375 ranges do not necessarily represent the highest climate suitability for crop yields. This might
376 reflect the fact that farming practices and plant breeding has modified the climatic
377 requirements of crops with regard to their wild progenitors [48], so that crops and their wild
378 progenitors no longer share the same climatic optimums. These findings have major
379 implication for agricultural science and breeding programs that increasingly look at crop wild
380 relative as promising reservoir of genetic diversity to enhance crop adaptation to heat or
381 drought (e.g. [21,24,49,50]). Accounting for differences in climate suitability between crops
382 and their wild progenitors will be a critical issue for the development of novel crop varieties
383 from these wild species.

384 Before concluding, it is important to mention some limitations of our study, which are mainly
385 related to the nature of the datasets available for this work. First, we cannot exclude that our
386 approach might overestimate the mismatches observed between crop's harvested areas and
387 climate suitability. This is notably because we cannot account for intra-specific (e.g.,
388 commercial varieties, landraces) variations in climatic ranges within each crop species.
389 However, intra-specific variations are expected to play a lesser role at global scale, compared
390 to a finer spatial scale[51]. Second, conclusions about the role of irrigation might be limited

391 since the nature of the data (i.e. % of land equipped for irrigation) does not depict the actual
392 irrigation of each crop. Finally, the agricultural data we used may appear a bit dated, as it
393 presents the average, global distribution of crop areas and yields for the 2000s [25]. It also
394 neglects year-to-year variability in the global distribution of crop areas and yields. Although
395 temporal changes in the global distribution of crop harvested areas can mitigate the negative
396 effects of climate on agricultural production [13], the extent to which these dynamics do
397 affect the magnitude of the harvested areas-climate suitability mismatch remains to be
398 quantified. Another promising extension of this work will be to consider the temporal
399 variability of crop yields, yield stability being key for the adaptation of global agriculture to
400 climate change [52].

401 To conclude, many strategies for coping with climate change in agriculture implicitly aim to
402 improve the match between the distribution of crop areas and climate. Accordingly, studies
403 have focused on the climatic niche of crops to predict future patterns of crop distribution and
404 to identify crops and wild relatives best adapted to future conditions. However, the fact that
405 multiple ecological, agricultural, socio-economic and historical factors govern the choice of
406 farmers to cultivate a particular species strongly limits the global adjustment of crop
407 distribution to climate, today. A main challenge for the coming years will therefore be to
408 comprehensively integrate these dimensions to define the socio-ecological niche of crops [53]
409 so as to design efficient strategies that can sustainably deal with climate change in agriculture.
410 Extrapolating the socio-ecological niche of crops to future climate conditions will also
411 provide crucial information for estimating the socio-economic costs that will need to be
412 invested in order to improve the match between crops and future climate.

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549 **Data availability**

550 The sources of all data used in this study are referenced in the Methods and all raw data are
551 freely accessible at the URLs provided in Extended Data Table 2. The dataset used for the
552 analyses is available from the corresponding author upon request (lucie.mahaut@cefe.cnrs.fr).

553 **Acknowledgements**

554 LM's work was funded by the French National Research Agency under the Programme
555 "Investissements d'Avenir" under the reference ANR 17 MPG A 0004. LHR's research on
556 sunflower climate adaptation is funded by Genome Canada, Genome BC, and The Natural
557 Sciences and Engineering Research Council of Canada. The Ministry of Economy and
558 Competitivy of Spain (Grants CGL2014-56567-R and CGL2017-83855-R; Ministerio de
559 Economía y Competitividad, Spain) fund RM research on crop's wild progenitors. SP thanks
560 the Bentham-Moxon Trust for funding a short stay at the University of British Columbia

561 (BMT35-2017). C.K.K. was supported by grant no. 2019-67012-29733/project accession no.
562 1019405 from the USDA National Institute of Food and Agriculture. C.V. was supported by
563 the European Research Council (ERC) Starting Grant Project "Ecophysiological and
564 biophysical constraints on domestication in crop plants" (Grant ERC-StG-2014-639706-
565 CONSTRAINTS). We thank Ian Ondo for his help with soil data, Emily Warschefsky and
566 Navin Ramankutty for feedback on the manuscript. We thank Gilles Dauby and Thomas
567 Couvreur for providing unpublished data from the Rainbio database. We also thank Nora
568 Castañeda-Álvarez and Matija Obreza for extracting occurrence records from GENESYS and
569 Dora A. L. Canhos and Sidnei De Souza for obtaining records from SpeciesLink database.

570 **Author contributions**

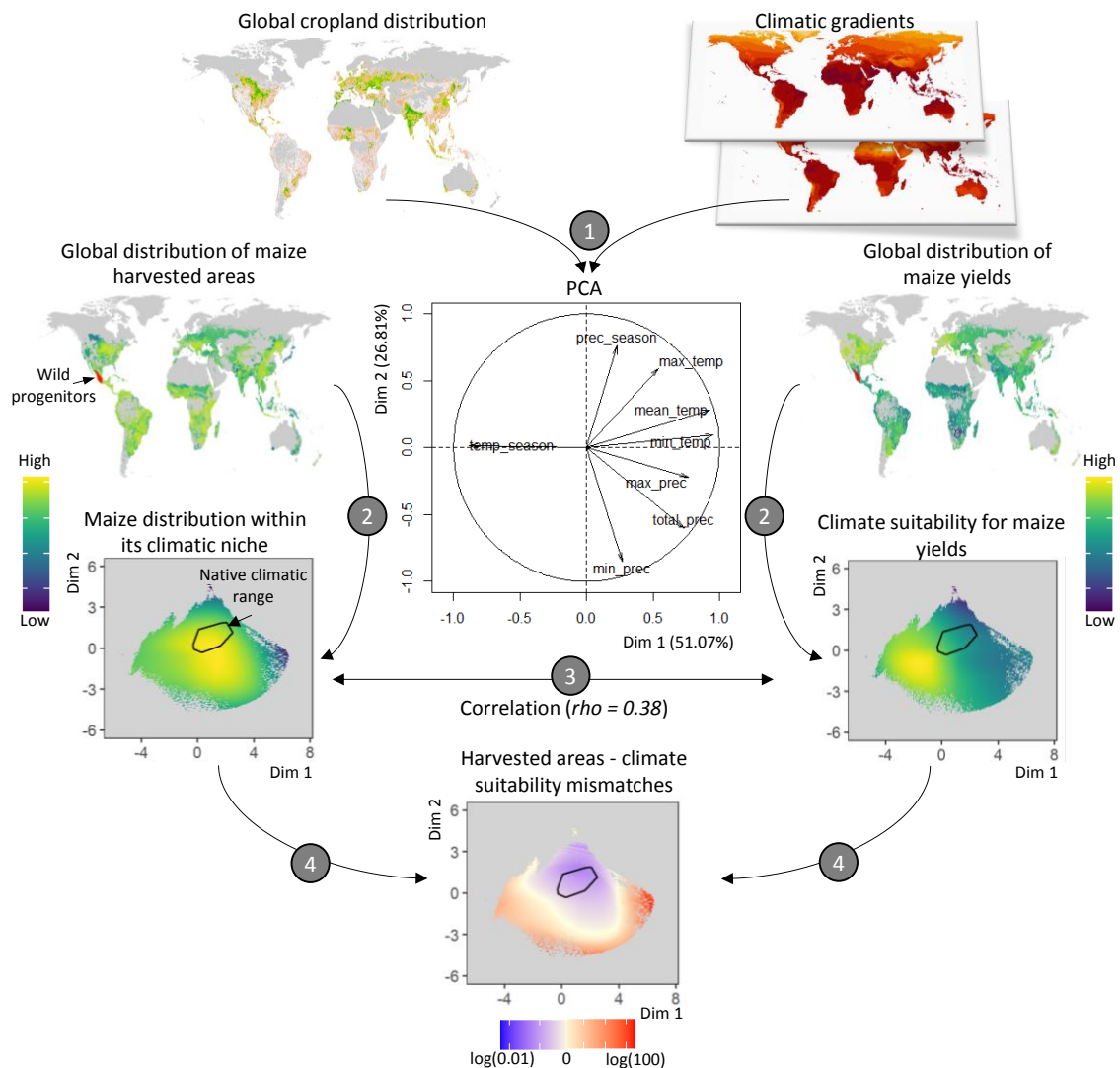
571 L.M. led the data analysis and writing. L.M., S.P., D.R. and C.V. designed the experiment.
572 F.B., C.K.K., R.M and C.P. contributed substantially to the crop wild progenitors' analysis
573 and writing. J.Y.B., S.P., D.R. and C.V. assisted with data analysis and writing. Z.M. and
574 L.H.R. assisted with study design and writing.

575 **Competing interests**

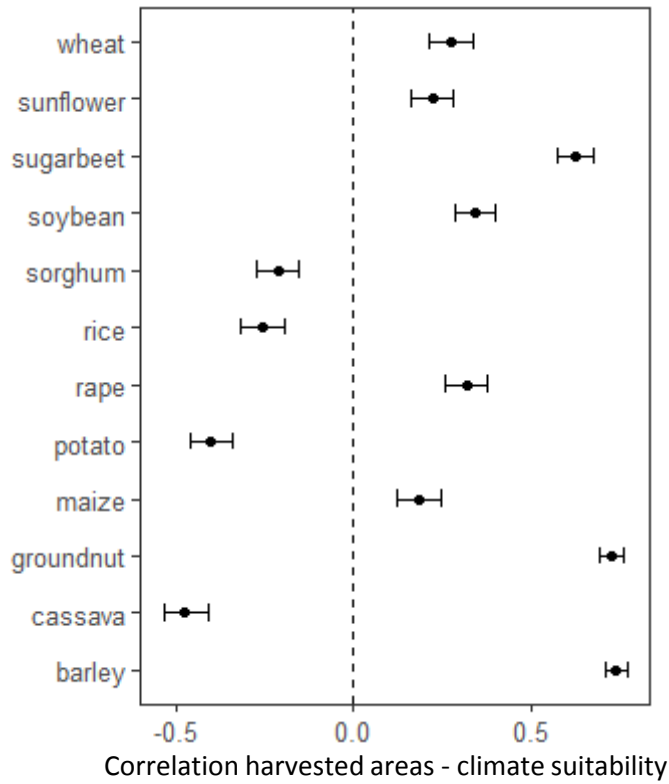
576 The authors declare no competing financial interests.

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580
 581 **Figure 1:** General framework for estimating (mis)matches between harvested areas and
 582 climate suitability for crop yields. First, we compute a unique 2D climatic space based on the
 583 global distribution of cropland and the two first dimensions of a PCA (Dim.1 and Dim. 2) that
 584 summarizes variations in eight bioclimatic variables related to mean, seasonality and extremes
 585 values of temperature (temp) and precipitation (prec). The portion of this climatic space that a
 586 crop occupies defines its climatic niche. Second, we project the global distributions of
 587 harvested areas and yields of twelve major food crops (here maize) as well as the distribution
 588 of their wild progenitors into the climatic niche of each crop (see Methods for details). The
 589 portion of the climatic niche that is occupied by wild progenitors (black polygons) represents
 590 the native range of the crop. We use multiple regression to model climate suitability as the
 591 marginal effects of Dim.1 and Dim.2 on crop yields while controlling for numerous non-
 592 climatic factors. Third, we quantify the relationship between harvested areas and climate
 593 suitability by computing Spearman's correlation index. Fourth, we analyse variation in the
 594 harvested areas-climate suitability relationship by computing a local mismatch index (see
 595 Methods for details). Positive values (red) indicate climatic zones with higher climate
 596 suitability with respect to harvested areas. Negative values (blue) indicate climatic zones with
 597 higher harvested areas with respect to climate suitability. Null values (beige) represent
 598 balanced harvested areas and climate suitability.

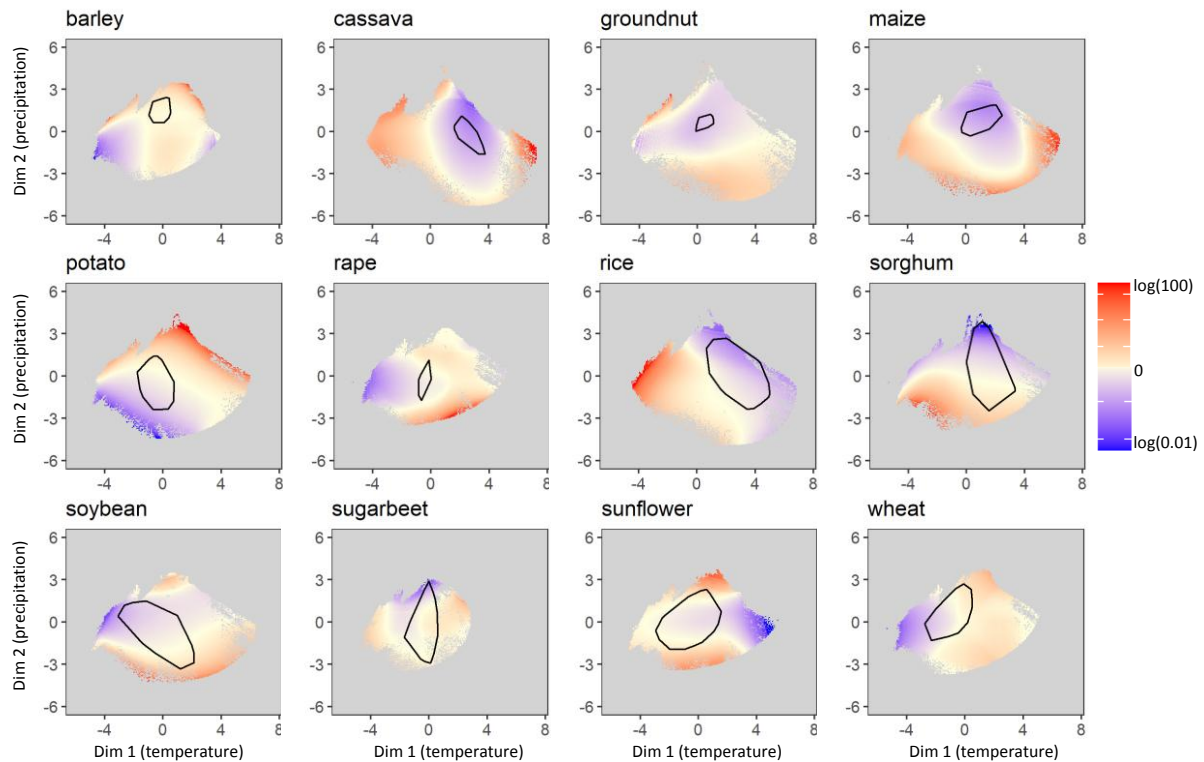


599

600 **Figure 2:** Correlation between the distribution of harvested areas and climate suitability for
 601 the yield of twelve major food crops. For each crop, we randomly sampled 1,000 pixels of the
 602 climate grid, computed Spearman correlation index between harvested area and climate
 603 suitability and repeated the process 1,000 times. Black dots indicate mean spearman
 604 correlation indices and horizontal bars indicate 95% confidence intervals.

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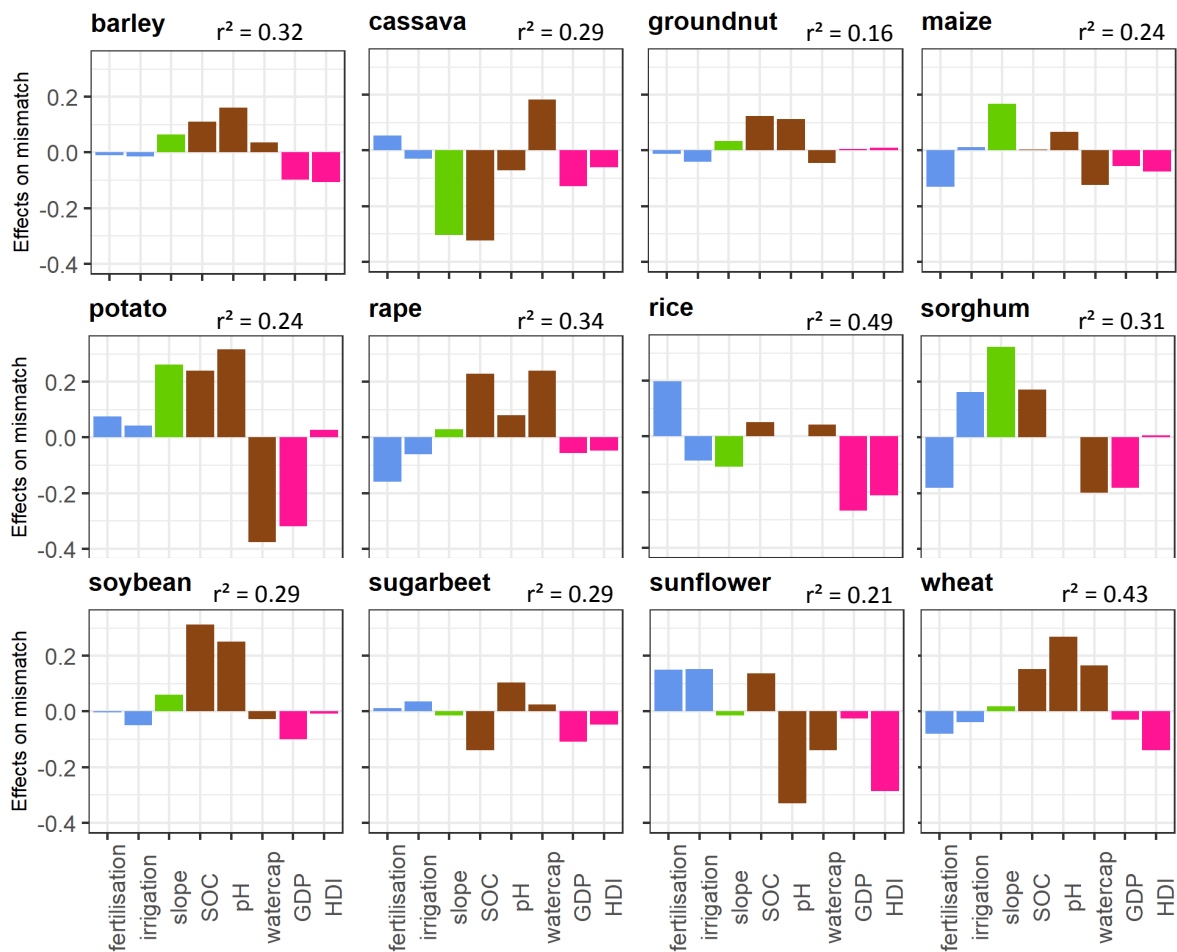


607

608 **Figure 3:** Variation in the harvested areas-climate suitability mismatch index within the
 609 climatic niche of twelve major food crops. Dim. 1 summarizes the variation in mean, seasonal
 610 and extreme temperature. Dim. 2 summarizes the variation in mean, seasonal and extreme
 611 precipitation. Beige colours indicate balanced harvested areas and climate suitability. Red
 612 represents zones where climate suitability is disproportionately high with respect to harvested
 613 areas. Conversely, blue indicates regions where harvested areas are disproportionately large
 614 with respect to climate suitability. Black polygons delineate the climatic space occupied by
 615 crop wild progenitors (i.e. native climatic range).

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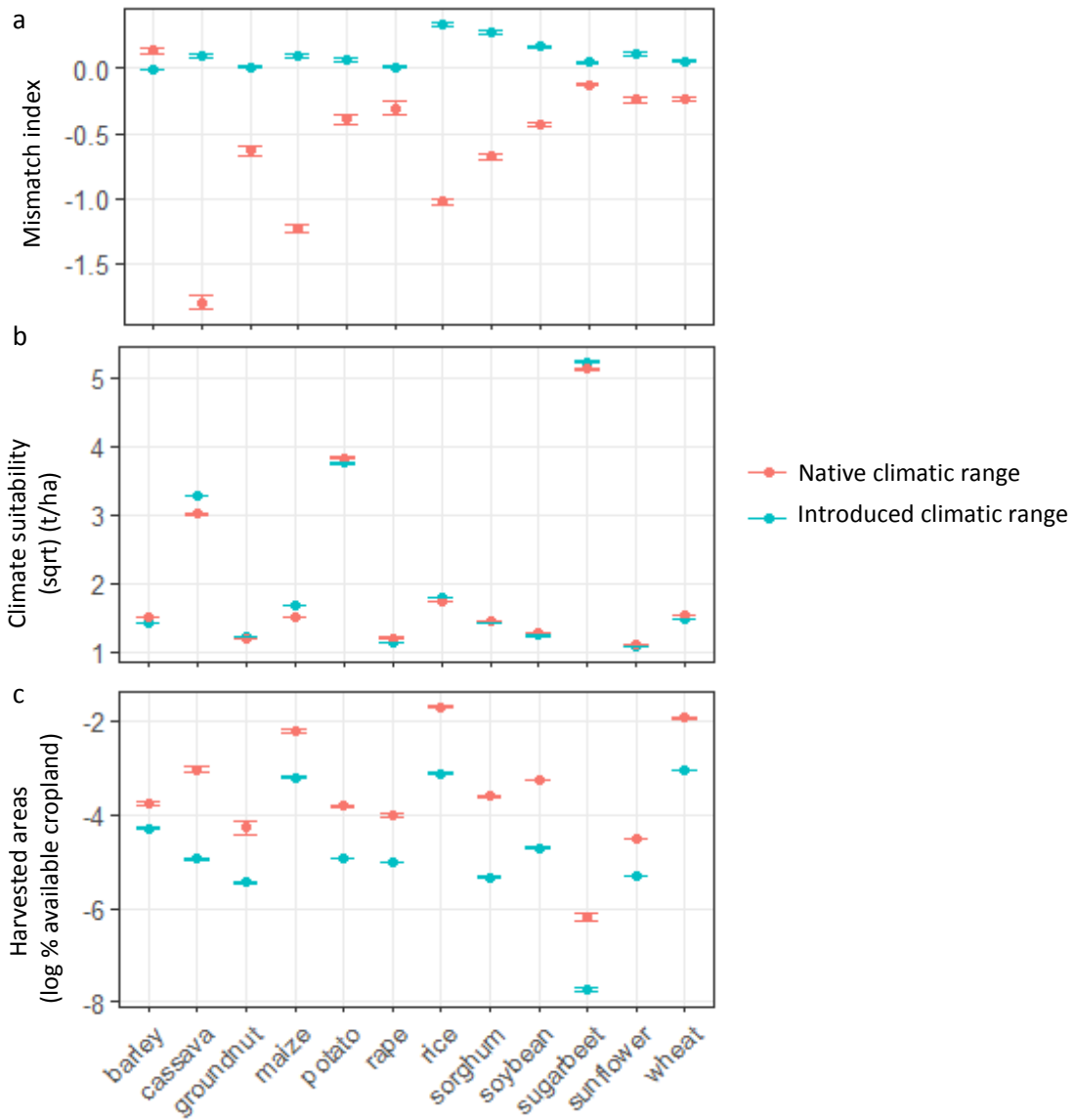


618

619 **Figure 4:** Estimated coefficients of the mismatch models for twelve major food crops. The
 620 effects of agricultural inputs (Fertilisation and Irrigation; blue), topography (slope; green), soil
 621 (SOC, pH, water capacity; brown) and socio-economic (GDP and HDI; pink) factors are
 622 modelled as linear terms. Positive effects on the absolute values of crop distribution – climate
 623 suitability mismatch indicate an increase in the decoupling between the distribution of
 624 harvested areas and climate suitability for crop yields while negative effects indicate an
 625 increasing match between both parameters. Coefficients of determination are shown (r^2).

626

627



628

629 **Figure 5:** Average mismatch index (a), climate suitability (b) and harvested areas (c) in the
 630 native (red) and introduced (blue) climatic ranges of twelve major food crops. Dots indicate
 631 average values +/- 95% confidence intervals.