

## Matches and mismatches between the global distribution of major food crops and climate suitability.

Lucie Mahaut, Samuel Pironon, Jean-Yves Barnagaud, François Bretagnolle, Colin K. Khoury, Zia Mehrabi, Ruben Milla, Charlotte Phillips, Loren H. Rieseberg, Cyrille Violle, et al.

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1	Matches and mismatches between the global distribution of major food crops and
2	climate suitability
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#### 24 Abstract

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

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48 Introduction

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

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

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

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

#### 97 Material and Methods

#### 98 Crop data set

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

#### 110 Crop progenitors data set

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

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

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

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

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

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

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

173 Data analyses

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

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

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

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

Then, we analysed variation in the relationships between harvested areas and climate suitability within the climatic niche of each crop by computing a local mismatch index (step 4 in Figure 1). We computed for each crop and for each pixel of the climatic niche the centiles of the smoothed values of harvested areas and the centiles of climate suitability. We calculated the log-ratio between climate suitability centiles and crop areas centiles. The resulting mismatch index varied between log(0.01) (climate suitability value belonging to the  $1^{st}$  centile/harvested areas value belonging to the  $100^{th}$  centile) and log(100) (climate suitability value belonging to the 100<sup>th</sup> centile/ harvested areas value belonging to the 1<sup>st</sup> centile). When equal to zero, this index indicates a balanced situation (i.e. absence of mismatch) between harvested areas and climate suitability. Positive values describe situations where climate suitability is disproportionately large with respect to the portion of cropland allocated to a crop while negative values indicate situations where crop harvested areas are disproportionately large with respect to climate suitability.

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

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

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

#### 246 **Results**

#### 247 Relationships between harvested areas and climate suitability

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

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

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

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

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

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

291 *Native vs introduced climatic ranges* 

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

#### 302 Discussion

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

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

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

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

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

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

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

Finally, our results bring novel insights to understand how the geographical expansion of 369 crops from their origin centres to the rest of the world has affected their climatic niche. 370 371 Despite the global homogenization of cropping patterns [20,47], we show that major crops are still farmed predominantly in their native climatic range. Such differences in the distribution 372 of harvested areas between native and introduced climatic ranges can highlight the biological 373 constraints of crop species to wide climate adaptation. However, we find that native climatic 374 375 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 requirements of crops with regard to their wild progenitors [48], so that crops and their wild 377 progenitors no longer share the same climatic optimums. These findings have major 378 implication for agricultural science and breeding programs that increasingly look at crop wild 379 380 relative as promising reservoir of genetic diversity to enhance crop adaptation to heat or drought (e.g. [21,24,49,50]. Accounting for differences in climate suitability between crops 381 and their wild progenitors will be a critical issue for the development of novel crop varieties 382 from these wild species. 383

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

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

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

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#### 549 Data availability

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

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#### 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

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.
- 577

#### 579 Figures



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





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



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

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

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