



Modelling potential range expansion of an underutilised food security crop in Sub-Saharan Africa

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Environmental Research Letters

DOI:

[10.1088/1748-9326/ac40b2](https://doi.org/10.1088/1748-9326/ac40b2)

E-pub ahead of print: 30/12/2021

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Koch, O., Mengesha, W. A., Pironon, S., Pagella, T., Ondo, I., Rosa, I., Wilkin, P., & Borrell, J. S. (2021). Modelling potential range expansion of an underutilised food security crop in Sub-Saharan Africa. *Environmental Research Letters*, 17(1), [014022]. <https://doi.org/10.1088/1748-9326/ac40b2>

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1 **Running head:** Modelling underutilised crop expansion

2 **Modelling potential range expansion of an underutilised food**
3 **security crop in Sub-Saharan Africa**

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19 **Abstract**

20 Despite substantial growth in global agricultural production, food and nutritional insecurity is
21 rising in Sub-Saharan Africa. Identification of underutilised indigenous crops with useful food
22 security traits may provide part of the solution. Enset (*Ensete ventricosum*) is a perennial
23 banana relative with cultivation restricted to southwestern Ethiopia, where high productivity
24 and harvest flexibility enables it to provide a starch staple for ~20 million people. An
25 extensive wild distribution suggests that a much larger region may be climatically suitable for
26 cultivation. Here we use ensemble ecological niche modelling to predict the potential range
27 for enset cultivation within southern and eastern Africa. We find contemporary bioclimatic
28 suitability for a 12-fold range expansion, equating to 21.9% of crop land and 28.4% of the
29 population in the region. Integration of crop wild relative diversity, which has broader climate
30 tolerance, could enable a 19-fold expansion, particularly to dryer and warmer regions. Whilst
31 climate change may cause a 37% – 52% reduction in potential range by 2070, large centres of
32 suitability remain in the Ethiopian Highlands, Lake Victoria region and the Drakensberg
33 Range. We combine our bioclimatic assessment with socioeconomic data to identify priority
34 areas with high population density, seasonal food deficits and predominantly small-scale
35 subsistence agriculture, where integrating enset may be particularly feasible and deliver
36 climate resilience. When incorporating the genetic potential of wild populations, enset
37 cultivation might prove feasible for an additional 87.2 - 111.5 million people, 27.7 – 33
38 million of which are in Ethiopia outside of enset's current cultivation range. Finally, we
39 consider explanations why enset cultivation has not expanded historically, and ethical
40 implications of expanding previously underutilised species.

41 **Keywords:** Agriculture, Ecological Niche Modelling, Enset, Ethiopia, Climate Change,
42 Ecological Intensification, Crop wild relatives.

43 **1. Introduction**

44 Food and nutritional insecurity is a growing challenge in Sub-Saharan Africa (SSA)
45 (Conceição *et al.* 2016; FAO and ECA 2018; Fraval *et al.* 2019), compounded by accelerating
46 population growth, higher standards of living, degraded ecosystem services, climate change
47 and volatile food markets (Poppy *et al.* 2014; Hall *et al.* 2017). Current efforts to address SSA
48 food security through agricultural policies tend to emphasize increased productivity via inputs
49 and technology (Conceição *et al.* 2016; Ittersum *et al.* 2016). However, a complementary
50 strategy, which may be particularly pertinent under climate change, is the adaptation of
51 agricultural systems through crop and cultivar choice (Rippke *et al.* 2016; J. S. Borrell *et al.*
52 2019; McMullin *et al.* 2019; Pironon *et al.* 2019; Rising and Devineni 2020). For example,
53 recent evidence suggests that prioritising traits such as perenniality (Kreitzman *et al.* 2020),
54 tolerance to drought or heat-induced stress (Heider *et al.* 2020) as well as crop diversity and
55 asynchrony (McMullin *et al.* 2019; Renard and Tilman 2019; Egli *et al.* 2020) may help
56 support smallholder resilience. Considering the antiquity and diversity of SSA agriculture,
57 renewed investigation of orphan and underutilised indigenous crops may yield candidates
58 with useful traits, where expanded cultivation could help meet food and nutritional security
59 goals (Shelef *et al.* 2017; Tadele and Bartels 2019; Ulian *et al.* 2020).

60 In this study we investigate the indigenous Ethiopian food security crop enset (*Ensete*
61 *ventricosum*, Musaceae), a close relative of the globally ubiquitous cultivated bananas
62 (*Musa*). Enset provides the starch staple for 20 million Ethiopians (J S Borrell *et al.* 2019),
63 and is one of 101 high potential crops identified by the African Orphan Crop Consortium
64 (Dawson *et al.* 2018). Also known as the ‘false banana’, enset is a giant herbaceous perennial
65 monocarp that accumulates standing biomass and can be harvested at any time prior to
66 flowering and senescence (~7-12 years) (Lock 1993; National Research Council 2006). Upon
67 harvesting, the entire pseudostem and corm is processed to extract starch, which is fermented

68 and stored until required for consumption (Tamrat *et al.* 2020). Enset is non-irrigated and is
69 among the highest yielding crops per hectare in the region, whilst vegetative propagation
70 enables rapid multiplication of favourable genotypes (Borrell *et al.* 2020). By maintaining
71 multiple age-classes, enset provides subsistence farmers the flexibility to harvest as required
72 (e.g. depending on availability of other crops or resources), buffering seasonal, social and
73 climate driven variability (J S Borrell *et al.* 2019). This suite of unusual food security traits
74 has earned enset the moniker ‘the tree against hunger’ (Brandt *et al.* 1997). Nevertheless,
75 despite its local agricultural dominance, utility and major cultural importance in the
76 southwestern Ethiopian highlands, enset has a remarkably narrow cultivated distribution and
77 is virtually unknown as a food plant outside of Ethiopia (J S Borrell *et al.* 2019).

78 Archaeological and historical evidence suggests that enset was domesticated in Ethiopia
79 (Brandt *et al.* 1997; Hildebrand 2010) and that cultivation has remained restricted to the
80 south-west (Negash 2020). There is limited evidence that cultivation was once more extensive
81 in northern Ethiopia, as observed in Bruce (1790). By contrast, inedible wild enset
82 populations are distributed across moist Afromontane Forest habitats in eastern and southern
83 Africa (Borrell *et al.*, 2019). This broad wild distribution provides an initial indication of the
84 potential to expand domesticated enset cultivation beyond its current range. As a major
85 African center of crop domestication, multiple Ethiopian crops including coffee (*Coffea*
86 *arabica*) (Davis *et al.* 2018) and finger millet (*Eleusine coracana*) (Fuller 2014) have been
87 successfully adopted beyond the species’ native range (Fuller and Lucas 2017). It is therefore
88 surprising that as a regional staple and a close relative of the globally cultivated banana, enset
89 has not been adopted outside of Ethiopia.

90 Climate change is predicted to seriously affect yields and distributions of major staple crops
91 in Africa (Schlenker and Lobell 2010; Challinor *et al.* 2014; Pironon *et al.* 2019), which may
92 catalyse renewed interest in adoption of alternative underutilised species (National Research

93 Council 2006; Ulian *et al.* 2020; McMullin *et al.* 2021). Understanding barriers to adoption
94 such as bioclimatic tolerance, prerequisite indigenous knowledge, access to material and
95 opportunity costs is key to sustainably exploiting currently underutilised species (Bioversity
96 International 2017; Jamnadass *et al.* 2020; McMullin *et al.* 2021). For example, a common
97 attribute of cultivated species is reduced genetic diversity as a consequence of a domestication
98 bottleneck (Gaut *et al.* 2018). Depending on the local bioclimatic conditions during the
99 domestication process, genetic variants may have become fixed, limiting adaptive potential in
100 parts of the species wild distribution (Warschefsky *et al.* 2014). Therefore, concurrently
101 modelling the distribution of crop wild relative progenitor populations, from which genetic
102 diversity could be introduced through breeding, may indicate further potential for crop
103 expansion. Similarly, subsistence farmer agricultural practice and crop choice is strongly
104 influenced by risk (Aryal *et al.* 2021), with the cost of crop adoption a trade-off against the
105 risk of food insecurity or perceived climate vulnerability of their current crop portfolio
106 (Akinyi *et al.* 2021).

107 In this study, we aim to identify both agrisystems and communities in which enset expansion
108 may be appropriate, by characterising both the present and future bioclimatic distribution in
109 which cultivation is viable, as well as the socioeconomic context in which adoption is feasible
110 (Shikuku *et al.* 2017; McMullin *et al.* 2021). We apply an ensemble ecological niche
111 modelling (ENM) framework to assess climatic suitability for expanded enset cultivation
112 across eastern and southern Africa and integrate this with poverty, demography and food
113 insecurity data to prioritise socioeconomic suitability. Relatively few studies have applied
114 ecological niche modelling to evaluate expansion potential in cultivated species (e.g. baobab,
115 Cuni and Patrick 2010; coffee, Moat *et al.* 2017), and fewer have attempted to integrate
116 anthropogenic features (e.g. *Colocasia* in Hawaii, Kodis *et al.* 2018). Enset has significant
117 potential because it can address acute food insecurity asset, even when grown in low numbers

118 (National Research Council 2006) and the wild distribution is considerably larger than the
119 current cultivated distribution (the inverse of many other domesticates, Diamond 2002).

120 We first generate ENMs for wild and domesticated enset across Ethiopia and assess niche
121 shifts associated with domestication. We use these models to evaluate enset's current and
122 potential distribution, as well as explanations for the lack of historical expansion. Second, we
123 evaluate the extent to which integrating wild enset genetic diversity could enable
124 domesticated enset to adapt to a broader region of cultivation, both now and under future
125 climate projections. Third, we analyse demographic and socioeconomic data to identify
126 priority areas in which enset cultivation could contribute to food and nutritional insecurity
127 needs with minimal barriers to adoption. Finally, we consider remaining political and cultural
128 barriers to expansion of enset, and parallels of this approach with other underutilised species.

129 **2. Methods**

130 **Agricultural surveys and data processing**

131 We collated 2515 georeferenced records of domesticated enset in the Ethiopian Highlands
132 from 2017-20. Observations included systematic agricultural surveys oriented to transect
133 elevational and climatic gradients from across the enset growing region, ensuring
134 comprehensive coverage of variation in bioclimatic and geographical space. We also collated
135 163 wild *E. ventricosum* observations from across Ethiopia and East and Southern Africa
136 using field surveys, online databases (GBIF.org 2018) and herbaria records (AAU, K).

137 We were cognisant that sampling bias in geographic space (e.g. due to accessibility) may
138 translate to bias in environmental space and overfitting (Boria *et al.* 2014). To ensure a
139 balanced representation of environmental conditions in our dataset, we filtered presence data
140 in environmental space following Varela *et al.* (2014), using 19 bioclimatic predictors from
141 CHELSA for the period 1979-2013 (Karger *et al.* 2017) and aggregated to 5 arc-minutes (~10

142 km²) resolution in ArcMap 10.7.1 (ESRI, USA). First, we plotted a Principal Component
143 Analysis of scaled environmental variables for all observations using the R package ade4
144 (Dray and Dufour 2007), and removed occurrence points with duplicated environmental
145 values on the first two principal components. This retained 414 domesticated and 99 wild
146 enset occurrence points. We applied further bias correction to domesticated samples by
147 calculating pairwise Euclidean distance and using Kmeans to identify 30 clusters that
148 minimise within sums of squares. We randomly sampled three occurrence points from each,
149 generating a sample evenly distributed across environmental space. We then partitioned 60
150 domesticated enset observations for model training and 30 for model evaluation from these
151 clusters. Generating pseudo-absences (PAs) enables parameterization of modelling
152 approaches that do not rely on true species absences. To account for uncertainty in PAs
153 samples, we generated 10 datasets of 10,000 PAs randomly selected across the reference area,
154 following the approach of Barbet-Massin et al. (2012).

155 **Variable selection and climate projections**

156 We defined the study area as comprising Ethiopia (hereafter “reference area”) and the 17
157 countries of East and Southern Africa in which wild enset has been recorded (“transfer area”)
158 (Figure 1). This modelling background extent was restricted to relevant agroecological zones
159 to obtain informative evaluation statistics and model output (Lobo *et al.* 2012), using the
160 “Agro-Ecological Zones for Africa South of the Sahara” dataset (HarvestChoice and
161 International Food Policy Research Institute, 2015), omitting arid and sub-tropical regions. To
162 reduce multicollinearity and model overfitting we restricted the number of environmental
163 variables using the “select07” approach (Dormann *et al.* 2013). Where pairs of variables were
164 correlated (Spearman’s rank correlation coefficient > 0.7), we retained the variable with the
165 highest explanatory power by calculating the univariate importance of all 19 bioclimatic
166 variables using the AIC of a quadratic GLM. Finally, ExDet (Mesgaran *et al.* 2014) was used

167 to select a set of variables only moderately correlated in the reference area as well as the
168 transfer area whilst also featuring low novelty in the transfer area. We therefore retained
169 maximum temperature of the warmest month (Bio 5), precipitation of the driest quarter (Bio
170 17) and mean annual precipitation (Bio 12) as response variables (Table S1). We omitted
171 edaphic variables as Ethiopian homegarden agriculture tends to alter local soil composition at
172 fine scales (Wolka *et al.* 2021). Similarly, we consciously excluded other remotely sensed
173 variables such as Normalized Difference Vegetation Index or Net Primary Production, as
174 although these may improve present time models, it is unclear how they could be applied to
175 future projections (Leitão *et al.* 2019).

176 For modelling the effect of climate change on the area suitable for enset cultivation,
177 projections of five global circulation models (GCMs) from the Coupled Model
178 Intercomparison Project Phase 5 (CMIP5) (CESM1-BGC, CESM1-CAM5, CMCC-CM,
179 MIROC5 and MPI-ESM-MR) were used for Representative Concentration Pathway Scenario
180 (RCP) 4.5 and RCP8.5 in 2050 and 2070. GCM selection was based on dissimilarity
181 following Sanderson *et al.* (2015), to reduce interdependence among the selected models.

182 **Ensemble modelling for wild and domesticated enset**

183 We use an ensemble of six different modelling techniques: Generalized Linear Models
184 (GLM), Generalized Additive Models (GAM), Generalized Boosting Models (GBM),
185 Random Forest (RF), Multiple Adaptive Regression Splines (MARS) and Maximum Entropy
186 (MAXENT), implemented in the R-package “biomod2” (Thuiller *et al.* 2016). Five modelling
187 runs with different testing/training data splits were carried out on 10 different sets of pseudo-
188 absences for each of the six modelling approaches, generating 300 models each for wild and
189 domesticated enset. An ensemble was generated from all models with a true skill statistic
190 (TSS) ≥ 0.6 and an area under the receiver operating characteristic curve ≥ 0.8 . We combined
191 models using the mean of probabilities weighted by each model’s TSS score. The maximized

192 sum of sensitivity and specificity (equivalent to maximizing TSS) was used to generate binary
193 presence-absence predictions (Barbet-Massin *et al.* 2012).

194 To compare domesticated and wild enset niches we used the niche similarity statistics
195 Schoener's D and Hellinger's I (Warren *et al.* 2008), as well as testing niche expansion,
196 unfilling and stability in the process of domestication using the ecospat package
197 (Broennimann *et al.* 2021). To assess areas climatically suitable for enset cultivation outside
198 of its current range, ensemble models were projected across the 18 countries of the study
199 region under current and future climate conditions. Mean probabilities of occurrence were
200 calculated across the five GCMs for each time period and RCP.

201 **Model evaluation**

202 Ensemble model discrimination ability was evaluated using AUC and TSS on a 30%
203 subsample of presences and pseudo-absences, across five independent runs. To evaluate
204 calibration (ability to correctly predict conditional probability of presence), we plotted the
205 continuous Boyce index (CBI) (Hirzel *et al.* 2006). The CBI is a threshold independent
206 measure of model performance, which measures the distribution of observed presences across
207 the projected suitability based on divergence from a random distribution. Good performance
208 is indicated by an increasing number of presences found with increasing predicted probability
209 of presence. In addition, we calculated the absolute validation index, a threshold dependent
210 measurement of the proportion of presences correctly identified above the chosen binary
211 probability of presence (Hirzel *et al.* 2006).

212 **Socioeconomic analysis of enset suitability**

213 After identifying bioclimatic suitability for enset cultivation, we performed further
214 prioritization based on five geographic, demographic, and socioeconomic criteria. First, to
215 mitigate unsustainable agricultural expansion, we retained only crop land outside of IUCN

216 category I/II protected areas, using the Spatial Production Allocation Model dataset for 2017
217 (International Food Policy Research Institute 2020) and World Database of Protected Areas
218 (UNEP-WCMC and IUCN 2020). Second, enset is characterised by high harvest flexibility
219 buffering seasonal food insecurity, therefore we integrated data from the Famine Early
220 Warnings System Network (USAID, 2019) to identify areas of seasonal food access
221 deficiencies from the period 2012-19. Average Integrated Food Security Phase Classification
222 for January/February, June/July and October (Months where continuous timeseries were
223 available) were obtained as a proxy for food access deficiencies per season. We retained areas
224 with an average classification of two (“stressed”) or higher in any season.

225 Enset successfully supports very high rural population densities and has among the highest
226 yield per hectare of regional crops (Borrell *et al.* 2020). Therefore third, we identified regions
227 with high rural population density using WorldPop (2018), which may be indicative of current
228 or future land shortages. The top 10th (~10,000 people) and 5th percentile (~18,000 people) of
229 resampled cells were classified as densely populated and very densely populated, respectively.

230 Fourth, enset is a low input, non-irrigated, predominantly subsistence cropping system. We
231 used Spatially Disaggregated Crop Production Statistics Data in Africa South of the Sahara
232 for 2017 (IFPRI, 2020) to identify areas with a high share of rain fed subsistence and low
233 input cropping practices. The top 20th (>~500 ha) and 10th percentile (>~1000 ha) of cells
234 were classified as of priority and of high priority respectively. Finally, we used the same data
235 to identify areas with low local diversity of staple crops. Crop diversity is an increasingly
236 recognised strategy for mitigating food insecurity (Fraval *et al.* 2019; Koch *et al.* 2021). We
237 calculated the Shannon Diversity Index for each cell based on the respective crops
238 contributing to low input and subsistence production. The lowest 2/3 and 1/3 were classified
239 as priority and high priority respectively. All indicators were scaled between 0-2 and the sum
240 of indicator scores was used as an overall priority score of each cell. Priority maps were then

241 overlaid with 2070 projections of binary suitability to account for climate change when
242 prioritizing expansion areas. All analyses were performed in R software version 3.6.2 (R Core
243 Team 2019).

244 **3. Results**

245 **Ensemble model performance**

246 The domesticated enset ensemble model achieved a high discriminative ability with an overall
247 TSS of 0.73 and AUC of 0.91. Individual model performance ranged from a TSS of 0.40-0.80
248 and AUC of 0.69-0.92. The performance of MARS and RF models was poorer compared to
249 other model types (Figure 2). A CBI score of 0.97 confirmed the very high predictive ability
250 of domesticated enset models in the reference area. Moreover, binary predictions of
251 domesticated enset models in reference space detected 83.3% of evaluation data as true
252 presences. The coefficient of variation between models was generally very low for moderate
253 to highly suitable areas (Figure 2), but uncertainty was greater in areas with low suitability.
254 Ensemble model performance for wild enset was similarly high with an overall TSS of 0.77,
255 AUC of 0.94 and CBI value of 0.94 (Table S2).

256 **Comparison of enset's wild and domesticated niches**

257 Similarity statistics confirm substantial overlap between the wild and domesticated niche ($D =$
258 0.72 , $I = 0.89$). However domesticated enset is confined to cooler maximum temperatures in
259 the warmest month (Bio5) and driest quarter precipitation (Bio17) has consistently higher
260 variable importance in ENMs (Figure 3). The expansion of domesticated enset's niche is
261 marginal ($E=0.06\%$), while the unfilling of wild ensets niche is more pronounced ($U= 6.5\%$).
262 Together the maximum temperature of warmest month and the precipitation of the driest
263 quarter have a combined relative importance of 98.5% for ensemble predictions, which offers

264 a good representation of the climate suitability predicted for enset cultivation in the
265 environmental space.

266 **Potential for expansion of enset cultivation**

267 Within Ethiopia, we estimate that approximately 251,300 km² are within the range suitable for
268 enset cultivation. Based on existing range maps from Borrell et al. (2019a), we estimate that
269 ~28.2% of this extent is currently utilised. Across East and Southern Africa our ensemble
270 model predicts ~906,000 km² to be climatically suitable for enset cultivation, covering 21.9%
271 (~208,000 km²) of croplands (Figure 2) and home to 28.4% of the total population of southern
272 and eastern Africa. Country specific predictions are reported in Tables S3-5.

273 The wild enset ensemble model identified a substantially broader range of suitable areas
274 (~1,270,000 km²), when compared to domesticated enset (906,000 km²). If we consider the
275 potential for future breeding to integrate wild enset genetic diversity and the associated
276 broader bioclimatic tolerance, ~1,375,000 km² is suitable for enset, encompassing 37.8%
277 (~361,000 km²) of the cropland in the study region. This represents a substantial further
278 expansion than if domesticated enset is considered alone.

279

280 **Areas suitable for enset cultivation under projected future climate**

281 Within its current Ethiopian range, enset cultivation is projected to contract by 10.8% under
282 RCP4.5 and 20.9% under RCP8.5 by 2070. However, if we account for the potential to shift
283 enset agriculture to all areas of suitability within Ethiopia, domestic enset's range could be
284 increased by 124.8% under RCP4.5 and 71.6% under RCP8.5. Across East and Southern
285 Africa, both RCP4.5 and RCP8.5 scenarios show pronounced reduction in the range suitable
286 for domesticated enset with respective declines of -31.3% and -47.4% by 2070 (Figure 4).
287 Under projected future climates, the range of suitability for wild enset exceeds that of

288 domesticated enset in most parts of the study area, thus the combined wild and domesticated
289 enset model predictions reduce climate change induced range contractions of the potential
290 enset cultivation area to -7% (RCP 4.5) and -29% (RCP 8.5). For 2050 scenarios see Figures
291 S4 and S5.

292 **Socioeconomic prioritization of enset adoption**

293 Using future bioclimatically suitable areas for 2070, we identified croplands characterised by
294 low crop diversity, minimal agricultural inputs and high population density with frequent
295 seasonal food security deficits. Based on this prioritization, we identify an additional current
296 population of 12.8 – 19 million Ethiopians (depending on scenario) for which enset
297 cultivation may be a beneficial, climate resilient asset to address food and nutritional
298 insecurity outside its current cultivation area. More broadly across East and Southern Africa
299 we identified 47 - 70.3 million people living in high priority areas, primarily localised to
300 southern Uganda, eastern Kenya and Western Rwanda (see Figure 5). When incorporating the
301 genetic potential of wild populations, enset cultivation might prove feasible for an additional
302 87.2 - 111.5 million people, 27.7 – 33 million of which are in Ethiopia outside of enset's
303 current cultivation range (see also Figures S6 and S7).

304 **4. Discussion**

305 **Niche shifts associated with domestication**

306 Comparison of wild and domesticated enset niches suggests that adaptation to on-farm
307 cultivation shifted the realised niche towards cooler maximum temperatures and increased the
308 importance of dry season precipitation. These changes are potentially indicative of the
309 transition from growth in a shaded, moist Afromontane forest environment, where water
310 availability is seasonally buffered, to cultivation in an open field environment. A requirement
311 for cooler maximum temperatures may have resulted in the moderate eastward expansion of

312 enset cultivation in Ethiopia to cropland at higher elevations. These bioclimatic limitations
313 suggest that for domesticated enset, better emulating the conditions of its wild environment
314 may contribute to broader bioclimatic tolerance, for example as a component of agroforestry
315 systems, as practiced in some parts of Sidama zone (Abebe *et al.* 2010). Nevertheless, wild
316 enset retains a broader overall niche space across all variables compared to domesticated
317 enset, commensurate with presumed greater extant genetic diversity and absence of a
318 domestication bottleneck. Surprisingly, the predicted suitability for both wild and
319 domesticated enset across southwestern Ethiopia (Figure 2), suggests that the absence of
320 contemporary wild populations across most of this range may have been due to extirpation,
321 either through habitat conversion (e.g. loss of forest cover (Friis *et al.* 2010)), overexploitation
322 (wild enset is inedible, but the leaves may be used (James S. Borrell *et al.* 2019)), lack of wild
323 seed dispersers or genetic swamping from domesticated lineages.

324 Whilst domestication in many other plant species has been associated with expansion outside
325 of their indigenous range (Diamond 2002), this has not occurred to any great extent in enset.
326 Our models show that Ethiopia is isolated from other centres of enset suitability by at least
327 450 km, potentially resulting in a barrier to dispersal. Indeed, much of what is known about
328 historic trade routes in Ethiopia suggests these were oriented towards Sudan and the Sahara as
329 well as the Red Sea coast to Arabia where no suitable conditions exist for enset cultivation
330 (Bent 1893; Pankhurst 1964). When combined with the additional barrier of indigenous
331 knowledge associated with intensive enset cultivation, the processing requirements, and the
332 fact that enset is propagated vegetatively which may travel less easily than seeds, this may
333 partly explain why enset was not adopted elsewhere. Nevertheless, this would not have
334 precluded concurrent domestication elsewhere in the wild range, as was likely the case for
335 other crops such as rice in Asia (Civáň *et al.* 2015), though no evidence for use of enset in
336 other cultures has been reported.

337 **Potential for expansion of enset cultivation**

338 We find that despite a highly restricted current distribution, there is significant potential for
339 climate-resilient enset expansion both within Ethiopia and across eastern and southern Africa
340 (Figure 4). The closest areas with high suitability are in Amhara and Oromia regions of
341 northern central Ethiopia. More widely, we also identify large areas of Kenya, Uganda and
342 Rwanda which are characterised by a similar highland climate. Overall, ensemble model
343 projections identified that 64.7% (~134,000 km²) of the cropland currently suitable for
344 domesticated enset cultivation lies outside of Ethiopia under current climatic conditions.

345 The integration of genetic diversity and useful traits from wild progenitor populations and
346 crop wild relatives is gaining increased attention as a pathway for climate change adaptation
347 (Brozynska *et al.* 2016; Migicovsky and Myles 2017). Here we illustrate this value by
348 showing that integrating crop wild relative diversity into enset breeding programmes may
349 enable broader climate tolerance. Under current climate, this could enable expansion of enset
350 cultivation by a further 144,000 km (15.1%) and under future scenarios up to ~73,000 km
351 (7.6%) of the current cropland in the study area. Wild diversity may offer additional benefits
352 beyond the potential for expansion. For example, higher fitness through improved tolerance of
353 higher temperatures, even within existing bioclimatic limits, could translate into yield
354 improvements (Zhao *et al.* 2017). Despite projected range declines for enset under high
355 emission climate change scenarios, more than ~54,000 km² (5.4%) of the current cropland are
356 projected to remain suitable for enset cultivation outside of Ethiopia by 2070.

357 **Socioeconomic suitability for enset cultivation**

358 Enset possesses a suite of traits that buffer acute food insecurity. We combined our climate
359 data with population, food insecurity and agricultural inputs data to identify regions and
360 communities with a similar socioeconomic context to those where enset is currently

361 successfully utilised. This approach revealed priority areas in Ethiopia, as well as Kenya,
362 Uganda and Rwanda with high future climate suitability, high rural population densities,
363 frequent seasonal food deficits, low agricultural inputs and low current crop diversity. While
364 achieving zero hunger is a major sustainable development goal (SDG2), agricultural
365 expansion risks undermining related global efforts to reduce biodiversity loss (Molotoks *et al.*
366 2017). Highly flexible and productive species such as enset provide one pathway for
367 improving local food security while minimising cropland expansion and resulting biodiversity
368 loss, particularly because environmental degradation may be highest during periods of acute
369 vulnerability, food insecurity and associated poverty (Asefa 2003).

370 **Remaining barriers to enset expansion**

371 Even if barriers are low, the uptake of novel cultivation practices represents a risk,
372 particularly for subsistence farmers (Meijer *et al.* 2015). Therefore, the bioclimatic and
373 socioeconomic matching performed here, offers no guarantee that farmers will perceive and
374 experience benefits. Previous approaches to disseminating agricultural innovations have
375 focused on demonstration farms, farmer-to-farmer learning and *in situ* inclusive development
376 of new approaches (Meijer *et al.* 2015), as part of extensive research on smallholder climate
377 adaptation (Bryan *et al.* 2009; Conway and Schipper 2011; Shikuku *et al.* 2017). Successful
378 examples include cassava (*Manihot esculenta*), which has expanded within Zambia to help
379 mitigate drought vulnerability and associated food shortages (Barratt *et al.* 2006). However,
380 we identify two remaining barriers that will require social and political approaches to
381 overcome. First, Ethiopia currently restricts the international transfer of plant material to
382 protect indigenous bioresources from inequitable exploitation (Tesgera 2019). Thus expansion
383 outside of Ethiopia would depend on bilateral Access and Benefit Sharing Agreements, the
384 implementation of which is highly variable internationally (Robinson *et al.* 2020). Second, the
385 contemporary distribution of enset cultivation is currently closely associated with cultural

386 groups who hold the required knowledge (Olango *et al.* 2014). This highlights that both
387 knowledge as well as plant material would need to be fairly and equitably shared for
388 successful transfer of enset cultivation (Swiderska 2006).

389 **Conclusions**

390 Expanding the range of cultivation of currently underutilised crops has significant potential to
391 support the diversification and resilience of global agrisystems under climate change.
392 Unifying interdisciplinary approaches involving both bioclimatic and socioeconomic
393 suitability may help prioritise communities for agricultural development interventions,
394 making successful adoption more likely. Whilst this represents a challenge to existing
395 agrisystem and food networks, it is also an opportunity to adopt an improved suite of
396 climate-resilient crops with multiple food security co-benefits.

397

398

399 **Funding and Acknowledgements**

400 This work was supported by the GCRF Foundation Awards for Global Agricultural and Food
401 Systems Research, entitled, ‘Modelling and genomics resources to enhance exploitation of the
402 sustainable and diverse Ethiopian starch crop enset and support livelihoods’ [Grant No.
403 BB/P02307X/1] and the GCRF I-FLIP grant ‘Enhancing enset agriculture with mobile agri-
404 data, knowledge interchange and climate adapted genotypes to support the Enset Center of
405 Excellence’ [BB/S018980/1]. JB was additionally supported by a Future Leader Fellowship at
406 the Royal Botanic Gardens, Kew.

407 **Author contributions**

408 OK and JB designed the study. JB and WA collected field observation. OK performed the
409 analyses, with SP, IO and JB providing technical input. JB and PW secured funding. JB
410 provided supervision. OK prepared the first draft and all authors contributed to the
411 interpretation of the results and preparation of the final manuscript.

412 **Data Availability**

413 Any data that support the findings of this study as well as the generated spatial data are
414 available on Figshare (<https://doi.org/10.6084/m9.figshare.16455648>) under the CC BY 4.0
415 licence.

416 **Conflict of Interest**

417 The authors declare no conflict of interest.

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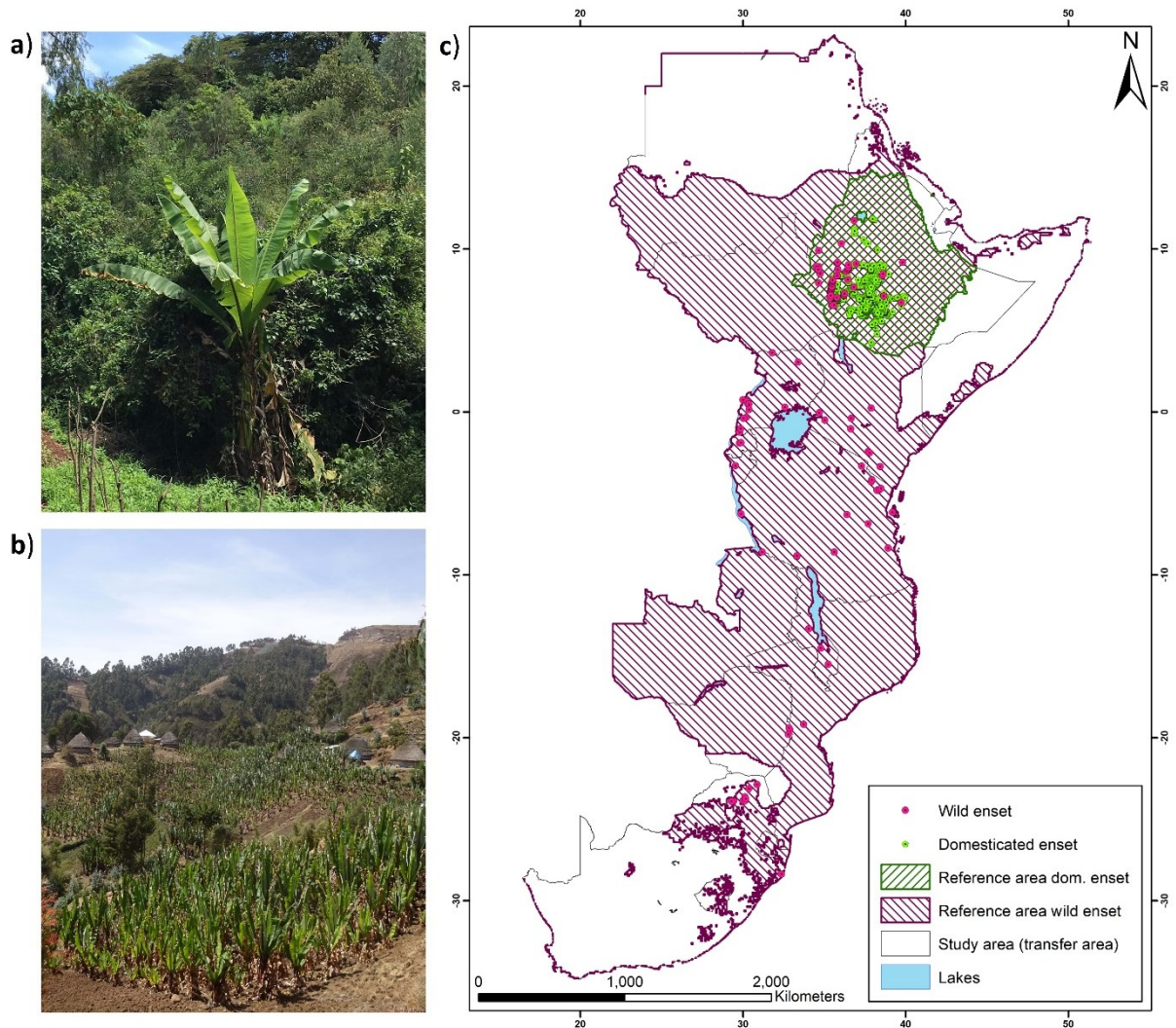
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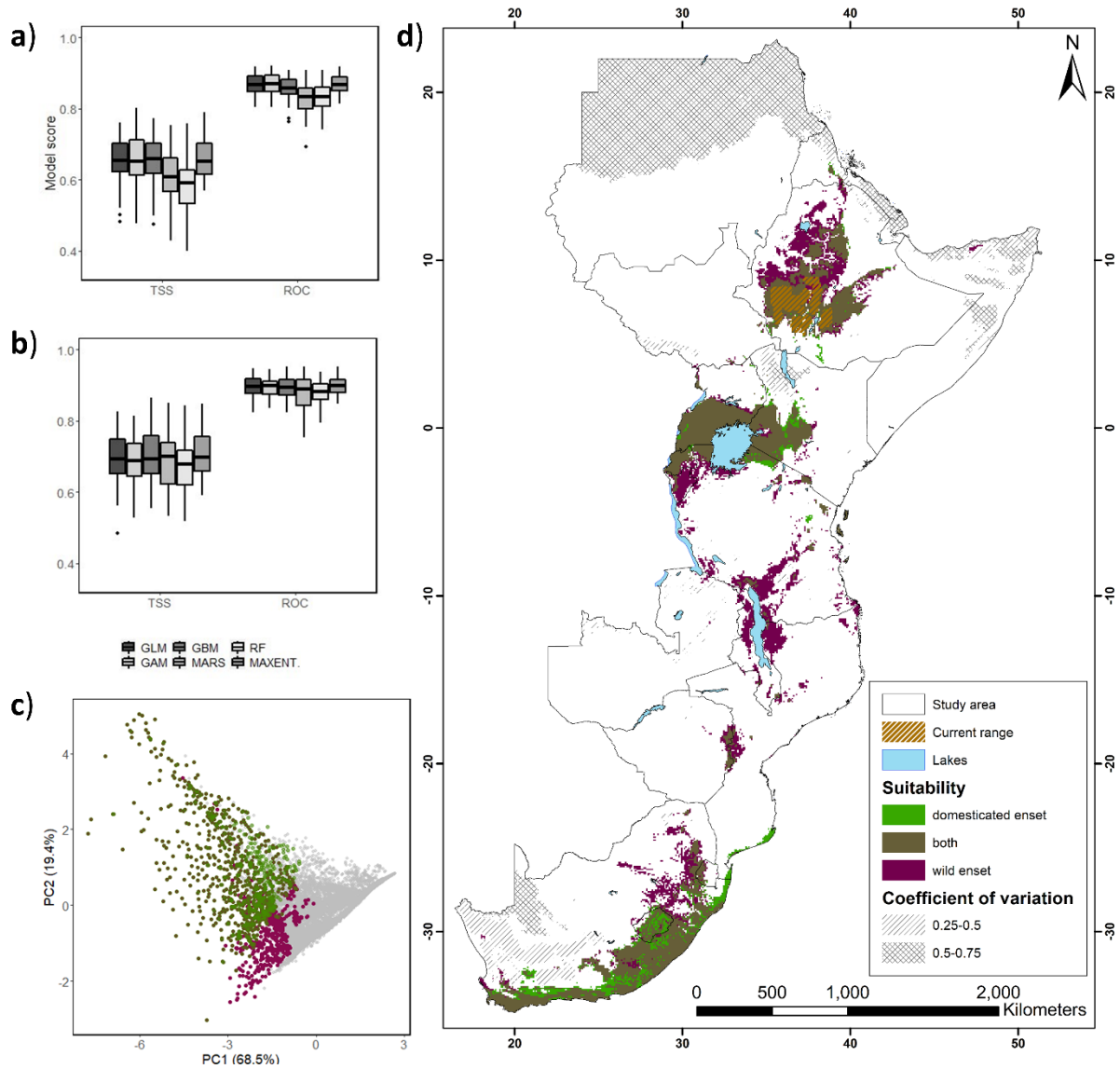
626

627 **Figures**



629 **Figure 1. Extent of the study area in eastern and southern Africa and distribution data**
630 **for wild and domesticated enset.** a) Image of wild enset from a river valley near Bonga,
631 Ethiopia. b) Cultivated enset from Basketo region, Ethiopia. c) Locations of 90 wild and 414
632 domesticated enset observations.

633

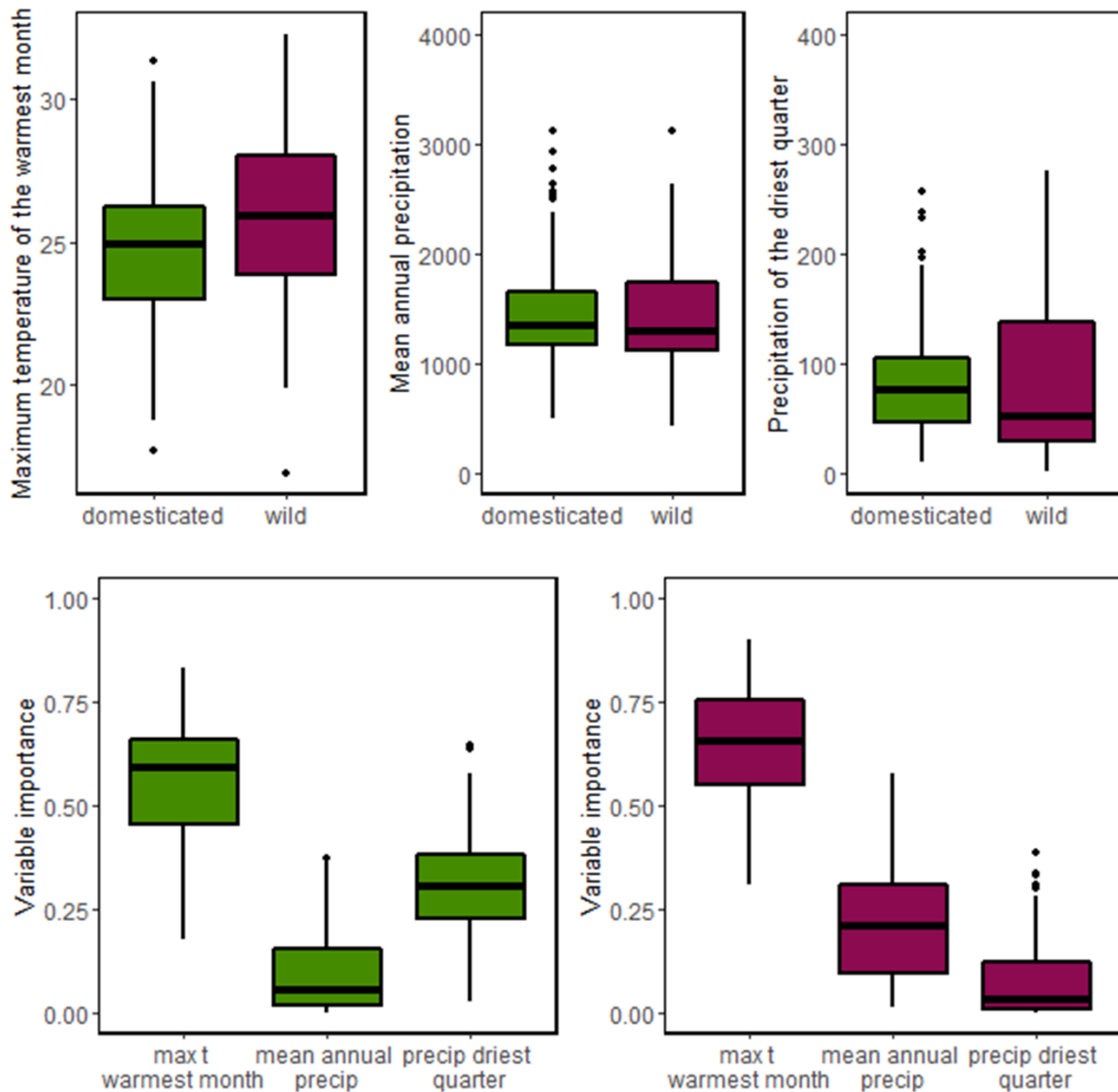


634

635 **Figure 2. Potential suitability for domesticated and wild enset under current climate and**
636 **expansion potential integrating the bioclimatic tolerance of wild enset populations. TSS and**
637 **ROC scores across distribution modelling algorithms for a) domesticated and b) wild enset**
638 **models. c) Comparison of the potential niche of enset in environmental space based on**
639 **principal component analysis of bioclimatic variables. Grey denotes background points. d)**
640 **binary representation of suitability, generated using the maximized TSS. The coefficient of**
641 **variation shows the degree of uncertainty across model predictions.**

642

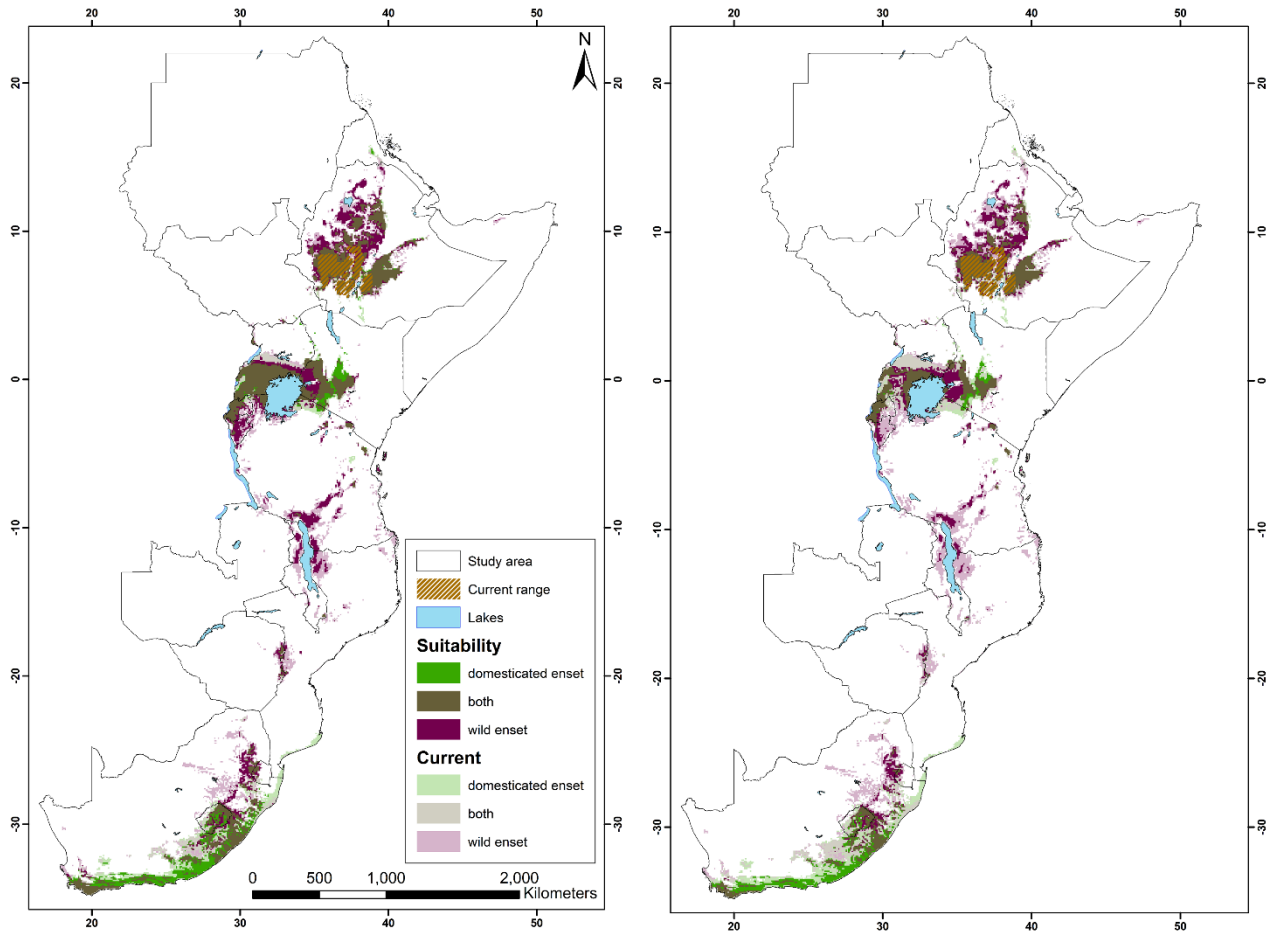
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644

645 **Figure 3. Comparison of the importance and range of bioclimatic variables for wild and**
646 **domesticated onset.** Bioclimatic values at onset presence points and model variable
647 importance. While maximum temperature of the warmest month is significantly lower for
648 domesticated onset ($t(113) = 3.74, p < 0.001$), differences in mean annual precipitation and
649 driest quarter precipitation are non-significant.

650



652 **Figure 4. Suitability range change for wild and domesticated enset for 2070 under a)**
653 **RCP4.5 and b) RCP8.5 scenarios. Projections for 2050 are provided in the supplementary**
654 **materials figures S4 and S5.**

655

656

