

1 **The climatic challenge: Which plants will people use in**
2 **the next century?**

3 **Borrell J.S.^{1*}, Dodsworth S.², Forest, F.¹, Perez-Escobar O.¹, Lee M. A.¹, Mattana E.³, Stevenson P.C.^{1,4},**
4 **Howes M.-J.R.^{1,5}, Pritchard H.W.³, Ballesteros D.³, Kusumoto B.^{1,6}, Ondo I.¹, Moat J.¹, Milliken, W. ³,**
5 **Ryan P.¹, Ulian T.³, Pironon S.¹**

6 ¹Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK.

7 ²School of Life Sciences, University of Bedfordshire, Luton, LU1 3JU, UK.

8 ³Royal Botanic Gardens, Kew, Wellcome Trust Millennium Building, Wakehurst Place, Ardingly, West
9 Sussex, RH17 6TN, U.K.

10 ⁴Natural Resources Institute, University of Greenwich, Chatham, ME4 4TB, U.K.

11 ⁵Institute of Pharmaceutical Science, King's College London, London, SE1 9NH, UK.

12 ⁶Faculty of Science, University of the Ryukyus, Nishihara, Okinawa, Japan

13

14 ***Corresponding author:** J. S. Borrell (J.borrell@kew.org); Royal Botanic Gardens, Kew, Richmond,
15 Surrey, TW9 3AE, UK.

16

17

18

19

20

21

22

23 **Abstract**

24 More than 31,000 useful plant species have been documented to fulfil needs and services for humans
25 or the animals and environment we depend on. Despite this diversity, today humans satisfy most
26 requirements with surprisingly few plant species; for example, just three crops – rice, wheat and maize
27 – comprise more than 50% of plant derived calories. Here, we synthesize the projected impact of
28 global climatic change on useful plants across the spectrum of plant domestication. We illustrate the
29 demographic, spatial, ecophysiological, chemical, functional, evolutionary and cultural traits that are
30 likely to characterise useful plants and their resilience in the next century. Using this framework, we
31 consider a range of possible pathways for future human use of plants. These are centred on two trade-
32 offs: i) *diversification* versus *specialization* in the range of species we utilize, and ii) *substitution* of the
33 species towards those better suited to future climate versus facilitating *adaptation* in our existing suite
34 of dominant useful plants. In the coming century, major challenges to agriculture and biodiversity will
35 be dominated by increased climatic variation, shifting species ranges, disruption to biotic interactions,
36 nutrient limitation and emerging pests and pathogens. These challenges must be mitigated, whilst
37 enhancing sustainable production to meet the needs of a growing population and a more resource
38 intensive standard of living. With the continued erosion of biodiversity, our future ability to choose
39 among these pathways and trade-offs is likely to be diminished.

40

41

42

43

44 **Keywords:** Biodiversity, climate change, conservation, crop breeding, crop wild relatives,
45 domestication, food security, medicinal plants, sustainable development, resilience.

46 **1. Introduction**

47 As human population increases and the standard of living improves over the next century, our reliance
48 on the effective and efficient utilisation of plants will grow (Godfray et al., 2010; Guo, Zhang, & Li,
49 2010). In this review our definition of useful plants follows RBG Kew (2016) in the broadest sense, as
50 “plant species which have been documented as fulfilling a particular need for humans, animals or the
51 wider environment”. Of the approximately 400,000 vascular plant species known to science, around
52 8% (31,000) have documented uses (RBG Kew, 2016), encompassing human and animal foods, fuels,
53 medicines, materials and crop wild relatives, and we note that many more species may be as yet
54 undocumented. While crop plants are perhaps most familiar, more than half of documented useful
55 plants (57%) are used for medicines and twice as many are used for materials (36.5%) than as foods
56 (17.8%) (Farnsworth & Soejarto, 1991; RBG Kew, 2016).

57 Global biodiversity loss as a result of habitat conversion, overexploitation and climate change is
58 projected to result in a 7-24% decline in vascular plant diversity by 2050 (C. Bellard, Bertelsmeier,
59 Leadley, Thuiller, & Courchamp, 2012; Vuuren, Sala, & Pereira, 2006), with climate adaptation
60 becoming a key challenge for many plant species over the next century. The impacts of climate change
61 are predicted to – and in many cases have already been demonstrated to – fundamentally alter several
62 aspects of plant biology including genomic architecture (Ahuja, de Vos, Bones, & Hall, 2010),
63 development (Gray & Brady, 2016), phenology (Springate & Kover, 2014), biotic interactions (Eckert
64 et al., 2010), demography (Miller & Gross, 2011) and distribution (Pecl et al., 2017). This in turn may
65 strongly impact on the quality and yield of the material and non-material products and benefits we
66 derive from them (Challinor et al., 2014; DaMatta, Grandis, Arenque, & Buckeridge, 2010).

67 An estimated 2,500 plant species from 160 taxonomic families have been altered by human selection
68 in the ~12,000 years since human plant domestication began (Smýkal, Nelson, Berger, & von
69 Wettberg, 2018; Zeven & de Wet, 1982). These species have been subjected to a spectrum of
70 domestication effort (Hammer & Khoshbakht, 2015; Meyer, Duval, & Jensen, 2012; Meyer &

71 Purugganan, 2013), with only around 200 species considered to be extensively domesticated (Meyer
72 et al., 2012; Vaughan, Balázs, & Heslop-Harrison, 2007), including, for example, extensively engineered
73 crops with annual production measured in the millions of tons (e.g. rice (*Oryza sativa*); Gross and Zhao
74 2014; Muthayya et al. 2014). By contrast, there is a substantially greater number of less extensively
75 utilised species, cultural, shade and ornamental plants, poisons and medicines harvested on a small
76 scale from wild or semi-wild populations (e.g. bamboo shoots (*Bambusa* sp) in western Thailand,
77 Delang, 2006; Ogle et al., 2003; Schippmann et al., 2002) which have been the subject to little or no
78 human-directed selection (Figure 1). Understanding how climate change will impact these useful
79 plants is critical to developing climate-resilient strategies that are sustainable and continue to derive
80 societal benefits from the plants we depend on. Climate change is a global multi-factor phenomenon
81 which includes increased temperatures, rising CO₂ concentrations and UV intensity, as well as changes
82 to the frequency and magnitude of rainfall events, including drought and flooding (IPCC, 2013). Useful
83 plants have been domesticated based on current (or recent past) growing conditions, and in the
84 future, may therefore experience very different conditions than they do today.

85 Typical features that mark a crop's divergence from a wild ancestor are together termed the
86 'domestication syndrome' (Harlan, 1971). These often include traits such as seed retention, increased
87 fruit or seed size or palatability, modified nutritive values (including increased protein, fat or sugar
88 content), rapid growth rates, altered reproductive strategy, changes in secondary metabolites, and
89 reduced resource allocation towards non-edible plant tissues as well as pest and pathogen defence
90 (Meyer et al., 2012). Domestication can therefore sometimes work against natural selection, resulting
91 in reduced fitness in a wild setting (Meyer et al., 2012), with knock-on impacts to beneficial insects
92 through changes to floral chemistry that in wild populations supports healthier pollinators (Egan et
93 al., 2018). Given projected future pressures, existing or newly domesticated plants may increasingly
94 be selected for tolerance to climatic variation, nutrient limitation (e.g. increased cost or reduced
95 availability of industrial fertilisers, and/or soil degradation) and emerging pests and pathogens,
96 generating in some cases a novel future 'domestication syndrome'. To better understand these

97 challenges, we explore a representative series of useful plant characteristics that are expected to be
98 impacted by climate change, from small to large scale (e.g. from genes to geographic distribution) and
99 from intrinsic to extrinsic factors (e.g. from physiological traits to pollination or human cultural
100 preferences). We survey phylogenetic position, geographic distribution, biotic interactions,
101 morphological traits and cultural importance - to consider likely indicators of future success in the
102 context of climate change and human utilization. Importantly, we consider these characteristics across
103 the domestication spectrum, along which is distributed the tremendous global diversity of useful
104 plants, from widely-domesticated crops to rare species harvested from the wild.

105 We align our review with a range of possible future strategies to meet these challenges (Figure 2).
106 These strategies are characterised by the interaction of two spectra; first, the trade-off between
107 replacing the major species we elect to use to better fit future environmental conditions (*Substitution*)
108 and selecting for improved performance from our existing species (*Adaptation*). Concurrently, society
109 faces a choice between an increasingly narrow suite of highly domesticated species (*Specialization*) or
110 substantially increasing the number of highly utilised species (*Diversification*). Our aim is to stimulate
111 discussion on the likely trajectory for useful plants under climate change as well as highlighting
112 opportunities and trade-offs, whilst better informing the option-values of strategies to sustainably
113 meet the growing human requirements we derive from useful plants.

114 **2. The evolutionary history of useful plants**

115 Several studies have investigated the phylogenetic distribution of useful plants, mostly using
116 angiosperm-wide or regional (i.e. flora) phylogenetic trees (Q. C. B. Cronk & Forest, 2017; Saslis-
117 Lagoudakis et al., 2012). Equally, many have explored the potential of phylogenetic trees for the
118 identification of species closely related to plants with chemical compounds of interest (i.e. so-called
119 “bioprospecting”) or crop wild relatives (Ernst et al., 2016; Halse-Gramkow et al., 2016). Fewer studies
120 however have directly addressed the effect, using a phylogenetic framework, that future climate

121 change might have on the conservation and preservation of plants useful for humans (Edwards, Still,
122 & Donoghue, 2007).

123 **2.1 The phylogenetic distribution of useful plants**

124 Plants that humans use tend to be phylogenetically clustered (Cronk, 2008; Cronk and Forest, 2017;
125 Meyer and Purugganan, 2013; Moerman, 1991; though see Şerban et al., 2008), and similarly, there is
126 initial evidence that the types of services or products plants provide may also be clustered (Cámara-
127 Leret et al., 2017). Patterns of plant use appear to depend on how common the use is, how common
128 the underlying trait is amongst plant taxa, and how phylogenetically close the taxa are to commonly
129 encountered plants (Cámara-Leret et al., 2017). For instance, a global analysis of plant utilisation
130 showed that common uses are more likely to show phylogenetic clustering than uncommon ones (Dai,
131 Zhang, Xu, Duffy, & Guo, 2017). Conversely, there is also evidence of phylogenetic clustering in plant
132 extinction risk (Forest et al., 2007; Vamosi & Wilson, 2008) suggesting that entire groups of functional
133 traits or uses could be universally vulnerable (Bascompte, Garcia, Ortega, Rezende, & Pironon, 2019).

134 At the broadest scale, most useful plants are angiosperms (Meyer et al., 2012), although there are
135 some key products derived from other plant groups, in particular from gymnosperms (e.g., pine nuts,
136 timber, medicinal compounds). Highly domesticated food crops show the clearest phylogenetic
137 clustering (Figure 3), however when all food plants (including spices) are considered, Şerban et al.
138 (2008) found little evidence of clustering in the angiosperm tree of life. This study, however,
139 encompasses plants consumed by humanity as a whole; it would be interesting to evaluate the
140 phylogenetic distribution of these species in cultural groups rather than in its entirety. Phylogenetic
141 analyses of useful plants in general have also been limited by lack of documentation on many
142 underutilised species, which is now beginning to be addressed (RBG Kew, 2016).

143 Most human calories consumed globally, are derived from only a handful of crops (e.g., rice, wheat
144 and maize) from the grass family (Poaceae). Within the remaining top 10 families globally utilised for
145 human calorific intake (FAO, 2015), the number of species from the bean family (Fabaceae) are

146 similarly ubiquitous (e.g. globally important soybean or lesser-used groundnuts; Smýkal *et al.* 2014)
147 while the majority of the remaining species dominating the human diet belong to only a handful of
148 other families such as Solanaceae (nightshades; potatoes), Arecaceae (palms; palm oil) and Asteraceae
149 (daisies; sunflower oil). This bias may reflect both the history of domestication of these taxa (i.e.
150 closely related species may be favoured through cultural experience and familiarity), but also the
151 natural presence of desirable traits among closely related species (i.e. nutritious, low toxicity).

152 More plant species are used for medicines, than for food (RBG Kew, 2016). These plants are more
153 widely dispersed across the plant tree of life, but still tend to show a degree of phylogenetic clustering,
154 likely as a result of complex secondary metabolite pathways that are perhaps less likely to evolve many
155 times independently (Halse-Gramkow *et al.*, 2016; Moerman, 1991). In a study focussing on the plants
156 used in traditional medicine in three distinct regions (New Zealand, Nepal, South Africa), Saslis-
157 Lagoudakis *et al.*, (2012) showed that the medicinal plants of these three floras share phylogenetic
158 patterns, indicating that related plants from the three regions are used to treat similar ailments, which
159 in turn suggests independent discoveries of medicinal properties. Garnatje *et al.*, (2017) termed this
160 'ethnobotanical convergence' and, where combined with 'omics', suggested that it has the potential
161 to identify new potential applications for plants.

162 **2.2 Genomic resources for useful plants**

163 Genomic resources are crucial for effective crop breeding, and the transition of species from
164 underutilised into extensively domesticated crops (or to push them further along the domestication
165 spectrum). Our understanding of the angiosperm phylogenetic tree is being further enhanced and
166 shaped by large-scale phylogenomic projects (e.g. 1KP, Kew's Plant and Fungal Trees of Life; Eiserhardt
167 *et al.*, 2018). The new detailed phylogenetic understanding provided by these programmes is crucial
168 for two main reasons. First to determine the directionality of evolution of particular traits (including
169 their genetic or genomic basis), and secondly to identify the wild relatives of crops, trace in time and
170 space their domestication and estimate their genetic divergence (Chomicki & Renner, 2014). New and

171 even larger genome sequencing initiatives aimed at sequencing the diversity of underrepresented
172 plant lineages, (e.g. 10KP; Cheng et al., 2018), will help to alleviate the current bias in genomic
173 resources, but they need to be matched by further biological characterisation of these taxa.

174 Combining such phylogenetic frameworks with ethnobotanical (Cámara-Leret et al., 2017), climatic,
175 trait and usage data (Ernst et al., 2016) will allow more sophisticated predictions of where and how
176 particularly useful traits have evolved across the angiosperm tree of life. Using biological responses to
177 plant extracts rather than standard categories may permit more phylogenetically diverse predictions
178 for bioprospecting, for instance in the medicinally important genus *Euphorbia* (Ernst et al., 2016). Such
179 approaches could permit identification of which species and traits could be used for breeding to
180 tolerate climate change (Mehrabi, Pironon, Kantar, Ramankutty, & Rieseberg, 2019), and in turn,
181 permit the identification of more diverse and unexpected uses for plants than would otherwise have
182 been the case.

183 The identification of new useful plants may also need to consider the context of hybridisation and
184 ploidy (i.e. cytogenetic information), particularly with accelerated range shifts and species
185 introductions. Many crop plants are polyploids, often allopolyploids (Meyer et al., 2012), the latter
186 resulting from hybridisation between species as well as whole genome duplication (e.g. *Triticum*
187 *aestivum* – allohexaploid bread wheat; *Solanum tuberosum* – allotetraploid potato). The result is more
188 than two sets of chromosomes with distinctive sub-genomes (from each parental donor). This can
189 result in reproductive isolation from crop wild relatives (which is an important consideration in
190 breeding efforts) but also impacts how species adapt and evolve in response to climate shifts and
191 other ecological factors (Soltis & Soltis, 2016).

192 **3. The impact of climate change on the distribution of useful plants**

193 **3.1 The impact across biomes**

194 Climate is a major driver of the spatial distribution of biodiversity (C. Bellard et al., 2012; Hoffmann &
195 Sgró, 2011), exerting a strong influence on the availability of various plants useful to humans around
196 the world. Changing climate is anticipated to result in a significant redistribution of the material and
197 non-material benefits provided by nature (Mooney et al., 2009), though this impact may differ among
198 regions, useful plant species and use types. Boreal and hemi-boreal areas, for example, are expected
199 to experience important climatic modifications with novel and disappearing climates mainly found in
200 north-eastern North America and Asia (Williams, Jackson, & Kutzbach, 2007). Given their relatively
201 poor species richness and endemism in both wild and cultivated useful plants (Pironon et al., *in*
202 *review*), poleward range extirpations might only affect a relatively limited number of species and
203 potential uses. However, increasing local losses could ultimately lead to global extinctions and,
204 additionally, it could strongly impact the lives of local indigenous populations given their poorer access
205 to replacement options (Garnett et al., 2018). On the other hand, boreal areas represent potential
206 opportunities for the expansion of both wild and domesticated species currently found at lower
207 latitudes (Odgaard et al., 2011, but see also Bebber et al., 2013). Temperate and Mediterranean useful
208 plants may therefore undergo range expansion at higher latitudes, despite declines at their rear-edge.
209 Although rear-edge populations of wild plants may be highly threatened by climate change, they have
210 often persisted under major past climatic fluctuations and contain unique and valuable adaptive
211 genetic diversity (Borrell et al., 2018; Hampe and Petit, 2005). Regions with highly heterogeneous
212 landscapes may facilitate the pursuit of suitable climatic conditions by species at a relatively small
213 scale, and therefore favour their persistence and survival (Ohlemüller et al., 2008). Despite the fact
214 that large negative effects have been observed, climate change tends to impact cultivated plants at a
215 lower intensity in temperate areas, in part because of the higher economic and technological capacity
216 of many countries in these regions (Challinor et al., 2014; Donatelli, Srivastava, Duveiller, Niemeier,
217 & Fumagalli, 2015; D. B. Lobell & Field, 2007), although well fertilized modern crop varieties seem
218 more sensitive to heat related losses (Schlenker & Lobell, 2010).

219 The impact of climate change on useful plants may be more severe in the tropics due to generally
220 more persistent food insecurity and a reduced capacity for agricultural adaptation (Muller, Cramer,
221 Hare, & Lotze-Campen, 2011). Large parts of the current tropical climatic space are predicted to
222 disappear together with the emergence of novel climates (C. Bellard et al., 2012; Céline Bellard et al.,
223 2014; Williams et al., 2007). Climate change may more acutely threaten the most important hotspots
224 of useful plants, both in terms of species richness and endemism (Pacifci et al., 2015, Pironon et al.,
225 *in review*). Major modern crops such as wheat, maize and rice have been observed to be highly
226 impacted by recent changes in temperature and precipitation regimes in the tropics (Challinor et al.,
227 2014; D. Lobell, Schlenker, & Costa-Roberts, 2011). Mountainous areas are potentially at greater risk
228 in the tropics where species tend to shift their ranges along topographical or habitat features rather
229 than latitude (Rumpf et al., 2018). Moreover, ongoing climate change is outpacing past climatic
230 modifications, which represents a major issue for tropical plants that evolved relatively slowly along
231 elevation (Morueta-Holme et al., 2015; VanDerWal et al., 2012), as opposed to temperate plants that
232 have been exposed to significant range shifts over past glaciations (Qian & Ricklefs, 2016).

233 There may be benefits to some localized agricultural systems as, for example, the number of cultivable
234 species is observed to increase on the elevational gradient from subtropical lowland to alpine in the
235 Himalayas (Chaudhary & Initiatives, 2016). For species such as coffee, climatically suitable areas are
236 predicted to shift from lowland to higher elevation (Moat et al., 2017), with losses partially
237 compensated by newly emerging climatically suitable areas in Indonesia (Schroth, Läderach, Blackburn
238 Cuero, Neilson, & Bunn, 2015) or Ethiopia (Moat et al., 2017). Overall, cultivation of useful plants is
239 likely to be characterised by accelerated re-distribution of species and agri-systems, with future
240 usefulness of plants potentially favouring those that are easier to transition to new locations or
241 environments, as well as species with lower inputs or better documented indigenous knowledge
242 management requirements. However, for non-cultivated useful plants which represent the largest
243 diversity of species used by human populations, relocation potential seems more limited.
244 Representing a major option value for humans, non-domesticated useful plants will therefore require

245 strong *in-situ* conservation efforts accounting for species natural dispersal following climate change
246 (Corlett & Westcott, 2013).

247 **3.2 The impact of range rarity**

248 Sensitivity to climate change does not only vary among regions (i.e. species range position) but also
249 among species. Species range size represents an important biogeographical feature often related to
250 vulnerability and extinction (Saupe et al., 2015). Under climate change, narrow ranged species are
251 expected to be at high risk due to shrinking habitat and low potential to reach new suitable areas
252 (Ohlemüller et al., 2008). The tropics may be at higher risk due to their expected higher turnover in
253 climatic conditions, and their extremely high concentration of endemic plant species, narrowly-
254 distributed human cultures, and therefore plant uses (Pironon et al., *in review*). Some of the
255 detrimental effects of climate change on useful plants have already been perceived by local
256 communities, such as in the Sierra Nevada del Cocuy-Güicán of Colombia, where climate change,
257 together with unsustainable land use and overharvesting are causing a decline in medicinal plant
258 resources (Rodríguez, Angueyra, Cleef, & Van Andel, 2018). Moreover, narrow-ranged species and
259 tropical areas might be even more vulnerable because they are also expected to be particularly
260 impacted by other global change drivers such as land use change or biotic invasions. On the other
261 hand, wide-ranged species have been demonstrated to have a high adaptability to changes in climatic
262 conditions (Newbold et al., 2016), even though many wild plants might not be able to expand quickly
263 due to dispersal lag (Svenning et al., 2008). It is also important here to note that the ecological niche
264 occupied by a species will also affect its ability to adapt to climate change, and that this might be
265 uncorrelated to its geographic range (i.e. a species with a large distribution range could more easily
266 be obliterated should it have a narrow ecological niche). For example, wetland rice, which is cultivated
267 globally, is more vulnerable to heat stress by climate change compared with other key crops (Teixeira,
268 Fischer, Velthuisen, Walter, & Ewert, 2013).

269 Overall, in this context, useful plants might suffer relatively less from extinction than other wild plants
270 as the geographical ranges of many have been largely expanded and intensified by humans through
271 some level of domestication, breeding, agricultural practices, global trade, or accidental introduction
272 (Coradin et al., 2018; Dempewolf et al., 2014; C. K. Khoury et al., 2014; Colin K. Khoury et al., 2016).
273 Future manipulation of useful plant distributions - and mitigation of negative climate change
274 repercussions on plant derived benefits - will be dependent on accurate climate projections enabling
275 identification of appropriate species and areas to utilise or cultivate across the landscape (Pironon *et*
276 *al. in review*). As a result, underutilized narrow-range or narrow-niche plants might represent
277 important targets for short-term conservation actions (Padulosi, Heywood, Hunter, & Jarvis, 2011),
278 perhaps through domestication.

279 **4. The impact of climate change on biotic interactions with useful plants**

280 A large proportion of plants, including those useful to humans, depend on biotic interactions for
281 pollination, predation of pest herbivores, seed dispersal, or persist where herbivores or harmful pest
282 and pathogens do not. Here, we predominantly consider insect interactions relating to pollination and
283 pests, as these are among the most extensively researched, though we note the importance of
284 interactions between pests and pathogens, seed dispersers, rhizobial symbionts and mycorrhizal
285 associations. Evidence about how climate change influences plant-insect interactions is growing and
286 indicates that these changes can have a negative impact, notably for pollination (Eckert et al., 2010)
287 and beneficial tri-trophic interactions such as those provided by natural pest regulation (Dyer,
288 Richards, Short, & Dodson, 2013), but may also exacerbate the occurrence of pests (Deutsch,
289 Tewksbury, & Tigchelaar, 2018).

290 **4.1 The impact on plant-pollinator interactions**

291 Outcomes for pollination include increased selection for selfing and perennialism (Otto, 2018),
292 reduced phenological and distributional overlap between plants and their pollinators, and decreased
293 variety in forage for pollinators (Memmott, Craze, Waser, & Price, 2007; Solga, Harmon, & Ganguli,

294 2014). *In extremis* the outcome may be the extinction of pollinators, plants or their interactions
295 (Bascompte et al., 2019; Memmott et al., 2007). The consequences of changing climate on pollinators
296 may not be fully apparent for decades (Burton & Lim, 2005) although severe discrete effects appear
297 likely in some circumstances (Garibaldi et al., 2016). While responses by plants and pollinators to
298 increasing temperature may occur concurrently, there is considerable variation in the direction and
299 magnitude of the response (Hegland, Nielsen, Lázaro, Bjerknes, & Totland, 2009) suggesting potential
300 spatial and temporal mismatch. For example, plants may flower earlier with increasing temperature
301 (Fitter & Fitter, 2002; Penuelas, 2002) but first emergence of pollinators may be slower to respond
302 (Gordo & Sanz, 2005; Hegland et al., 2009), and the success of pollination services is highly dependent
303 on synchrony between flower and pollinator. This is particularly apparent in highly specific pollinator
304 plant interactions. The first flight date of the solitary bee *Andrena nigroaenea*, advances more in
305 response to higher temperatures than the flowering date of the orchid *Ophrys sphegodes* which *A.*
306 *nigroaenea* males inadvertently pollinate through pseudocopulation owing to the flower mimicking
307 the odour and appearance of the female bee (Ayasse et al., 2000). Ironically, advanced emergence of
308 both genders leads to greater competition for males by female bees with the plant losing out. Small
309 temperature rises increase the probability of males and females flying at the same time and before
310 orchid flowering, reducing the frequency of pseudocopulation and pollination success for the flower
311 (Robbirt, Roberts, Hutchings, & Davy, 2014).

312 Pollinator ranges are also fluctuating, in some cases characterized by migration to cooler latitudes and
313 higher altitudes, although these changes are not always compensated at opposing range limits (Potts
314 et al., 2016). For example, in 67 bumble bee species across Europe and North America, southward
315 range contractions of up to 300 km have been recorded compared to historical distributions, with
316 closely related species showing similar shifts – yet typically the northward range expansions are
317 limited by availability of forage, particularly for oligolectic species and specialists since plant range
318 expansions are too slow. This results in an overall range contraction with potential temporal and
319 spatial mismatches for plants dependent on these pollinators (Bascompte et al., 2019; Kerr et al.,

320 2015). Changing pollinator ranges could lead to a loss in pollinator diversity or abundance leading to
321 lower food production (Potts et al., 2016). Seasonal behaviour and ranges of many pollinators may
322 change but differentially, leading to disruption of life cycles, plant-pollinator interactions and
323 population structure and composition (Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008). Different
324 groups of pollinators may be too slow to adapt to rapid temperature changes disrupting crop
325 pollination especially if the overlap of climatic conditions for crops and their pollinators is limited
326 (Giannini et al., 2013; Polce et al., 2014; Settele et al., 2016).

327 The combined and interactive effects of different stressors (e.g. pesticide exposure, diseases, habitat
328 loss and climate change) for pollinators are also predicted to be important (Vanbergen et al., 2013).
329 Thus, the likely consequences of multiple interacting factors such as habitat loss exacerbated by
330 climate change may lead to greater impacts on pollination services by limiting capacity to compensate
331 for range shifts (Thorne et al., 2010). This may lead to landscapes dominated by adaptable generalists
332 at the expense of less adaptable specialists (Settele et al., 2016), with consequences for plants with
333 specialist pollinator syndromes. For example, butterfly species that were mobile and habitat
334 generalists increased in distribution consistent with exploiting warmer temperatures whereas less
335 motile generalists and habitat specialists declined in distribution consistent with being limited by
336 habitat loss (T. Warren, 2001). So, the combined effects of landscape and climate may cause specialists
337 to decline, reducing population diversity and placing plant species at risk.

338 Changes to climate other than temperature may also detrimentally impact biotic interactions. Cocoa
339 production for example is uniquely dependent upon the pollination services of Ceratopogonid midges
340 (Bogdanski et al., 2008). There is increasing evidence that pollinator limitation (Forbes and Northfield,
341 2015; Groeneveld et al., 2010) is influenced by drought rather than temperature since the lifecycle of
342 the pollinator relies on high forest floor moisture for larval development (Arnold et al., 2018). It is
343 possible that similar impacts may manifest themselves in wild populations of *Theobroma* species
344 influencing future diversification within the genus, since it shows greater diversity at lower altitudes

345 that may be warmer and wetter (Richardson, Whitlock, Meerow, & Madriñán, 2015) and changes to
346 this status may influence diversity and abundance of pollinators and their services in different
347 habitats.

348 **4.2 The impact on pest regulation**

349 Trophic interactions where beneficial invertebrates provide natural pest regulation may also be
350 affected, particularly since the natural enemies of many pests also rely on non-crop habitats for food,
351 refuge and as alternative hosts (Gurr, Wratten, Landis, & You, 2016). However, by comparison to
352 pollinators much less is reported about natural enemies of pests. Dyer et al. (2013), for example,
353 report that higher temperatures and CO₂ concentrations led to developmental asynchrony between
354 the parasitic wasp *Cotesia marginiventris* and its host, the larvae of the moth *Spodoptera exigua*, and
355 in some cases, to the mortality of the wasp. More recently, Roslin et al., (2017) reported that insect
356 predation increases towards the Equator and lower elevations suggesting a strong association with
357 higher temperature which may influence the range and effectiveness of natural regulation of pests
358 with consequences for crop production. Thus, natural pest regulation that is dependent on insect
359 predators or parasitism may decline as a direct consequence of a changing climate, which could
360 particularly impact plants that have been domesticated and are now cultivated at large scales.

361 Climate may also influence the severity and temporal phenology of herbivory that may result in major
362 consequences for useful plants. This is particularly so for domesticated species that have been bred
363 for uniform traits so are more susceptible to major outbreaks of insects. For example, the tent
364 caterpillar *Malacosoma disstria* is a major pest of poplar and birch trees, which have regional
365 importance for silviculture. However an increase in temperature of between 1.7 and 3.4°C has resulted
366 in more advanced spring phenology for trees than insects, potentially mitigating against risks of major
367 outbreaks (Schwartzberg et al., 2014). Conversely, models evaluating relationships between
368 temperature, population growth and metabolic rates in insects show that global increases in

369 temperature could lead to an escalation in preharvest losses of rice, maize, and wheat with increases
370 estimated to be up to 25% per degree of temperature increase (Deutsch et al., 2018).

371 **4.3 Generalism vs specialism in biotic interactions**

372 In the future, the effective and efficient use of plants in food production, provisioning and supporting
373 ecosystem services may increasingly depend on the discovery and conservation of other related
374 species for which plant pollinator interactions are less affected by climate change. Alternatively,
375 continued management of useful plants may also extend to the network of species with which they
376 interact. Concurrently, there may be increasing demand for plant species less reliant on pollinators
377 and plant selection favouring selfing or clonal reproduction. This may be the case, for example, with
378 *Theobroma* species (cacao) for which selfing is an alternative pollination system although with poorer
379 yield and higher risk of fruit abortion (J. Warren, Misir, & Kalai, 1995). While current concerns focus
380 primarily on short-term impacts, climate change has disrupted ecosystems and trophic interactions
381 over much greater time scales affecting abundance and ranges leading to communities dominated by
382 generalists (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013). Understanding how climate influences
383 trophic interactions and community dynamics will be critical to predicting how managed and
384 unmanaged ecosystems react to change in the short and longer term, and crucially could involve cases
385 where rapid evolution alters provision of ecosystem services (*sensu lato* Rudman et al., 2017).

386 **5. The future of useful plant traits**

387 In the future, useful plants are very likely to be growing in different conditions than they are today,
388 either through inability to track their climate envelope, reduction or disappearance of their historical
389 climate niche (see section 4) or reluctance or inability of users to shift to new species. Projected
390 changes will include warmer temperatures, more frequent drought or flooding, increased UV
391 exposure and rising CO₂ concentrations (IPCC, 2013; Figure 4). Concurrently, there may be agricultural
392 pressures to reduce energy intensive or environmentally harmful inputs such as fertilizers and
393 pesticides. The interactions of these environmental variables with plant traits is complex and the traits

394 which best promote resistance and resilience to climate change will be strongly context and scale
395 dependent. There are two general strategies to enable plant resilience to climate change: i) selecting
396 for positive adaptive traits to a given abiotic stress or ii) selecting for traits to avoid a particular stress
397 factor (e.g. increased seed dormancy or changes to phenology). The appropriate strategy in any given
398 situation is likely to be dependent on the duration, direction and magnitude of projected climatic
399 changes, as well as the resource allocation and morphological trade-off with other desirable plant
400 traits.

401 Plants can also alter the environment they are exposed to through ‘niche construction’ mechanisms
402 (*sensu* Laland et al., 2016), such as phenology, seed dispersal, dormancy and germination (Donohue,
403 2005). Domestication has directly or indirectly influenced many of these traits (i.e. “human driven
404 niche construction” (*sensu* Smith, 2007) with seed traits that had been of selective advantage for wild
405 seed-bearing plants, including seed dormancy, not necessarily being advantageous for crops. These
406 differences in functional seed traits might, for example, limit the capacity of cultivated plants to cope
407 with periods of drought in contrast to their wild relatives (e.g. Castillo-Lorenzo et al., 2019; Castillo-
408 Lorenzo et al., 2018).

409 We emphasise that whilst many trait shifts in response to climate change may be negative, or erode
410 plant usefulness, some aspects of future climate, such as elevated CO₂ levels, may present
411 opportunities for increased yield or value. Finally, whilst we principally consider adaptation involving
412 genetic change in this manuscript, acclimatization (i.e. phenotypic plasticity) may also facilitate
413 adaptation, though this ultimately has a genetic basis.

414 **5.1 Adaptation to changing precipitation**

415 The direction of precipitation changes, either increasing or decreasing, is likely to be spatially variable,
416 with the frequency and magnitude of droughts expected to increase across many regions. Plant traits
417 that promote drought tolerance fall into two categories; water saving and water acquisition traits.
418 Water saving traits include a shorter habit, smaller leaves, early maturity, plasticity in leaf chemistry

419 for osmotic control and the capacity for prolonged stomatal closure which reduces seasonal
420 evapotranspiration (Cattivelli et al., 2008). Increased investment in roots as well as deeper, finer roots,
421 rather than shallow tap roots, promotes water acquisition when water is scarce (Fry, Evans, Sturrock,
422 Bullock, & Bardgett, 2018). Conversely, other regions will be exposed to more frequent and severe
423 flooding. The ability to maintain high levels of soluble sugars in plant tissues during germination is one
424 proposed mechanism for tolerance to fresh water (Peña-Fronteras et al., 2009) and salt water flooding
425 (Colmer, Vos, & Pedersen, 2009). Traits associated with the rapid closure of root stomata, larger
426 interconnected aerenchyma that allows oxygen translocation and rapid petiole elongation also confer
427 flood tolerance in addition to traits that support seed dormancy under anoxic conditions (Else,
428 Janowiak, Atkinson, & Jackson, 2009).

429 **5.2 Adaptation to increased temperature and CO₂ levels**

430 Unlike precipitation, both temperatures and CO₂ concentrations are expected to rise across most
431 regions, although this will vary in magnitude (IPCC 2013). Smaller, fibrous and slow-growing leaves
432 with thicker cell walls, narrowly spaced veins, greater hair densities and high lignin content are
433 generally associated with heat tolerance (Kering, Guretzky, Funderburg, & Mosali, 2011). However,
434 these traits are generally undesirable in human food crops and, in animal feed, can lead to increased
435 enteric methane emissions (M. A. Lee, Davis, Chagunda, & Manning, 2017). Other traits, such as a
436 greater photosynthetic rates, increased membrane thermostability (e.g. cellular lipids and/or sugars)
437 and the maintenance of RUBISCO production may confer heat tolerance in a way which does not limit
438 yields (Larkindale & Huang, 2004). Synthesis of some of the intra-cellular compounds which protect
439 plant tissues from heat may also protect them from UV damage (Wahid, Gelani, Ashraf, & Foolad,
440 2007). An example is the production of anthocyanins in leaves and fruits, the consumption of which
441 may also offer human health benefits (Cassidy, 2018). Rising temperatures may lead to increased
442 productivity in some cases and CO₂ can also have a fertilising effect on plants. Yet this effect is not
443 universal and often becomes saturated even at relatively low CO₂ concentrations (M. Lee, Manning,

444 Rist, Power, & Marsh, 2010). Traits which promote a continued CO₂ fertilisation effect as
445 concentrations increase may therefore be beneficial and include greater photosynthetic nitrogen use
446 efficiency, a high relative growth rate (particularly of meristems) and an ability to maintain a
447 consistent partitioning coefficient, with plants investing an equal proportion of the additional energy
448 into photosynthetic capacity (e.g. increased number or surface area of leaves) and crop (e.g. increased
449 number or mass of seeds) (Bishop, Betzelberger, Long, & Ainsworth, 2015; Oguchi, Ozaki, Hanada, &
450 Hikosaka, 2016).

451 **5.3 Adaptation in nutritional and chemical traits**

452 Changes in precipitation, temperature and CO₂ levels have been shown to influence chemical
453 composition across a diverse range of useful plants (Holopainen et al., 2018; Hummel et al., 2018;
454 Loladze, 2014). These changes could have a substantial impact on the benefits derived from certain
455 species, relevant to their uses for nutrition, as medicines and other uses for humanity. For example,
456 Laenoi et al., (2018) showed that in four modern varieties of rice, both yield and grain quality
457 responded differently across seasons and in general had lower concentrations of nutrients including
458 N, P, Fe and Zn in the wet season. Similarly, exposure to UVB light, which is predicted to increase with
459 climate change, can negatively affect the nutritional quality of certain soya bean cultivars (Choudhary
460 & Agrawal, 2015). As atmospheric CO₂ rises, plants are predicted to have increased starch and reduced
461 protein content, which is associated with a decline in digestibility (Ziska, Epstein, & Schlesinger, 2009).
462 Indeed, increased CO₂ leads not only to decreased protein, but also reduced levels of iron and zinc in
463 crops such as wheat, rice, potatoes, soy, and peas, and in fruits and vegetables, which are important
464 sources of nutrients especially in many low-income countries (Fanzo, Davis, McLaren, & Choufani,
465 2018; Green et al., 2018). Conversely, some studies conclude that elevated CO₂ levels can increase
466 grain (including wheat and canola) yield, which is an important factor to support livelihoods. The
467 negative effect on grain nutritional value is, however, likely to have long term consequences for
468 human health (Jin, Armstrong, & Tang, 2019). Furthermore, abiotic stresses including light,

Formatted: Subscript

469 temperature, drought and altered soil composition that may be linked with climate change have
470 already been shown to have a negative impact on the nutritional value of forage crops, affecting
471 livestock health (Kulkarni et al., 2018). Ozone (O₃) is a contributor to climate change and it reduced
472 the nutritive quality of forage crops including ryegrass (*Lolium perenne* L.) and clover (*Trifolium*
473 *subterraneum* L.) (Kulkarni et al., 2018). Thus, from the emerging evidence available to date, climate
474 change could mean higher yields of less nutritious crops with consequences for both human and
475 livestock health.

476 There is, however, evidence to suggest that extreme environmental conditions may increase
477 production of certain secondary metabolites in plants in response to stress factors, such as flavonoids
478 in vegetables, and phenolics with antioxidant activity in quinoa (Dong, Gruda, Lam, Li, & Duan, 2018).
479 Such compounds may be produced by plants in response to environmental stressors, but are also
480 relevant to maintaining human health beyond functional nutrition (Howes & Simmonds, 2014). Plant
481 secondary metabolites not only provide benefits to human health by maintaining a dietary range, but
482 their increased production could have relevance to the medicinal or social uses of plants and their
483 chemical constituents. For example, higher CO₂ can increase morphine production in the wild poppy
484 (*Papaver setigerum*) and digoxin production in *Digitalis lanata* (Ziska et al., 2009). Increased yields of
485 such pharmaceutically important compounds may be useful to meet therapeutic demands in the
486 future, but levels of other secondary metabolites with toxic or other potentially adverse effects (e.g.
487 allergens) may also be increased, with consequences for the value of currently useful plants and for
488 human health.

489 **5.4 Adaptations in seed and germination biology**

490 Climate change is altering the drivers for seed dormancy and germination, and in the future may
491 preclude, delay, or enhance regeneration from seeds (Walck, Hidayati, Dixon, Thompson, & Poschlod,
492 2011). As a result, there is no clear positive or negative response in useful plants and we cannot predict
493 whether emergence will continue to match with the season favourable for establishment (Fernández-

494 Pascual, Mattana, & Pritchard, 2018). Breaking dormancy and germination are complex physiological
495 events. The more developmental stages from imbibition to germination, the increasing likelihood that
496 changes in the environment could affect or disrupt reproduction by seeds. For example, seeds with
497 morphophysiological dormancy could have different thermal thresholds for the internal growth of the
498 embryo and radicle protrusion. This appears to be the case for some species with rudimentary
499 embryos in Ranunculaceae (Porceddu, Mattana, Pritchard, & Bacchetta, 2017). Wild plants show a
500 high intraspecific variation in traits underpinning seedling emergence, growth and establishment
501 (Cochrane, Yates, Hoyle, & Nicotra, 2015). However, it is not yet possible to make generalizations
502 about how this variation is allocated across geographic ranges and further research to identify the
503 distribution of seed traits within foundation species and the mechanisms driving them is required
504 (Cochrane et al., 2015). In wild populations of useful plants, persistence in the soil seed bank may be
505 affected by the abiotic environment (Long et al., 2015). Warmer soil can increase seed bank decay due
506 to increased germination rates, for facultative pyrogenic plants, whose physical seed dormancy (i.e.,
507 seeds with an impermeable coat) is broken by high temperature thresholds (Ooi, Denham, Santana,
508 & Auld, 2014).

509 **5.5 Selection of life history traits**

510 The time taken to domesticate crops has decreased since the earliest domestication events (Meyer et
511 al., 2012; Vaughan et al., 2007), suggesting that accelerating the development of certain traits in
512 underutilized plants is possible. Similarly the processes and timing leading to domestication can vary
513 across groups of plants, depending especially on how they are reproduced – by seed or vegetatively
514 by cuttings – as well as which plant part is being selected for (Fuller et al., 2014). Trees and longer-
515 lived plants, for example, have historically been domesticated at a slower rate than annuals with
516 shorter life cycles, due to extended juvenile stages which delay the point at which desirable (often
517 reproductive) traits can be evaluated and selected. This in turn means that perennial crops often retain
518 higher genetic diversity than annual crops (Miller & Gross, 2011). Therefore, if we sought to accelerate

519 the domestication of underutilized species, on the one hand we may prefer to focus on shorter
520 lifecycle species i.e. annuals. Yet conversely, whilst the majority of annual crops are grown from seed,
521 more than 75% of perennial crops are clonally propagated, which overcomes the challenges of a long
522 juvenile stage and eliminates the variation of sexual reproduction (Miller & Gross, 2011). Whilst
523 annuals predominate in our current food system (McClure, Sawler, Gardner, Money, & Myles, 2014),
524 from a plant domestication perspective, it is not yet clear which life history traits will be most
525 advantageous in the future.

526 **5.6 Multi-trait adaptation**

527 Climate change is multifactorial, therefore traits that confer resistance or resilience to multiple
528 climatic effects (whilst simultaneously retaining traits for enhanced production and nutrition) would
529 be preferable. For example, reaching maturity earlier in the season, flowering at cooler times of the
530 day, expression of protective secondary metabolites which offer osmotic control, and deeper, finer
531 roots may offer combined protection against warming, drought and UV (Shah et al., 2011). If flooding
532 is projected, then traits which promote additional growth, phenological shifts or dormancy in adverse,
533 often anoxic, conditions will be favourable. The interactions between different climatic variables can
534 also lead to synergistic or antagonistic effects on useful plants. For example, it is known that
535 simultaneously increasing rainfall and nitrogen enrichment can increase plant productivity to a greater
536 degree than the sum of their separate effects, since the additional water washes the dissolved
537 nitrogen over roots, aiding nutrient uptake (M. Lee et al., 2010). The interactive effects of CO₂ with
538 warming or drought varies substantially between plant species and can be synergistic, antagonistic or
539 neutral, with additional complexity added since the outcome can be further modified by factors such
540 as phenological stage, intensity and stress duration (Kadam et al., 2014).

541 Given the complexities associated to the prediction of future climates for a given location, particularly
542 at a finer-scale, combined with inter-annual variation in conditions, then it may be preferable to
543 cultivate multiple genotypes with different traits as an insurance against different climatic outcomes.

544 Concurrently, many traits will be linked and therefore the selection of some traits will automatically
545 cause a rise or trade-offs in other traits (Díaz et al., 2016), thus a more thorough understanding of
546 linked traits will be required for breeding optimisation. It will be important to consider the direction,
547 magnitude and likelihood of multiple aspects of climate change and the full suite of plant traits if we
548 are to adequately adapt to our changing world. Technical advances, such as genomic selection or
549 prediction, which uses genome-wide markers to predict individual's breeding values, may permit
550 selection for multiple traits whilst maintaining genetic diversity (Crossa et al., 2017).

551 **6. The cultural influences on our use of plants**

552 Although agriculture began up to 12,000 years ago (Meyer & Purugganan, 2013), in many parts of the
553 world people have continued to exploit seasonally available food sources from the wild.
554 Domestications occurred independently on different continents within different temporal contexts,
555 and the possible climatic and socio-economic reasons are still debated, along with the co-evolutionary
556 mechanisms behind these recurrent parallel processes (Fuller et al., 2014). Change accelerated
557 dramatically in the mid-twentieth century with the green revolution focusing on increasing yields of a
558 small number of species. This was accompanied by new farming practises with high use of fertilizers
559 and agrochemicals, altered irrigation techniques (Pingali, 2012), and accelerated cultural selection of
560 a smaller suite of focal useful plants (Meyer et al., 2012). More recently, this trend has been countered
561 by efforts to increase the number of crops and foster the conservation and sustainable use of the
562 whole biodiversity portfolio for human use. For example the FAO Commission on Genetic Resources
563 for Food and Agriculture recently recognised the value of “Globally Important Agricultural Heritage
564 Systems” (FAO 2018), which are traditional systems with high agrobiodiversity, resilient ecosystems,
565 and linkage of farming practices to cultural identity and local ecological knowledge (e.g. the Ethiopian
566 Highlands; Borrell et al., 2018). Other initiatives that have gained traction include the African Orphan
567 Crops Consortium (<http://africanorphancrops.org>), The Millennium Seed Bank (MSB) in the UK,
568 supported by a global network of partner institutions and The Global Crop Diversity Trust's Svalbard

569 Global Seed Vault in Norway to safeguard through duplicate storage as much of the world's unique
570 crop genetic material as possible (Ulian, Pritchard, Cockel, & Mattana, 2019).

571 **6.1 Transitions between major and minor useful plants**

572 The plants a community or society may choose to cultivate or harvest from the wild may be strongly
573 influenced by climate and biogeography, but these factors also interact with technological
574 developments, socio-economic changes and cultural preferences. Many crops that are currently
575 'minor' have been major crops or had wider distributions in the recent or ancient past (Austin, 2006).
576 Species use may change for many reasons, including shifts to more beneficial alternative species, as a
577 result of overharvesting (Parejko, 2003), changes in their major use preference (i.e. food to
578 construction, fodder to medicine) or the development of new uses for existing crops (e.g. grain crops
579 adapted for biofuel production) (Hill, 2007). In northern Sudan, several indigenous African crops
580 including sorghum, lablab and cowpea, were major crops until recently, but have become less
581 important (Ryan, 2018). Lablab (*Lablab purpureus*) in particular has been described as a 'lost crop' in
582 Africa, yet in India, lablab still has considerable importance, showing spatial variation in societal value
583 of crops even outside of their regions of origin. This demonstrates that whilst there has been a decline
584 and homogenisation of global plant species utilization, it is possible for currently minor species to
585 become more widely utilized once again. Some species have been exploited for other purposes, before
586 being additionally used for food (Meyer et al., 2012). For example *Theobroma cacao*, now used
587 worldwide to produce chocolate, was originally used in the production of a fermented beverage and
588 is still used for preparing *mole* in Mexico, whilst others can lose some of their applications, for example
589 more palatable and easier to process enset landraces may be less suited to fibre production (Borrell,
590 Biswas, et al., 2018).

591 **6.2 Human influence on plant resilience**

592 There are several strategies to facilitate climate adaptation whilst continuing to derive material and
593 non-material benefits from useful plants. In the short-term, the conservation of extant genetic

594 diversity, particularly in a period of rapid environmental change, is critical to enable future crop
595 development. Human selection for useful plant traits is sometimes at odds with natural selection of
596 fitness traits, thus maintaining diversity across all traits, not just target traits, is considered important
597 (Fu, 2015). For the majority of useful plants that are not cultivated, cultural choices are crucial to
598 enable conservation of wild populations. Conservation may also be key to enabling discovery of
599 currently unknown or undocumented useful plants (Dempewolf et al., 2014; Garnett et al., 2018;
600 Rodríguez et al., 2018). In the medium-term, plant breeding and genomic prediction tools are likely to
601 enable faster development of resilience traits (for example; breeding of dieback resilient *Fraxinus* in
602 the UK). Concurrently, for wild populations, assisted gene flow or migration strategies could be
603 employed to facilitate adaptation (Aitken & Bemmels, 2016).

604 In the longer term, the *ex situ* conservation strategies for preservation of genetic resources of useful
605 plants will need to be adapted to the effects that climate change will have in some seed traits and how
606 these traits are represented in the range of species considered as useful plants. For example, seed
607 storability has been a key trait selected during crop domestication. Indeed, 84% of the world's major
608 crops or crop complexes listed in Annex I of the International Treaty for Plant Genetic Resources for
609 Food and Agriculture produce seeds that are considered orthodox (i.e. tolerate desiccation and
610 storage at low temperatures, the standard seed storage conditions) and these seeds can be stored *ex*
611 *situ* for relatively long-periods of time (Pritchard, 2016). However, seed storability (i.e. desiccation
612 tolerance and longevity) is affected by changes to the parental environments, and the environmental
613 conditions expected under climate change scenarios may potentially reduce seed storability for
614 diverse species (Kochanek, Buckley, Probert, Adkins, & Steadman, 2010). Additionally, there is an
615 increasing number of plant species that are or have the potential to become useful plants for which
616 seed storability may be reduced or intractable using the standard seed storage conditions (i.e.
617 recalcitrant seeds that do not tolerate desiccation and/or storage at low temperatures and clonally
618 reproduced crops) (Li & Pritchard, 2009). This is particularly important in the tropics where there is
619 the largest concentration of recalcitrant seeded species (Wyse & Dickie, 2017). Historically,

620 recalcitrant seeds (desiccation intolerant) and clonally reproduced crops have required field gene
621 banks and *in vitro* collections. These methods are higher risk as, for example, field gene banks are
622 exposed to pests and the unfavourable environmental changes predicted under climate change. New
623 approaches such as Cryobiotechnology, including cryogenic storage and explant recovery *in vitro*
624 (Pritchard, 2018), provides a long-term solution for previously intractable species and is also likely to
625 improve longevity of orthodox seeded species (Walters, Wheeler, & Stanwood, 2004).

626 Finally, we note that genetic engineering is likely to play an increasingly important and sophisticated
627 role in manipulating the diversity of useful plants. In the short term, this is likely to benefit a relatively
628 narrow range of extensively domesticated (and better studied) species, and in the context of this
629 review could be considered a form of *Adaptation-Specialization* (Figure 1). A full discussion of this
630 broad topic is outside of the scope of this review, and we refer the reader to Ortiz et al., (2014).

631 **6.3 Preservation of indigenous knowledge associated with useful plants**

632 The efficient exploitation of many underutilised useful plants depends to a large degree upon the
633 preservation of associated, and often diverse indigenous knowledge (for example the complex
634 cultivation and processing practices for enset in Ethiopia, Borrell et al., 2018). It is important to
635 recognise that many communities still cultivate relatively few species, and are reliant on harvested
636 (wild) plants for construction, medicine, tools, food, firewood (and also game animals dependent on
637 plants) (Mollel, Fischer, Hemp, & Fischer, 2017). Indigenous knowledge combined with science has
638 been suggested as one of the most effective approaches to achieving agricultural climate adaptation
639 (Makondo & Thomas, 2018). There is increasing evidence that a large proportion of this knowledge is
640 endangered, with the future of many underutilised plants depending upon addressing cultural biases
641 against the use of local or traditional food crops (Berkes, Colding, & Folke, 2000; Makondo & Thomas,
642 2018). For example modernising cultural attitudes see some traditional wild harvested plants as
643 children's food, or indigenous species are overlooked because they are perceived as 'backwards' in
644 favour of introduced 'modern' crops (Yemataw, Tesfaye, Zeberga, & Blomme, 2016).

645 **6.4. Useful plants as an option value**

646 Conservation of species and ecosystems is essential to preserve useful plant diversity but is inhibited
647 by the scale of the challenge and limited resources. In this regard, phylogenetic diversity (which in
648 many cases may also be spatially correlated with biodiversity hotspots) has been considered as a
649 suitable representative of feature diversity (but see Kelly et al., 2014 and Owen et al., 2019 for further
650 discussion of this topic) and consequently, maximizing phylogenetic diversity would be an efficient
651 way to identify potential future value of plant diversity, including plants useful to humans (i.e. the
652 concept of option values; Faith, 1992). In the future, the desire to create sustainable products will
653 require new solutions to overcome the overexploitation of wild raw resources. New challenges (e.g.
654 reduction in single use plastics, emerging diseases) may also require development of entirely new
655 classes of useful plant product, from as yet unexploited branches of the plant tree of life.

656 **7. Conclusion**

657 Useful plants underpin human well-being and the global economy, but the majority are under-
658 documented and under-developed. Lack of knowledge on the ecological characteristics of many useful
659 plant species emphasises the urgent need to synthesise the future impact of climate change on our
660 useful plant resource system over the next century. In this review we have identified a range of
661 characteristics that may be typical of the useful plants we will increasingly rely on in the future as well
662 as conceivable pathways for society's use of plants (Figure 2).

663 Different combinations of characteristics or traits are likely to be favoured under different pathways.
664 A trend towards *adaptation*, for example, may intensify the pattern of domestication that is already
665 established, with continued emphasis on our existing extensively domesticated species. This would be
666 concomitant with development of novel genomic and breeding approaches to make further
667 performance gains whilst technological solutions may also be sought for pest regulation, plant-
668 pollinator interactions and appropriate irrigation or nutrient inputs. Conversely, *substitution* may
669 favour different species, better suited to future conditions i.e. useful plants that already display

670 desired traits to tolerate climate change, but in which productivity traits may not yet have been
671 extensively developed. In this case, useful plant development may focus on species with higher
672 temperature tolerance, improved photosynthesis and water use efficiency. The key difference
673 between *adaptation* and *substitution* is that the former relies on technology to develop traits in
674 species with existing desirable yield or product attributes, enabling them to tolerate future climatic
675 conditions, whereas *substitution* favours species already (or likely to be) tolerant of future climatic
676 conditions, with development of 'useful' features or traits being secondary.

677 Concurrently, a trend towards specialization is likely to favour wide-spread generalist species, selected
678 to be tolerant to a wide range of climatic conditions. They may have more generalist pollinators (or
679 no pollinator), and a range of uses or co-products enabling multiple benefits to be derived from a
680 limited pool of species. It is likely that many of the species used under a specialization scenario are
681 already moderately or extensively domesticated, though some may be subject to reduced intra-
682 specific diversity. The alternative trend, *diversification*, entails increasing use of larger numbers of
683 species. A key pillar to support this trend would be conservation, to support maintenance of option
684 values, particularly in species-rich areas such as the tropics. Conservation of crop and crop wild relative
685 genetic diversity would be prioritized, together with accelerated documentation of indigenous
686 knowledge associated with weakly domesticated or wild harvested species. From a phylogenetic
687 perspective, a better understanding of the frequency of different uses across and within plant families
688 would aid management of useful plant resources, as well as facilitate the identification of novel useful
689 plants.

690 The strategies considered here are a simplified representation of a continuous spectrum of pathways
691 and a subset of useful plant characteristics. These pathways should be framed by the current global
692 trend towards lower numbers of species and reduced genetic diversity. Therefore, on our current
693 trajectory without adequate *in situ* and *ex situ* conservation of species and genetic diversity, the
694 *adaptation* and *specialization* pathways become increasingly unavoidable. Whereas conservation and

695 seed banking interventions now, could help ensure that the full range of pathways are available in the
696 future. In the near term, global and national agricultural and conservation policies will substantially
697 influence society's long-term trajectory across these spectra of strategies. Useful plant documentation
698 efforts, for example, should be a priority in the same way that seed banks have sought to safeguard
699 physical plant diversity. Similarly, robust multilateral systems of access and benefit-sharing will be
700 critical to ensure equitable benefit from useful plants, and are key to enabling strategies such as
701 *substitution* and *diversification*. We conclude that whilst we currently have a choice of strategies, the
702 continued loss of diversity combined with climate change means that without effective safeguards
703 and planning, in the future the range of strategies available to us will become much more limited.

704 **Acknowledgements**

705 We are thankful to all students, assistants, collection curators, partners and researchers that
706 supported collation of data on global useful plant diversity and documentation. We thank Dr Mark
707 Nesbitt for thoughtful comments on the manuscript. This research did not receive any specific grant
708 from funding agencies in the public, commercial, or not-for-profit sectors.

709 **Contributions**

710 JB and SP conceived and edited the manuscript. All authors contributed to the writing of the
711 manuscript. All authors approved the final version of the manuscript.

712 **Declarations of interest**

713 None

714 **References**

- 715 Ahuja, I., de Vos, R. C. H., Bones, A. M., & Hall, R. D. (2010). Plant molecular stress responses face
716 climate change. *Trends in Plant Science*, 15(12), 664–674.
717 <https://doi.org/10.1016/j.tplants.2010.08.002>
- 718 Aitken, S. N., & Bemmels, J. B. (2016). Time to get moving: Assisted gene flow of forest trees.

- 719 *Evolutionary Applications*, 9(1), 271–290. <https://doi.org/10.1111/eva.12293>
- 720 Arnold, S. E. J., Bridgemoan, P., Perry, G. B., Spinelli, G. R., Pierre, B., Murray, F., ... Stevenson, P. C.
721 (2018). The significance of climate in the pollinator dynamics of a tropical agroforestry system.
722 *Agriculture, Ecosystems and Environment*, 254(November 2017), 1–9.
723 <https://doi.org/10.1016/j.agee.2017.11.013>
- 724 Austin, D. F. (2006). Fox-tail Millets (Setaria: Poaceae)—Abandoned Food in Two Hemispheres.
725 *Economic Botany*, 60(2), 143–158. [https://doi.org/10.1663/0013-0001\(2006\)60\[143:fmspfi\]2.0.co;2](https://doi.org/10.1663/0013-0001(2006)60[143:fmspfi]2.0.co;2)
- 727 Ayasse, M., Löfstedt, C., Ibarra, F., Schiestl, F. P., Francke, W., Hansson, B., & Paulus, H. F. (2000).
728 Evolution of Reproductive Strategies in the Sexually Deceptive Orchid *Ophrys Sphegodes*: How
729 Does Flower-Specific Variation of Odor Signals Influence Reproductive Success? *Evolution*, 54(6),
730 1995–2006. [https://doi.org/10.1554/0014-3820\(2000\)054\[1995:eorsit\]2.0.co;2](https://doi.org/10.1554/0014-3820(2000)054[1995:eorsit]2.0.co;2)
- 731 Bascompte, J., Garcia, M. B., Ortega, R., Rezende, E. L., & Pironon, S. (2019). Mutualistic interactions
732 reshuffle the effects of climate change on plants across the tree of life. *Science Advances*.
- 733 Bebbler, D. P., Ramotowski, M. A. T., & Gurr, S. J. (2013). Crop pests and pathogens move polewards
734 in a warming world. *Nature Climate Change*, 3(11), 985–988.
735 <https://doi.org/10.1038/nclimate1990>
- 736 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of Climate
737 Change on the Future of Biodiversity. *Ecology Letters*, 15(4), 365–377.
738 <https://doi.org/10.1111/j.1461-0248.2011.01736.x>Impacts
- 739 Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., & Courchamp, F. (2014).
740 Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography*, 23(12),
741 1376–1386. <https://doi.org/10.1111/geb.12228>
- 742 Berkes, F., Colding, J., & Folke, C. (2000). Rediscovery of Traditional Ecological Knowledge as Adaptive
743 Management. *Ecological Applications*, 10(5), 1251–1262.
- 744 Bishop, K. A., Betzelberger, A. M., Long, S. P., & Ainsworth, E. A. (2015). Is there potential to adapt
745 soybean (*Glycine max* Merr.) to future [CO₂]? An analysis of the yield response of 18 genotypes
746 in free-air CO₂ enrichment. *Plant, Cell and Environment*, 38(9), 1765–1774.
747 <https://doi.org/10.1111/pce.12443>
- 748 Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and the past,
749 present, and future of biotic interactions. *Science*, 341(August), 499–504.
750 <https://doi.org/10.1126/science.1237184>
- 751 Bogdanski, A. K., Klein, A.-M., Steffan-Dewenter, I., Tschardtke, T., Bos, M. M., Veddeler, D., &
752 Tyljanakis, J. M. (2008). Caveats To Quantifying Ecosystem Services: Fruit Abortion Blurs Benefits
753 From Crop Pollination. *Ecological Applications*, 17(6), 1841–1849. <https://doi.org/10.1890/06-1763.1>
- 755 Borrell, J. S., Biswas, M. K., Goodwin, M., Blomme, G., Schwarzacher, T., Heslop-Harrison, P. J. S., ...
756 Wilkin, P. (2018). Enset in Ethiopia: a poorly characterised but resilient starch staple. *Annals of*
757 *Botany*, xx–xxx, 1–20. <https://doi.org/10.1093/aob/mcy214>
- 758 Borrell, J. S., Wang, N., Nichols, R. A., & Buggs, R. J. A. (2018). Genetic diversity maintained among
759 fragmented populations of a tree undergoing range contraction. *Heredity*, 121, 304–318.
760 <https://doi.org/10.1038/s41437-018-0132-8>
- 761 Burton, I., & Lim, B. (2005). Achieving adequate adaptation in agriculture. *Increasing Climate*

- 762 *Variability and Change: Reducing the Vulnerability of Agriculture and Forestry*, 191–200.
763 https://doi.org/10.1007/1-4020-4166-7_9
- 764 Cámara-Leret, R., Faurby, S., Macía, M. J., Balslev, H., Gödel, B., Svenning, J.-C., ... Salsis-Lagoudakis,
765 C. H. (2017). Fundamental species traits explain provisioning services of tropical American palms.
766 *Nature Plants*, 3(2). <https://doi.org/10.1038/nplants.2016.220>
- 767 Cassidy, A. (2018). Berry anthocyanin intake and cardiovascular health. *Molecular Aspects of Medicine*.
768 <https://doi.org/10.1016/j.mam.2017.05.002>
- 769 Castillo-Lorenzo, E., Finch-Savage, W. E., Seal, C. E., & Pritchard, H. W. (2019). Adaptive significance of
770 functional germination traits in crop wild relatives of Brassica. *Agricultural and Forest
771 Meteorology*, 264, 343–350.
- 772 Castillo-Lorenzo, E., Pritchard, H. W., Finch-Savage, W. E., & Seal, C. E. (2018). Comparison of seed and
773 seedling functional traits in native Helianthus species and the crop H. annuus (sunflower). *Plant
774 Biology*.
- 775 Cattivelli, L., Rizza, F., Badeck, F. W., Mazzucotelli, E., Mastrangelo, A. M., Francia, E., ... Stanca, A. M.
776 (2008). Drought tolerance improvement in crop plants: An integrated view from breeding to
777 genomics. *Field Crops Research*. <https://doi.org/10.1016/j.fcr.2007.07.004>
- 778 Challinor, A., Watson, J., Lobell, D., Howden, S., Smith, D., & Chhetri, N. (2014). A meta-analysis of crop
779 yield under climate change and adaptation. *Nature Climate Change*, 4, 287–291.
780 <https://doi.org/10.1038/nclimate2153>
- 781 Chaudhary, P., & Initiatives, L. (2016). Consistency of local perceptions of climate change in the
782 Kangchenjunga Himalaya Landscape Consistency of local perceptions of climate change in the
783 Kangchenjunga Himalaya landscape. *Current Science*, 101(4), 504–513.
- 784 Cheng, S., Melkonian, M., Smith, S. A., Brockington, S., Archibald, J. M., Delaux, P.-M., ... Wong, G. K.-
785 S. (2018). 10KP: A phylodiverse genome sequencing plan. *GigaScience*, 7(3).
786 <https://doi.org/10.1093/gigascience/giy013>
- 787 Chomicki, G., & Renner, S. S. (2014). Watermelon origin solved with molecular phylogenetics including
788 Linnaean material: another example of museomics. *New Phytologist*, 205(2), 526–532.
789 <https://doi.org/10.1111/nph.13163>
- 790 Choudhary, K. K., & Agrawal, S. B. (2015). Assessment of Fatty Acid Profile and Seed Mineral Nutrients
791 of Two Soybean (Glycine maxL.) Cultivars Under Elevated Ultraviolet-B: Role of ROS, Pigments
792 and Antioxidants. *Photochemistry and Photobiology*, 92(1), 134–143.
793 <https://doi.org/10.1111/php.12544>
- 794 Christenhusz, M. J. M., Fay, M. F., & Chase, M. W. (2017). *Plants of the world: an illustrated
795 encyclopedia of vascular plants*.
- 796 Cochrane, A., Yates, C. J., Hoyle, G. L., & Nicotra, A. B. (2015). Will among-population variation in seed
797 traits improve the chance of species persistence under climate change? *Global Ecology and
798 Biogeography*, 24(1), 12–24.
- 799 Colmer, T. D., Vos, H., & Pedersen, O. (2009). Tolerance of combined submergence and salinity in the
800 halophytic stem-succulent *Tecticornia pergranulata*. *Annals of Botany*, 103(2), 303–312.
801 <https://doi.org/10.1093/aob/mcn120>
- 802 Coradin, L., Larranaga, N., van Zonneveld, M., Blonder, B., Hunter, D., & Hormaza, J. I. (2018). Human
803 diets drive range expansion of megafauna-dispersed fruit species. *Proceedings of the National
804 Academy of Sciences*, 115(13), 3326–3331. <https://doi.org/10.1073/pnas.1718045115>

- 805 Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in*
806 *Ecology and Evolution*, 28(8), 482–488. <https://doi.org/10.1016/j.tree.2013.04.003>
- 807 Cristina Giannini, T., Acosta, A. L., Silva, C. I. da, de Oliveira, P. E. A. M., Imperatriz-Fonseca, V. L., &
808 Saraiva, A. M. (2013). Identifying the areas to preserve passion fruit pollination service in
809 Brazilian Tropical Savannas under climate change. *Agriculture, Ecosystems and Environment*,
810 171(May), 39–46. <https://doi.org/10.1016/j.agee.2013.03.003>
- 811 Cronk, Q. C. (2008). Crop domestication in the Compositae : a family-wide trait assessment, 1141–
812 1157. <https://doi.org/10.1007/s10722-008-9315-0>
- 813 Cronk, Q. C. B., & Forest, F. (2017). The Evolution of Angiosperm Trees: From Palaeobotany to
814 Genomics. In *Comparative and Evolutionary Genomics of Angiosperm Trees* (pp. 1–17).
815 <https://doi.org/10.1007/7397>
- 816 Crossa, J., Pérez-rodríguez, P., Cuevas, J., Montesinos-lópez, O., Jarquín, D., Campos, G. D. L., ...
817 Varshney, R. K. (2017). Genomic Selection in Plant Breeding : Methods , Models , and
818 Perspectives. *Trends in Plant Science*, xx, 1–15. <https://doi.org/10.1016/j.tplants.2017.08.011>
- 819 Dai, X., Zhang, W., Xu, J., Duffy, K. J., & Guo, Q. (2017). Global pattern of plant utilization across
820 different organisms: Does plant apparency or plant phylogeny matter? *Ecology and Evolution*,
821 7(8), 2535–2545. <https://doi.org/10.1002/ece3.2882>
- 822 DaMatta, F. M., Grandis, A., Arenque, B. C., & Buckeridge, M. S. (2010). Impacts of climate changes on
823 crop physiology and food quality. *Food Research International*, 43(7), 1814–1823.
824 <https://doi.org/10.1016/j.foodres.2009.11.001>
- 825 Delang, C. O. (2006). Not just minor forest products: The economic rationale for the consumption of
826 wild food plants by subsistence farmers. *Ecological Economics*, 64–73.
827 <https://doi.org/10.1016/j.eco>
- 828 Dempewolf, H., Eastwood, R. J., Guarino, L., Khoury, C. K., Müller, J. V., & Toll, J. (2014). Adapting
829 Agriculture to Climate Change: A Global Initiative to Collect, Conserve, and Use Crop Wild
830 Relatives. *Agroecology and Sustainable Food Systems*, 38(4), 369–377.
831 <https://doi.org/10.1080/21683565.2013.870629>
- 832 Deutsch, C. A., Tewksbury, J. J., & Tigchelaar, M. (2018). Increase in crop losses to insect pests in a
833 warming climate, 919(August), 916–919.
- 834 Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The
835 global spectrum of plant form and function. *Nature*, 529(7585), 167–171.
836 <https://doi.org/10.1038/nature16489>
- 837 Donatelli, M., Srivastava, A. K., Duveiller, G., Niemeyer, S., & Fumagalli, D. (2015). Climate change
838 impact and potential adaptation strategies under alternate realizations of climate scenarios for
839 three major crops in Europe. *Environmental Research Letters*, 10(7).
840 <https://doi.org/10.1088/1748-9326/10/7/075005>
- 841 Dong, J., Gruda, N., Lam, S. K., Li, X., & Duan, Z. (2018). Effects of Elevated CO2 on Nutritional Quality
842 of Vegetables: A Review. *Frontiers in Plant Science*, 9. <https://doi.org/10.3389/fpls.2018.00924>
- 843 Donohue, K. (2005). Niche construction through phenological plasticity: life history dynamics and
844 ecological consequences. *New Phytologist*, 166(1), 83–92. Retrieved from internal-
845 [pdf://0095503774/Donohue-2005-Niche construction through phenol.pdf](pdf://0095503774/Donohue-2005-Niche%20construction%20through%20phenol.pdf)
- 846 Dyer, L. A., Richards, L. A., Short, S. A., & Dodson, C. D. (2013). Effects of CO2 and Temperature on
847 Tritrophic Interactions. *PLoS ONE*, 8(4). <https://doi.org/10.1371/journal.pone.0062528>

848 Eckert, C. G., Kalisz, S., Geber, M. A., Sargent, R., Elle, E., Cheptou, P. O., ... Winn, A. A. (2010). Plant
849 mating systems in a changing world. *Trends in Ecology and Evolution*, 25(1), 35–43.
850 <https://doi.org/10.1016/j.tree.2009.06.013>

851 Edwards, E. J., Still, C. J., & Donoghue, M. J. (2007). The relevance of phylogeny to studies of global
852 change, 22(5). <https://doi.org/10.1016/j.tree.2007.02.002>

853 Egan, P. A., Adler, L. S., Irwin, R. E., Farrell, I. W., Palmer-young, E. C., Stevenson, P. C., ... Egan, P. A.
854 (2018). Crop Domestication Alters Floral Reward Chemistry With Potential Consequences for
855 Pollinator Health, 9(September), 1–14. <https://doi.org/10.3389/fpls.2018.01357>

856 Eiserhardt, W. L., Antonelli, A., Bennett, D. J., Botigué, L. R., Burleigh, J. G., Dodsworth, S., ... Baker, W.
857 J. (2018). A roadmap for global synthesis of the plant tree of life. *American Journal of Botany*,
858 105(3), 614–622. <https://doi.org/10.1002/ajb2.1041>

859 Else, M. A., Janowiak, F., Atkinson, C. J., & Jackson, M. B. (2009). Root signals and stomatal closure in
860 relation to photosynthesis, chlorophyll a fluorescence and adventitious rooting of flooded
861 tomato plants. *Annals of Botany*, 103(2), 313–323. <https://doi.org/10.1093/aob/mcn208>

862 Ernst, M., Saslis-Lagoudakis, C. H., Grace, O. M., Nilsson, N., Toft Simonsen, H., Horn, J. W., ... Rønsted,
863 N. (2016). Molecular phylogenetics as a predictive tool in plant-based drug discovery in the genus
864 *Euphorbia* L. *Planta Medica*, 81(S 01), S1–S381. <https://doi.org/10.1055/s-0036-1596164>

865 Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity, 1–10.

866 Fanzo, J., Davis, C., McLaren, R., & Choufani, J. (2018). The effect of climate change across food
867 systems: Implications for nutrition outcomes. *Global Food Security*, 18, 12–19.
868 <https://doi.org/10.1016/j.gfs.2018.06.001>

869 Farnsworth, N. R., & Soejarto, D. D. (1991). Global importance of medicinal plants. *The Conservation*
870 *of Medicinal Plants*, 26, 25–51.

871 Fernández-Pascual, E., Mattana, E., & Pritchard, H. W. (2018). Seeds of future past: climate change
872 and the thermal memory of plant reproductive traits. *Biological Reviews*.

873 Fitter, A. H., & Fitter, R. S. R. (2002). Rapid changes in flowering time in British plants. *Science*,
874 296(5573), 1689–1691. <https://doi.org/10.1126/science.1071617>

875 Food and Agriculture Organization of the United Nations. (2015). *FAO Statistical Pocketbook*. Food and
876 Agriculture Organization of the United Nations.

877 Forbes, S.J., & Northfield, T. D. (2015). Increased pollinator habitat enhances cacao fruit set and
878 predator conservation. *Ecological Applications*, 27(3), 887–899.
879 <https://doi.org/10.1111/ijlh.12426>

880 Forest, F., Grenyer, R., Rouget, M., Davies, T. J., Cowling, R. M., Faith, D. P., ... Savolainen, V. (2007).
881 Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, 445(February
882 2007), 757–760. <https://doi.org/10.1038/nature05587>

883 Fry, E. L., Evans, A. L., Sturrock, C. J., Bullock, J. M., & Bardgett, R. D. (2018). Root architecture governs
884 plasticity in response to drought. *Plant and Soil*, 433(1–2), 189–200.
885 <https://doi.org/10.1007/s11104-018-3824-1>

886 Fu, Y. B. (2015). Understanding crop genetic diversity under modern plant breeding. *Theoretical and*
887 *Applied Genetics*, 128(11), 2131–2142. <https://doi.org/10.1007/s00122-015-2585-y>

888 Fuller, D. Q., Denham, T., Arroyo-kalin, M., Lucas, L., Stevens, C. J., Qin, L., & Allaby, R. G. (2014).
889 Convergent evolution and parallelism in plant domestication revealed by an expanding

890 archaeological record, *111*(17). <https://doi.org/10.1073/pnas.1308937110>

891 Garibaldi, L. A., Vanbergen, A. J., Biesmeijer, J. C., Aizen, M. A., Imperatriz-Fonseca, V., Ngo, H. T., ...
892 Potts, S. G. (2016). Safeguarding pollinators and their values to human well-being. *Nature*,
893 *540*(7632), 220–229. <https://doi.org/10.1038/nature20588>

894 Garnatje, T., Peñuelas, J., & Vallès, J. (2017). Ethnobotany, Phylogeny and “Omics” for Human Health
895 and Food Security. *Trends in Plant Science*, *22*(3), 187–191.
896 <https://doi.org/10.1016/j.tplants.2017.01.001>

897 Garnett, S. T., Fernández-Llamazares, Á., Brondizio, E. S., Duncan, T., Malmer, P., Jonas, H., ... Geyle,
898 H. (2018). A spatial overview of the global importance of Indigenous lands for conservation.
899 *Nature Sustainability*, *1*(7), 369–374. <https://doi.org/10.1038/s41893-018-0100-6>

900 Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., ... Toulmin, C.
901 (2010). Food Security : The Challenge of Feeding 9 Billion People. *Science*, *327*(February), 812–
902 818. <https://doi.org/DOI:10.1126/science.1185383>

903 Gordo, O., & Sanz, J. J. (2005). Phenology and climate change: A long-term study in a Mediterranean
904 locality. *Oecologia*, *146*(3), 484–495. <https://doi.org/10.1007/s00442-005-0240-z>

905 Gray, S. B., & Brady, S. M. (2016). Plant developmental responses to climate change. *Developmental*
906 *Biology*, *419*(1), 64–77. <https://doi.org/10.1016/j.ydbio.2016.07.023>

907 Green, H., Broun, P., Cook, D., Cooper, K., Drewnowski, A., Pollard, D., ... Roulin, A. (2018). Healthy and
908 sustainable diets for future generations. *Journal of the Science of Food and Agriculture*, *98*(9),
909 3219–3224. <https://doi.org/10.1002/jsfa.8953>

910 Groeneveld, J. H., Tschardtke, T., Moser, G., & Clough, Y. (2010). Experimental evidence for stronger
911 cacao yield limitation by pollination than by plant resources. *Perspectives in Plant Ecology,*
912 *Evolution and Systematics*, *12*(3), 183–191. <https://doi.org/10.1016/j.ppees.2010.02.005>

913 Gross, B. L., & Zhao, Z. (2014). Archaeological and genetic insights into the origins of domesticated
914 rice. *Proceedings of the National Academy of Sciences*, *111*(17), 6190–6197.
915 <https://doi.org/10.1073/pnas.1308942110>

916 Guo, Z., Zhang, L., & Li, Y. (2010). Increased dependence of humans on ecosystem services and
917 biodiversity. *PLoS ONE*, *5*(10). <https://doi.org/10.1371/journal.pone.0013113>

918 Gurr, G. M., Wratten, S. D., Landis, D. A., & You, M. (2016). Habitat Management to Suppress Pest
919 Populations: Progress and Prospects. *Annual Review of Entomology*, *62*(1), 91–109.
920 <https://doi.org/10.1146/annurev-ento-031616-035050>

921 Halse-Gramkow, M., Ernst, M., Dunn, R. R., & Saslis-Lagoudakis, C. H. (2016). Phylogenetics of
922 psychoactive plants in neuro-targeted bioprospecting. *Planta Medica*, *81*(S 01), S1–S381.
923 <https://doi.org/10.1055/s-0036-1596186>

924 Hammer, K., & Khoshbakht, K. (2015). A domestication assessment of the big five plant families.
925 *Genetic Resources and Crop Evolution*, *62*(5), 665–689. <https://doi.org/10.1007/s10722-014-0186-2>

926

927 Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters.
928 *Ecology Letters*, *8*(5), 461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>

929 Harlan, J. (1971). Agricultural Origins: Centers and Noncenters. *Science*, *239*(4843), 17–18.

930 Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknæs, A. L., & Totland, Ø. (2009). How does climate warming
931 affect plant-pollinator interactions? *Ecology Letters*, *12*(2), 184–195.

- 932 <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- 933 Hill, J. (2007). Review article Environmental costs and benefits of transportation biofuel production
934 from food- and lignocellulose-based energy crops . A review. *Agronomy for Sustainable*
935 *Development*, 27, 1–12. <https://doi.org/10.1051/agro>
- 936 Hoffmann, A. A., & Sgró, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, 470(7335),
937 479–485. <https://doi.org/10.1038/nature09670>
- 938 Holopainen, J. K., Blande, J. D., Virjamo, V., Ghimire, R. P., Julkunen-Tiitto, R., & Kivimäenpää, M.
939 (2018). Climate Change Effects on Secondary Compounds of Forest Trees in the Northern
940 Hemisphere. *Frontiers in Plant Science*, 9(October), 1–10.
941 <https://doi.org/10.3389/fpls.2018.01445>
- 942 Howes, M. J. R., & Simmonds, M. S. J. (2014). The role of phytochemicals as micronutrients in health
943 and disease. *Current Opinion in Clinical Nutrition and Metabolic Care*, 17(6), 558–566.
944 <https://doi.org/10.1097/MCO.000000000000115>
- 945 Hummel, M., Hallahan, B. F., Brychkova, G., Ramirez-Villegas, J., Guwela, V., Chataika, B., ... Spillane,
946 C. (2018). Reduction in nutritional quality and growing area suitability of common bean under
947 climate change induced drought stress in Africa. *Scientific Reports*, 8(1), 1–11.
948 <https://doi.org/10.1038/s41598-018-33952-4>
- 949 IPCC. (2013). IPCC Fifth Assessment Report (AR5) - The physical science basis. *IPCC*.
- 950 Jin, J., Armstrong, R., & Tang, C. (2019). Impact of elevated CO₂ on grain nutrient concentration varies
951 with crops and soils – A long-term FACE study. *Science of The Total Environment*, 651, 2641–
952 2647. <https://doi.org/10.1016/j.scitotenv.2018.10.170>
- 953 Kadam, N. N., Xiao, G., Melgar, R. J., Bahuguna, R. N., Quinones, C., Tamilselvan, A., ... Jagadish, K. S.
954 V. (2014). Chapter Three - Agronomic and Physiological Responses to High Temperature,
955 Drought, and Elevated CO₂ Interactions in Cereals. In D. B. T.-A. in A. Sparks (Ed.) (Vol. 127, pp.
956 111–156). Academic Press. [https://doi.org/https://doi.org/10.1016/B978-0-12-800131-
957 8.00003-0](https://doi.org/https://doi.org/10.1016/B978-0-12-800131-8.00003-0)
- 958 Kelly, S., Grenyer, R., & Scotland, R. W. (2014). Phylogenetic trees do not reliably predict feature
959 diversity. *Diversity and Distributions*, 20, 600–612. <https://doi.org/10.1111/ddi.12188>
- 960 Kering, M. K., Guretzky, J., Funderburg, E., & Mosali, J. (2011). Effect of Nitrogen Fertilizer Rate and
961 Harvest Season on Forage Yield, Quality, and Macronutrient Concentrations in Midland Bermuda
962 Grass. *Communications in Soil Science and Plant Analysis*, 42, 1958–1971.
963 <https://doi.org/10.1080/00103624.2011.591470>
- 964 Kerr, J. T., Pindar, A., Galpern, P., Packer, L., Potts, S. G., Roberts, S. M., ... Gall, L. F. (2015). Climate
965 change impacts on bumblebees converge across continents. *Science*, 349(6244), 177–180.
- 966 Khoury, C. K., Achicanoy, H. A., Bjorkman, A. D., Navarro-Racines, C., Guarino, L., Flores-Palacios, X., ...
967 Struik, P. C. (2016). Origins of food crops connect countries worldwide. *Proceedings of the Royal*
968 *Society B: Biological Sciences*, 283(1832), 1–9. <https://doi.org/10.1098/rspb.2016.0792>
- 969 Khoury, C. K., Ramirez-Villegas, J., Guarino, L., Bjorkman, A. D., Dempewolf, H., Rieseberg, L. H., ...
970 Struik, P. C. (2014). Increasing homogeneity in global food supplies and the implications for food
971 security. *Proceedings of the National Academy of Sciences*, 111(11), 4001–4006.
972 <https://doi.org/10.1073/pnas.1313490111>
- 973 Kochanek, J., Buckley, Y. M., Probert, R. J., Adkins, S. W., & Steadman, K. J. (2010). Pre-zygotic parental
974 environment modulates seed longevity. *Austral Ecology*, 35(7), 837–848. Retrieved from

- 975 internal-pdf://83.244.69.127/Kochanek-2010-Pre-zygotic parental environment.pdf
- 976 Kulkarni, K. P., Tayade, R., Asekova, S., Song, J. T., Shannon, J. G., & Lee, J.-D. (2018). Harnessing the
977 Potential of Forage Legumes, Alfalfa, Soybean, and Cowpea for Sustainable Agriculture and
978 Global Food Security. *Frontiers in Plant Science*, *9*. <https://doi.org/10.3389/fpls.2018.01314>
- 979 Laenoi, S., Rerkasem, B., Lordkaew, S., & Prom-u-thai, C. (2018). Seasonal variation in grain yield and
980 quality in different rice varieties. *Field Crops Research*, *221*, 350–357.
981 <https://doi.org/10.1016/j.fcr.2017.06.006>
- 982 Laland, K., Matthews, B., & Feldman, M. W. (2016). An introduction to niche construction theory.
983 *Evolutionary Ecology*, *30*(2), 191–202.
- 984 Larkindale, J., & Huang, B. (2004). Thermotolerance and antioxidant systems in *Agrostis stolonifera*:
985 Involvement of salicylic acid, abscisic acid, calcium, hydrogen peroxide, and ethylene. *Journal of*
986 *Plant Physiology*, *161*(4), 405–413. <https://doi.org/10.1078/0176-1617-01239>
- 987 Lee, M. A., Davis, A. P., Chagunda, M. G. G., & Manning, P. (2017). Forage quality declines with rising
988 temperatures, with implications for livestock production and methane emissions.
989 *Biogeosciences*, *14*(6), 1403–1417. <https://doi.org/10.5194/bg-14-1403-2017>
- 990 Lee, M., Manning, P., Rist, J., Power, S. A., & Marsh, C. (2010). A global comparison of grassland
991 biomass responses to CO₂ and nitrogen enrichment. *Philosophical Transactions of the Royal*
992 *Society of London. Series B, Biological Sciences*, *365*(1549), 2047–2056.
993 <https://doi.org/10.1098/rstb.2010.0028>
- 994 Li, D., & Pritchard, H. W. (2009). The science and economics of ex situ plant conservation, (October).
995 <https://doi.org/10.1016/j.tplants.2009.09.005>
- 996 Lobell, D. B., & Field, C. B. (2007). Global scale climate-crop yield relationships and the impacts of
997 recent warming. *Environmental Research Letters*, *2*(1). <https://doi.org/10.1088/1748-9326/2/1/014002>
- 999 Lobell, D., Schlenker, W., & Costa-Roberts, J. (2011). Climate Trends and Global crop production since
1000 1980. *Science*, *333*(June), 1186–1189.
- 1001 Loladze, I. (2014). Hidden shift of the ionome of plants exposed to elevated CO₂ depletes minerals at
1002 the base of human nutrition. *eLife*, *2014*(3), 1–29. <https://doi.org/10.7554/eLife.02245>
- 1003 Long, R. L., Gorecki, M. J., Renton, M., Scott, J. K., Colville, L., Goggin, D. E., ... Finch-Savage, W. E.
1004 (2015). The ecophysiology of seed persistence: a mechanistic view of the journey to germination
1005 or demise. *Biological Reviews*, *90*(1), 31–59. Retrieved from internal-pdf://80.19.69.64/Long-
1006 2015-The ecophysiology of seed persistenc.pdf
- 1007 Makondo, C., & Thomas, D. S. G. (2018). Climate change adaptation : Linking indigenous knowledge
1008 with western science for effective adaptation. *Environmental Science and Policy*, *88*(January),
1009 83–91. <https://doi.org/10.1016/j.envsci.2018.06.014>
- 1010 Matzke, N. J. (2018). BioGeoBEARS: BioGeography with Bayesian (and likelihood) Evolutionary Analysis
1011 with R Scripts (Version v1.1.1).
- 1012 McClure, K. A., Sawler, J., Gardner, K. M., Money, D., & Myles, S. (2014). Genomics: A potential
1013 panacea for the perennial problem. *American Journal of Botany*, *101*(10), 1780–1790.
1014 <https://doi.org/10.3732/ajb.1400143>
- 1015 Mehrabi, Z., Pironon, S., Kantar, M., Ramankutty, N., & Rieseberg, L. (2019). Shifts in the abiotic and
1016 biotic environment of cultivated sunflower under future climate change.

- 1017 Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of
1018 plant-pollinator interactions. *Ecology Letters*, *10*(8), 710–717. <https://doi.org/10.1111/j.1461->
1019 [0248.2007.01061.x](https://doi.org/10.1111/j.1461-0248.2007.01061.x)
- 1020 Meyer, R. S., Duval, A. E., & Jensen, H. R. (2012). Patterns and processes in crop domestication: an
1021 historical review and quantitative analysis of 203 global food crops. *New Phytologist*, *196*, 29–
1022 48.
- 1023 Meyer, R. S., & Purugganan, M. D. (2013). Evolution of crop species: genetics of domestication and
1024 diversification. *Nature Reviews Genetics*, *14*, 840. Retrieved from
1025 <https://doi.org/10.1038/nrg3605>
- 1026 Miller, A. J., & Gross, B. L. (2011). From forest to field: Perennial fruit crop domestication. *American*
1027 *Journal of Botany*, *98*(9), 1389–1414. <https://doi.org/10.3732/ajb.1000522>
- 1028 Moat, J., Williams, J., Baena, S., Wilkinson, T., Gole, T. W., Challa, Z. K., ... Davis, A. P. (2017). Resilience
1029 potential of the Ethiopian coffee sector under climate change. *Nature Plants*, *3*(7), 17081.
1030 <https://doi.org/10.1038/nplants.2017.81>
- 1031 Moerman, D. E. (1991). The medicinal flora of native North America: An analysis. *Journal of*
1032 *Ethnopharmacology*, *31*, 1–42.
- 1033 Mollel, N. P., Fischer, M., Hemp, A., & Fischer, M. (2017). Usable wild plant species in relation to
1034 elevation and land use at Mount Kilimanjaro , Tanzania. *Alpine Botany*, *127*(2), 145–154.
1035 <https://doi.org/10.1007/s00035-017-0187-9>
- 1036 Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S., ... Yahara, T.
1037 (2009). Biodiversity, climate change, and ecosystem services. *Current Opinion in Environmental*
1038 *Sustainability*, *1*(1), 46–54. <https://doi.org/10.1016/j.cosust.2009.07.006>
- 1039 Morueta-Holme, N., Jonas, J. D., Segnitz, R. M., Svenning, J.-C., Sandoval-Acuña, P., & Engemann, K.
1040 (2015). Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt.
1041 *Proceedings of the National Academy of Sciences*, *112*(41), 12741–12745.
1042 <https://doi.org/10.1073/pnas.1509938112>
- 1043 Muller, C., Cramer, W., Hare, W. L., & Lotze-Campen, H. (2011). Climate change risks for African
1044 agriculture. *Proceedings of the National Academy of Sciences*, *108*(11), 4313–4315.
1045 <https://doi.org/10.1073/pnas.1015078108>
- 1046 Muthayya, S., Sugimoto, J. D., Montgomery, S., & Maberly, G. F. (2014). An overview of global rice
1047 production, supply, trade, and consumption. *Annals of the New York Academy of Sciences*,
1048 *1324*(1), 7–14. <https://doi.org/10.1111/nyas.12540>
- 1049 Newbold, T., Hudson, L. N., Contu, S., Hill, S. L. L., Lysenko, I., Palma, A. De, ... Purvis, A. (2016).
1050 Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local
1051 assemblages worldwide, 1–24. <https://doi.org/10.5519/0066354>
- 1052 Odgaard, M. V., Bøcher, P. K., Dalgaard, T., & Svenning, J. C. (2011). Climatic and non-climatic drivers
1053 of spatiotemporal maize-area dynamics across the northern limit for maize production-A case
1054 study from Denmark. *Agriculture, Ecosystems and Environment*, *142*(3–4), 291–302.
1055 <https://doi.org/10.1016/j.agee.2011.05.026>
- 1056 Ogle, B. M., Tuyet, H. T., Duyet, H. N., Dung, N. N. X., & Xuan Dung, N. N. (2003). Food, Feed or
1057 Medicine: The Multiple Functions of Edible Wild Plants in Vietnam. *Economic Botany*, *57*(1), 103–
1058 117. [https://doi.org/10.1663/0013-0001\(2003\)057\[0103:FFOMTM\]2.0.CO;2](https://doi.org/10.1663/0013-0001(2003)057[0103:FFOMTM]2.0.CO;2)
- 1059 Oguchi, R., Ozaki, H., Hanada, K., & Hikosaka, K. (2016). Which plant trait explains the variations in

1060 relative growth rate and its response to elevated carbon dioxide concentration among
1061 *Arabidopsis thaliana* ecotypes derived from a variety of habitats? *Oecologia*, 180(3), 865–876.
1062 <https://doi.org/10.1007/s00442-015-3479-z>

1063 Ohlemüller, R., Anderson, B. J., Araújo, M. B., Butchart, S. H. M., Kudrna, O., Ridgely, R. S., & Thomas,
1064 C. D. (2008). The coincidence of climatic and species rarity: High risk to small-range species from
1065 climate change. *Biology Letters*, 4(5), 568–572. <https://doi.org/10.1098/rsbl.2008.0097>

1066 Ooi, M. K. J., Denham, A. J., Santana, V. M., & Auld, T. D. (2014). Temperature thresholds of physically
1067 dormant seeds and plant functional response to fire: variation among species and relative impact
1068 of climate change. *Ecology and Evolution*, 4(5), 656–671. Retrieved from internal-
1069 pdf://0355681663/Ooi-2014-Temperature thresholds of physically.pdf

1070 Ortiz, R., Jarvis, A., Fox, P., Aggarwal, P. K., & Campbell, B. M. (2014). *Plant genetic engineering, climate*
1071 *change and food security*.

1072 Otto, S. P. (2018). Adaptation, speciation and extinction in the Anthropocene. *Proc. R. Soc. B*,
1073 285(1891), 20182047. <https://doi.org/10.1098/RSPB.2018.2047>

1074 Owen, N. R., Gumbs, R., Gray, C. L., & Faith, D. P. (2019). captures more than just functional diversity.
1075 *Nature Communications*, 8–10. <https://doi.org/10.1038/s41467-019-08600-8>

1076 Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., ... Rondinini,
1077 C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5, 215.
1078 Retrieved from <https://doi.org/10.1038/nclimate2448>

1079 Padulosi, S., Heywood, V., Hunter, D., & Jarvis, A. (2011). Underutilized species and climate change:
1080 current status and outlook. *Crop Adaptation to Climate Change*, 507–521.
1081 <https://doi.org/10.1002/9780470960929>

1082 Parejko, K. (2003). Pliny the Elder's Silphium: First Recorded Species Extinction. *Conservation Biology*,
1083 17(3), 925–927. <https://doi.org/10.1007/s10669-006-7484-y>

1084 Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... Williams, S. E. (2017).
1085 Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being.
1086 *Science*, 355(6332). <https://doi.org/10.1126/science.aai9214>

1087 Peña-Fronteras, J. T., Villalobos, M. C., Baltazar, A. M., Merca, F. E., Ismail, A. M., & Johnson, D. E.
1088 (2009). Adaptation to flooding in upland and lowland ecotypes of *Cyperus rotundus*, a
1089 troublesome sedge weed of rice: Tuber morphology and carbohydrate metabolism. *Annals of*
1090 *Botany*, 103(2), 295–302. <https://doi.org/10.1093/aob/mcn085>

1091 Penuelas, J. (2002). Responses to a Warming World. *Science*, 294(5543), 793–795.
1092 <https://doi.org/10.1126/science.1066860>

1093 Pingali, P. L. (2012). Green Revolution: Impacts, limits, and the path ahead. *Proceedings of the National*
1094 *Academy of Sciences*, 109(31), 12302–12308. <https://doi.org/10.1073/pnas.0912953109>

1095 Pironon, S., Etherington, T. R., Borrell, J. S., Kuhn, N., Macias-Fauria, M., Ondo, I., ... Willis, K. J. (n.d.).
1096 Potential adaptive strategies for 29 Sub-Saharan crops under future climate change (Under
1097 review).

1098 Pironon, S., Ondo, I., Diazgranados, M., Baquero, A. C., Allkin, R., Canteiro, C., ... Willis, K. J. (n.d.).
1099 Exploring the global distribution of people's plants. (Under review).

1100 Polce, C., Garratt, M. P., Termansen, M., Ramirez-Villegas, J., Challinor, A. J., Lappage, M. G., ...
1101 Biesmeijer, J. C. (2014). Climate-driven spatial mismatches between British orchards and their
1102 pollinators: Increased risks of pollination deficits. *Global Change Biology*, 20(9), 2815–2828.

- 1103 <https://doi.org/10.1111/gcb.12577>
- 1104 Porceddu, M., Mattana, E., Pritchard, H. W., & Bacchetta, G. (2017). Dissecting seed dormancy and
 1105 germination in *Aquilegia barbaricina*, through thermal kinetics of embryo growth. *Plant Biology*,
 1106 19(6), 983–993. Retrieved from internal-pdf://62.46.69.111/Porceddu-2017-Dissecting seed
 1107 dormancy and ger.pdf
- 1108 Pritchard, H. W. (2016). Priority science for the preservation of priority crops. *Indian J Plant Genet*
 1109 *Resour*, 29, 297.
- 1110 Pritchard, H. W. (2018). The rise of plant cryobiotechnology and demise of plant cryopreservation?
 1111 *Cryobiology*, 85, 160–161.
- 1112 Qian, H., & Ricklefs, R. E. (2016). Out of the Tropical Lowlands: Latitude versus Elevation. *Trends in*
 1113 *Ecology and Evolution*, 31(10), 738–741. <https://doi.org/10.1016/j.tree.2016.07.012>
- 1114 RBG Kew. (2016). State of the World's Plants 2016. *Royal Botanic Gardens, Kew*, 1–80.
 1115 <https://doi.org/10.1287/mnsc.1070.0706>
- 1116 Richardson, J. E., Whitlock, B. A., Meerow, A. W., & Madriñán, S. (2015). The age of chocolate: a
 1117 diversification history of *Theobroma* and Malvaceae. *Frontiers in Ecology and Evolution*,
 1118 3(November), 1–14. <https://doi.org/10.3389/fevo.2015.00120>
- 1119 Robbirt, K. M., Roberts, D. L., Hutchings, M. J., & Davy, A. J. (2014). Potential disruption of pollination
 1120 in a sexually deceptive orchid by climatic change. *Current Biology*, 24(23), 2845–2849.
 1121 <https://doi.org/10.1016/j.cub.2014.10.033>
- 1122 Rodríguez, M. A., Angueyra, A., Cleef, A. M., & Van Andel, T. (2018). Ethnobotany of the Sierra Nevada
 1123 del Cocuy-Güicán: Climate change and conservation strategies in the Colombian Andes. *Journal*
 1124 *of Ethnobiology and Ethnomedicine*, 14(1), 1–12. <https://doi.org/10.1186/s13002-018-0227-6>
- 1125 Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., ... Slade, E. M. (2017).
 1126 Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356(6339), 742 LP-
 1127 744. <https://doi.org/10.1126/science.aaj1631>
- 1128 Rudman, S. M., Kreitzman, M., Chan, K. M. A., & Schluter, D. (2017). Ecosystem Services : Rapid
 1129 Evolution and the Provision of Ecosystem Services. *Trends in Ecology & Evolution*, 32(6), 403–
 1130 415. <https://doi.org/10.1016/j.tree.2017.02.019>
- 1131 Rumpf, S. B., Willner, W., Schütz, M., Dullinger, S., Moser, D., Wessely, J., ... Klöner, G. (2018). Range
 1132 dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of*
 1133 *Sciences*, 115(8), 1848–1853. <https://doi.org/10.1073/pnas.1713936115>
- 1134 Ryan, P. (2018). *Nubia Past and Present; agriculture, crops and food*. London and Khartoum: The British
 1135 Museum.
- 1136 Saslis-Lagoudakis, C. H., Savolainen, V., Williamson, E. M., Forest, F., Wagstaff, S. J., Baral, S. R., ...
 1137 Hawkins, J. A. (2012). Phylogenies reveal predictive power of traditional medicine in
 1138 bioprospecting. *Proceedings of the National Academy of Sciences*, 109(39), 15835–15840.
 1139 <https://doi.org/10.1073/pnas.1202242109>
- 1140 Saupe, E. E., Portell, R. W., Qiao, H., Soberón, J., Hendricks, J. R., Lieberman, B. S., & Hunter, S. J. (2015).
 1141 Niche breadth and geographic range size as determinants of species survival on geological time
 1142 scales. *Global Ecology and Biogeography*, 24(10), 1159–1169.
 1143 <https://doi.org/10.1111/gcb.12333>
- 1144 Schippmann, U., Leaman, D. J., & Cunningham, A. B. (2002). *Impact of Cultivation and Gathering of*
 1145 *Medicinal Plants on Biodiversity: Global Trends and Issues*. *Materials Science Research*

- 1146 *International* (Vol. 3). <https://doi.org/10.1515/hfsg.1998.52.4.365>
- 1147 Schlenker, W., & Lobell, D. B. (2010). Robust negative impacts of climate change on African agriculture.
1148 *Environmental Research Letters*, 5(1). <https://doi.org/10.1088/1748-9326/5/1/014010>
- 1149 Schroth, G., Läderach, P., Blackburn Cuero, D. S., Neilson, J., & Bunn, C. (2015). Winner or loser of
1150 climate change? A modeling study of current and future climatic suitability of Arabica coffee in
1151 Indonesia. *Regional Environmental Change*, 15(7), 1473–1482. <https://doi.org/10.1007/s10113-014-0713-x>
1152
- 1153 Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L.
1154 (2014). Simulated climate warming alters phenological synchrony between an outbreak insect
1155 herbivore and host trees, 1041–1049. <https://doi.org/10.1007/s00442-014-2960-4>
- 1156 Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate Change Can Cause Spatial
1157 Mismatch of Trophically Interacting Species. *Ecology*, 89(12), 3472–3479.
- 1158 Şerban, P., Wilson, J. R. U., Vamossi, J. C., & Richardson, D. M. (2008). Plant Diversity in the Human Diet:
1159 Weak Phylogenetic Signal Indicates Breadth. *BioScience*, 58(2), 151–159.
1160 <https://doi.org/10.1641/b580209>
- 1161 Settele, J., Bishop, J., & Potts, S. G. (2016). Climate change impacts on pollination. *Nature Plants*, 2(7).
1162 <https://doi.org/10.1038/nplants.2016.92>
- 1163 Shah, F., Huang, J., Cui, K., Nie, L., Shah, T., Chen, C., & Wang, K. (2011). Impact of high-temperature
1164 stress on rice plant and its traits related to tolerance. *Journal of Agricultural Science*, 149(5), 545–
1165 556. <https://doi.org/10.1017/S0021859611000360>
- 1166 Smith, B. D. (2007). Niche construction and the behavioral context of plant and animal domestication.
1167 *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 16(5), 188–
1168 199. Retrieved from internal-pdf://240.30.69.80/Smith-2007-Niche construction and the
1169 behavior.pdf
- 1170 Smýkal, P., Coyne, C. J., Ambrose, M. J., Maxted, N., Schaefer, H., Blair, M. W., ... Varshney, R. K. (2014).
1171 Legume Crops Phylogeny and Genetic Diversity for Science and Breeding. *Critical Reviews in Plant*
1172 *Sciences*, 34(1–3), 43–104. <https://doi.org/10.1080/07352689.2014.897904>
- 1173 Smýkal, P., Nelson, M., Berger, J., & von Wettberg, E. (2018). The Impact of Genetic Changes during
1174 Crop Domestication on Healthy Food Development. *Agronomy*, 8(3), 26.
1175 <https://doi.org/10.3390/agronomy8030026>
- 1176 Solga, M. J., Harmon, J. P., & Ganguli, A. C. (2014). Timing is Everything: An Overview of Phenological
1177 Changes to Plants and Their Pollinators. *Natural Areas Journal*, 34(2), 227–234.
1178 <https://doi.org/10.3375/043.034.0213>
- 1179 Soltis, P. S., & Soltis, D. E. (2016). Ancient WGD events as drivers of key innovations in angiosperms.
1180 *Current Opinion in Plant Biology*, 30, 159–165. <https://doi.org/10.1016/j.pbi.2016.03.015>
- 1181 Springate, D. A., & Kover, P. X. (2014). Plant responses to elevated temperatures: A field study on
1182 phenological sensitivity and fitness responses to simulated climate warming. *Global Change*
1183 *Biology*, 20(2), 456–465. <https://doi.org/10.1111/gcb.12430>
- 1184 Svenning, A. J., Normand, S., Skov, F., Svenning, J., Normand, S., & Skov, F. (2008). Postglacial Dispersal
1185 Limitation of Widespread Forest Plant Species in Nemoral Europe. *Ecography*, 31(3), 316–
1186 326. <https://doi.org/10.1111/j.2008.0906-7590.05206.x>
- 1187 Teixeira, E. I., Fischer, G., Velthuizen, H. Van, Walter, C., & Ewert, F. (2013). Global hot-spots of heat
1188 stress on agricultural crops due to climate change. *Agricultural and Forest Meteorology*, 170,

- 1189 206–215. <https://doi.org/10.1016/j.agrformet.2011.09.002>
- 1190 Thorne, J. H., Fordyce, J. A., Forister, M. L., Shapiro, A. M., McCall, A. C., O'Brien, J., ... Waetjen, D. P.
1191 (2010). Compounded effects of climate change and habitat alteration shift patterns of butterfly
1192 diversity. *Proceedings of the National Academy of Sciences*, 107(5), 2088–2092.
1193 <https://doi.org/10.1073/pnas.0909686107>
- 1194 Ulian, T., Pritchard, H. W., Cockel, C. P., & Mattana, E. (2019). *Enhancing food security through seed*
1195 *banking and use of wild plants: case studies from the Royal Botanic Gardens, Kew*. In
1196 *Encyclopedia of Food Security and Sustainability*. (P. Ferranti, E. Berry, & A. Jock, Eds.). New York:
1197 Elsevier.
- 1198 Vamosi, J. C., & Wilson, J. R. U. (2008). Nonrandom extinction leads to elevated loss of angiosperm
1199 evolutionary history. *Ecology Letters*, 11, 1047–1053. <https://doi.org/10.1111/j.1461->
1200 [0248.2008.01215.x](https://doi.org/10.1111/j.1461-0248.2008.01215.x)
- 1201 Vanbergen, A. J., Garratt, M. P., Vanbergen, A. J., Baude, M., Biesmeijer, J. C., Britton, N. F., ... Wright,
1202 G. A. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and*
1203 *the Environment*, 11(5), 251–259. <https://doi.org/10.1890/120126>
- 1204 VanDerWal, J., Murphy, H. T., Kutt, A. S., Perkins, G. C., Bateman, B. L., Perry, J. J., & Reside, A. E.
1205 (2012). Focus on poleward shifts in species distribution underestimates the fingerprint of
1206 climate change. *Nature Climate Change*, 3, 239. Retrieved from
1207 <https://doi.org/10.1038/nclimate1688>
- 1208 Vaughan, D. A., Balázs, E., & Heslop-Harrison, J. S. (2007). From crop domestication to super-
1209 domestication. *Annals of Botany*, 100(5), 893–901. <https://doi.org/10.1093/aob/mcm224>
- 1210 Vuuren, D. P. van, Sala, O. E., & Pereira, H. M. (2006). The Future of Vascular Plant Diversity Under
1211 Four Global Scenarios. *Ecology and Society*, 11(2).
- 1212 Wahid, A., Gelani, S., Ashraf, M., & Foolad, M. R. (2007). Heat tolerance in plants: An overview.
1213 *Environmental and Experimental Botany*. <https://doi.org/10.1016/j.envexpbot.2007.05.011>
- 1214 Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and
1215 plant regeneration from seed. *Global Change Biology*, 17(6), 2145–2161.
1216 <https://doi.org/10.1111/j.1365-2486.2010.02368.x>
- 1217 Walters, C., Wheeler, L., & Stanwood, P. C. (2004). Longevity of cryogenically stored seeds.
1218 *Cryobiology*, 48(3), 229–244. Retrieved from [internal-pdf://83.125.69.111/Walters-2004-](https://doi.org/10.1016/j.cryobiol.2004.03.001)
1219 [Longevity of cryogenically stored.pdf](https://doi.org/10.1016/j.cryobiol.2004.03.001)
- 1220 Warren, J., Misir, S., & Kalai. (1995). Isozyme markers for self-compatibility and yield in theobroma
1221 cacao (Cacao). *Heredity*, 74(4), 354–356. <https://doi.org/10.1038/hdy.1995.53>
- 1222 Warren, T. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat
1223 change. *Nature*, 414(169), 65–69. <https://doi.org/10.1093/nq/s7-VII.169.229-b>
- 1224 Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and
1225 disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, 104(14),
1226 5738–5742. <https://doi.org/10.1073/pnas.0606292104>
- 1227 Wyse, S. V., & Dickie, J. B. (2017). Predicting the global incidence of seed desiccation sensitivity. *Journal*
1228 *of Ecology*, 105(4), 1082–1093.
- 1229 Yemataw, Z., Tesfaye, K., Zeberga, A., & Blomme, G. (2016). Exploiting indigenous knowledge of
1230 subsistence farmers' for the management and conservation of Enset (*Ensete ventricosum*
1231 (Welw.) Cheesman) (musaceae family) diversity on-farm. *Journal of Ethnobiology and*

- 1232 *Ethnomedicine*, 12(1), 34. <https://doi.org/10.1186/s13002-016-0109-8>
- 1233 Yu, G., Smith, D. K., Zhu, H., Guan, Y., & Lam, T. T. (2017). GGTREE : an R package for visualization and
1234 annotation of phylogenetic trees with their covariates and other associated data, 28–36.
1235 <https://doi.org/10.1111/2041-210X.12628>
- 1236 Zeven, A., & de Wet, J. (1982). *Dictionary of cultivated plants and their regions of diversity*.
1237 <https://doi.org/10.1016/j.contraception.2015.02.004>
- 1238 Ziska, L. H., Epstein, P. R., & Schlesinger, W. H. (2009). Commentary Rising CO₂, Climate Change, and
1239 Public Health : Exploring the Links to Plant Biology, 117(2), 155–158.
1240 <https://doi.org/10.1289/ehp.11501>

1241

1242

1243

1244

1245

1246

1247 **Figure Legends**

1248 **Figure 1. A schematic diagram of the potential distribution of useful plants across the domestication**
1249 **spectrum.** The total number of useful plants is reported as exceeding 31,000 (Kew, 2016), however
1250 the actual and relative size of domestication classes is unknown.

1251 **Figure 2. climate change adaptation strategies and trade-offs for the future utilization of useful**
1252 **plants.**

1253 **Figure 3. Phylogenetic distribution of selected plant crops across the seed plant families.** A) Crops
1254 species were identified *sensu* FAO (2010). Families containing at least one crop taxon are indicated
1255 with red bars placed in front of the phylogenetic tips. Plant families without any crop are colour coded

1256 in blue. We note however that families without crop taxa may nevertheless include useful plants not
1257 considered in this analysis. A bar plot with the proportion (%) of crop plant taxa per number of species
1258 is also provided. A familial phylogeny of seed plants was produced by collapsing species into families
1259 using the R package BioGeoBEARS (Matzke, 2018) while crop plant families were plotted as trait data
1260 in phylogenetic tips using the R package ggtree (Yu, Smith, Zhu, Guan, & Lam, 2017). The total number
1261 of species per family was obtained from Christenhusz et al. (2017).

1262 **Figure 4. Traits that are likely to characterise future useful plants under climate change.** Schematic
1263 diagram with a non-exhaustive selection of desirable useful plant traits in response to a range of
1264 emerging environmental stressors associated with climate change.

1265