

1 **Running title:** The Exigent threat of Dodders in Eastern Africa

2

3 **Title:** Physiological and ecological warnings that Dodder pose an exigent threat to
4 farmlands in Eastern Africa

5

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16 **Sentence Summary:** Microscopy and habitat suitability modeling provide an early
17 warning that dodder's invasion in Eastern Africa poses a threat to important cash crops

18

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30

31 **Abstract**

32 Invasive holoparasitic plants of the genus *Cuscuta* (dodder) threaten Africa's
33 ecosystems, due to their rapid spread and attack on various host plant species. Most
34 *Cuscuta* species cannot photosynthesize, hence rely on host plants for nourishment.
35 After attachment through a peg-like organ called a haustorium, the parasites deprive
36 hosts of water and nutrients leading to their death. Despite their rapid spread in Africa,
37 dodders have attracted limited research attention, although data on their taxonomy, host
38 range and epidemiology are critical for their management. Here, we combine taxonomy
39 and phylogenetics to reveal presence of field dodder (*Cuscuta campestris*) and *C.*
40 *kilimanjari* (both either naturalized or endemic to East Africa), and for the first time in
41 continental Africa, presence of the giant dodder (*C. reflexa*) a south Asian species.
42 These parasites have a wide host range, parasitizing species across 13 angiosperm
43 orders. Evaluating the possibility of *C. reflexa* to expand this host range to tea, coffee,
44 and mango, crops of economic importance to Africa, revealed successful parasitism,
45 following haustorial formation and vascular bundle connections in all three crops.
46 However, only mango mounted a successful post-attachment resistance response.
47 Furthermore, species distribution models predicted high habitat suitability for all three
48 *Cuscuta* species across major tea- and coffee-growing regions of Eastern Africa,
49 suggesting an imminent risk to these crops. Our findings provide relevant insights into a
50 little-understood threat to biodiversity and economic wellbeing in Eastern Africa, and
51 providing critical information to guide development of management strategies to avert
52 their spread.

53

54 **Key words:** *Cuscuta*, *Cuscuta* resistance, Parasitic plants, species distribution models

55

56 Introduction

57 Invasive parasitic plants are a major threat to plant communities, due to their profound
58 negative impacts on global biodiversity and agricultural productivity (Press and Phoenix,
59 2005). In Africa, some parasitic plants, such as *Striga spp.* are well researched because
60 of their direct negative impacts on cereal staples (reviewed by Parker, 2012). However,
61 others such as dodder (*Cuscuta spp.*), noxious vines of the Convolvulaceae family,
62 have received little attention.

63 The genus *Cuscuta* comprises over 200 species of obligate parasites that infect a wide
64 range of herbaceous and woody plants, including important crop species (Lanini and
65 Kogan, 2005). *Cuscuta spp.* are widely distributed across the world, and reportedly
66 colonize a wide range of hosts across various habitats (Lanini and Kogan, 2005).
67 Overall, members of this genus occur on all continents, except Antarctica, with most
68 species reported in the Americas and Mexico, which are also considered their centre of
69 diversity (Yuncker, 1932; Stefanović *et al.*, 2007). In Africa, only a handful of studies
70 have reported dodder occurrence (Zerman and Saghir, 1995; Garcia, 1999; Garcia and
71 Martin, 2007; Garcia *et al.*, 2014). However, their distribution patterns remain unknown.
72 According to the Flora of Tropical East Africa (Verdcourt, 1963), several species,
73 namely *C. australis*, *C. campestris* Yuncker, *C. suaveolens* Seringe, *C. kilimanjari* Oliv,
74 *C. hyalina* Roth, *C. Engelm.*, *C. epilinum* and *C. planiflora* Tenore, are endemic to or
75 naturalized in Eastern Africa. However, some non-native species have recently been
76 anecdotally reported although information about where they were introduced from is
77 unclear.

78 *Cuscuta*'s widespread success is attributed to its parasitic life history strategy and ability
79 to steal most of the resources needed for growth and reproduction from its hosts.
80 Particularly, most *Cuscuta* species do not photosynthesize, due to reduced levels (or
81 lack thereof) of chlorophylls, although some show localized photosynthesis (Parker and
82 Riches, 1993; Braukmann *et al.*, 2013; Kim and Westwood, 2015). Consequently, they
83 entirely depend on their hosts for nourishment.

84 *Cuscuta* life cycle follows a systematic pattern that begins with seed germination,
85 attachment and penetration of a suitable host (through a specialized organ called
86 haustorium), development of vegetative tissues, flowering and seed production. Due to

87 a limited amount of food reserves in their seeds, seedlings must attach to an
88 appropriate host within 3-5 days of germination (Lanini and Kogan, 2005), and establish
89 vascular bundle connections that act as a conduit for siphoning water, nutrients and
90 photo-assimilates. Thereafter, the parasite develops flowers and eventually produces
91 viable seeds that shed back to the soil (Dawson *et al.*, 1994; Albert *et al.*, 2008). At this
92 point, the host succumbs to parasitism often leading to its death.

93 Morphological identification of *Cuscuta* species is difficult because of lack of
94 morphological descriptors based on leaf structure. All members have slender vines, with
95 scale-like leaves and no roots. Previous taxonomic identification relied on floral and fruit
96 characters. In this regard, the early monograph by Engelmann, (1857) categorized
97 *Cuscuta* into 3 groups, based on stigma and style morphology. These were later
98 adopted by Yuncker, (1932) as subgenera. Specifically, subgenus *Monogynella* is
99 characterized by fused styles, whereas subgenera *Cuscuta* and *Grammica* have 2
100 distinct styles, distinguished by respective elongate and globose stigmas. Yuncker later
101 revised the monograph and subdivided these subgenera into 8 sections, based on fruit
102 dehiscence, and 29 subsections based on a combination of characters, such as flower
103 numbers, size, texture and shape, as well as density of inflorescence among others.

104 We hypothesized that different *Cuscuta* species currently occur in Eastern Africa, and
105 their distribution patterns are due to various biotic factors, such as presence of suitable
106 hosts, and interactions with the environment. This is because, in general, occurrence of
107 a species in a particular locality is shaped by life history characteristics, environmental
108 requirements, population genetics and their associations with ecology over time.
109 Therefore, we first used a combination of morphological descriptors and sequencing of
110 the plastid locus (Ribulose biphosphate carboxylase large- *rbcL* and *trnL*) as well as
111 nuclear ITS region, to identify *Cuscuta* species presently invading ecosystems in Kenya.
112 We then determined their host range by compiling a comprehensive list of current
113 *Cuscuta* hosts and extrapolated the possibility of the parasite to expand this range to
114 crop trees, by infecting coffee (*Coffea arabica*), tea (*Camelia sinensis*) and mango
115 (*Mangifera indica*) under greenhouse conditions. We selected these crops because of
116 their agricultural/economic importance. In Kenya, they contribute to the country's GDP

117 through export earnings and cover an estimated area of 114,700, 218,538 and 60,497
118 ha for coffee, tea and mango respectively (FAO, 2017).

119 Finally, we used geographical information system (GIS)-based species distribution
120 modelling (SDM) to estimate geographical distribution of the identified *Cuscuta spp.*
121 across Eastern Africa, based on current climatic conditions and vegetation. Specifically,
122 we adopted presence-only SDMs using the maximum entropy (MaxEnt) algorithm,
123 which combines occurrence records with environmental variables to build correlative
124 models for predicting habitat suitability for a species (Phillips *et al.*, 2006). This
125 algorithm has been previously used to predict distribution of parasitic plants, such as *C.*
126 *chinensis* (Ren *et al.*, 2020), *Striga hermonthica* (Cotter *et al.*, 2012) and, mistletoes
127 (Zhang *et al.* 2016).

128 We found that the current dodder invasion in Kenya i) comprises *C. campestris*, *C.*
129 *kilimanjari* and *C. reflexa*; ii) has a wide host range that could potentially include tea and
130 coffee; and iii) has a wide distribution with potential to invade new habitats. These
131 findings will inform policies for management of the parasite in Eastern Africa.

132

133

134 **Results**

135 **Floral morphological characters reveal 3 *Cuscuta* species**

136 Floral characters revealed 3 distinct *Cuscuta* species in accessions collected from
137 Kenya (Fig. 1). Summarily, flowers across all specimens had clusters comprising 5
138 petals, 5 sepals and 5 stamens, and were identified to the species level as follows:

139 ***C. campestris* Yuncker (subgenus *Grammica*)**: accessions here comprised slender,
140 threadlike yellow to orange stems with a diameter of about 0.3 mm (Supplemental Fig.
141 S1A). Flowers were small, and white, about 2 mm in diameter, with greenish-yellow
142 capsules that appeared in compact cymose clusters. Calyx lobes were obtuse, or
143 somewhat acute, whereas corolla lobes were triangular. Stamens were shorter than the
144 lobes, with filaments of about 1mm. They had 2 separate slender styles, about 1 mm
145 long, with globose stigmas that did not split at the base. Four ovules, about 1 mm long,
146 were present (Fig. 1Aa-d).

147 ***C. kilimanjari* Oliv**: accessions here had thick, coarse and purple vines, about 1 mm in
148 diameter (Supplemental Fig. S1B). Flowers were pale white, waxy, about 4 mm wide.
149 Both sets of calyx and corolla were obtuse, whereas stamens were shorter than the
150 lobes, with short and thick filaments. This category had 2 separate short and thick
151 styles, less than 1 mm long and 0.3 mm wide. Styles bore white spherical stigmas, with
152 ovaries that had purple spots (Fig. 1Ba-d).

153 ***C. reflexa* Roxb**: vines were greenish-yellow, >2 mm in diameter (Supplemental Fig.
154 S1C), with large flowers about 6 mm wide. The flowers had a single thick and short
155 style, with 2 elongated stigmas, and ovaries that contained 4 white ovules, of different
156 sizes (Fig. 1Ca-d).

157

158 **Phylogenetic analysis**

159 Parsimony consensus trees for accessions under this study, alongside other *Cuscuta*
160 species from GenBank, revealed consistent topologies across all 3 (*rbcL*, *trnL* and ITS)
161 regions (Fig. 2). In brief, 3 major clades, corresponding to the 3 *Cuscuta* subgenera,
162 were resolved across the datasets with good bootstrap support. Specifically, *C.*
163 *campestris* accessions from the current study were resolved in the first major clade with
164 other reported species of subgenus *Grammica*, sister to *C. campestris* taxa from

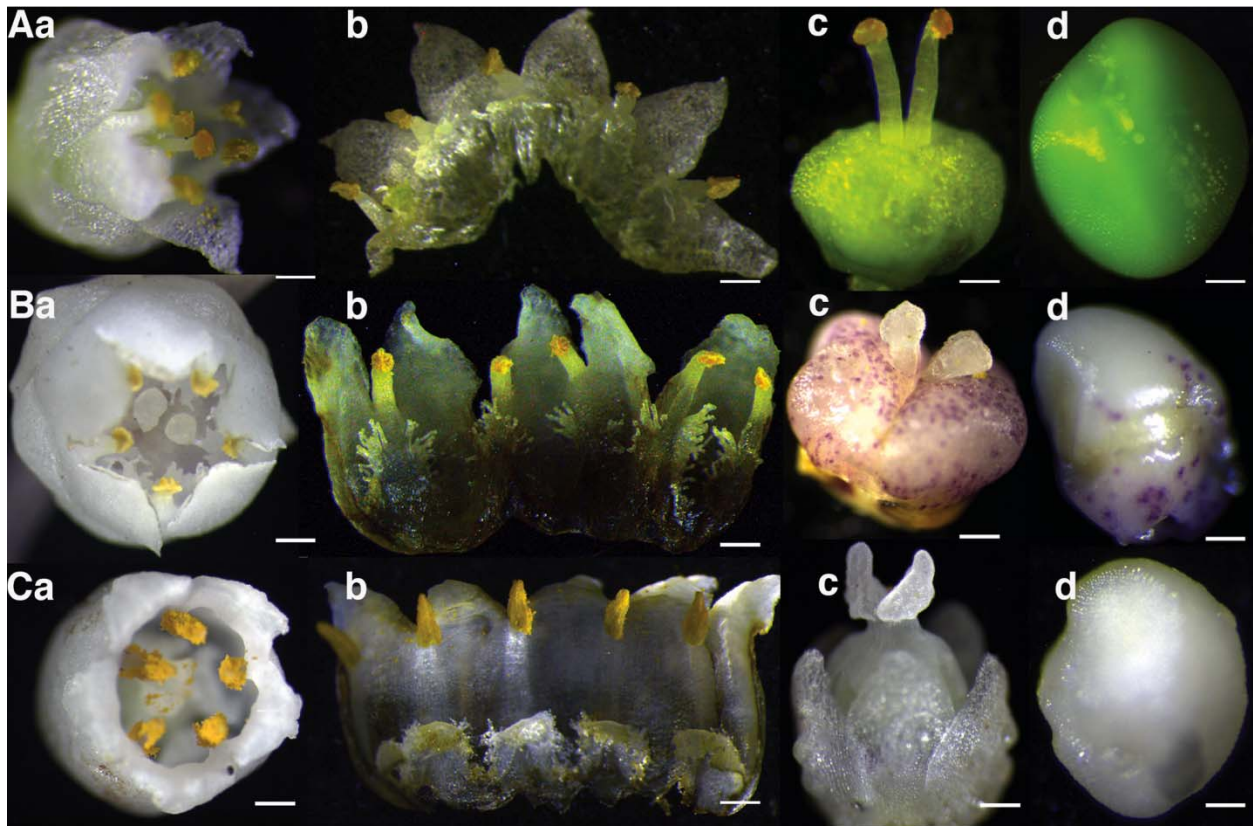


Fig. 1 Profiles of floral morphology among *Cuscuta* accessions collected across Kenya, showing variations in gynoecia, ovule shape, size and colour across species. Aa-Ad *C. campestris*- evidenced by small, white flowers with separate styles that bear globose stigmas; Ba-Bd *C. kilimanjari*- confirmed by thick separate styles with spherical stigmas; Ca-Cd *C. reflexa*- evidenced by short fused styles that bear ligulate stigmas. Bars Aa = 0.4 mm; Ab = 0.4 mm; Ac = 0.4 mm; Ad = 0.1 mm Ba = 0.8 mm; Bb = 0.8 mm; Bc = 1 mm; Bd = 1 mm; Ca = 1.2 mm; Cb = 1.2 mm; Cc = 1 mm and Cd = 0.2 mm.

165 GenBank (Fig. 2). Within the same clade, our *C. kilimanjari* accessions were resolved
166 and nested with a South American clade of subgenus *Grammica*. The second major
167 clade comprised members of subgenus *Cuscuta*, with emphasis on species previously
168 reported to occur in Africa. The third major clade comprised subgenus *Monogynella*,
169 with our *C. reflexa* taxa nested inside a Genbank-derived *C. reflexa* group and basal to
170 both subgenera *Cuscuta* and *Grammica*. Unrooted Maximum Likelihood gene trees
171 confirmed that subgenus *Monogynella* were basal to subgenus *Grammica*, across all
172 genes tested, as well as in the combined dataset (Supplemental Fig. S2)

173

174 **Dodder has a wide host range with potential to infect crops of great economic** 175 **importance**

176 A total of twenty-six (26) host plant species across 13 angiosperm orders, comprising
177 shrubs (40%), trees (44%) and herbs (16%) were parasitized by the aforementioned

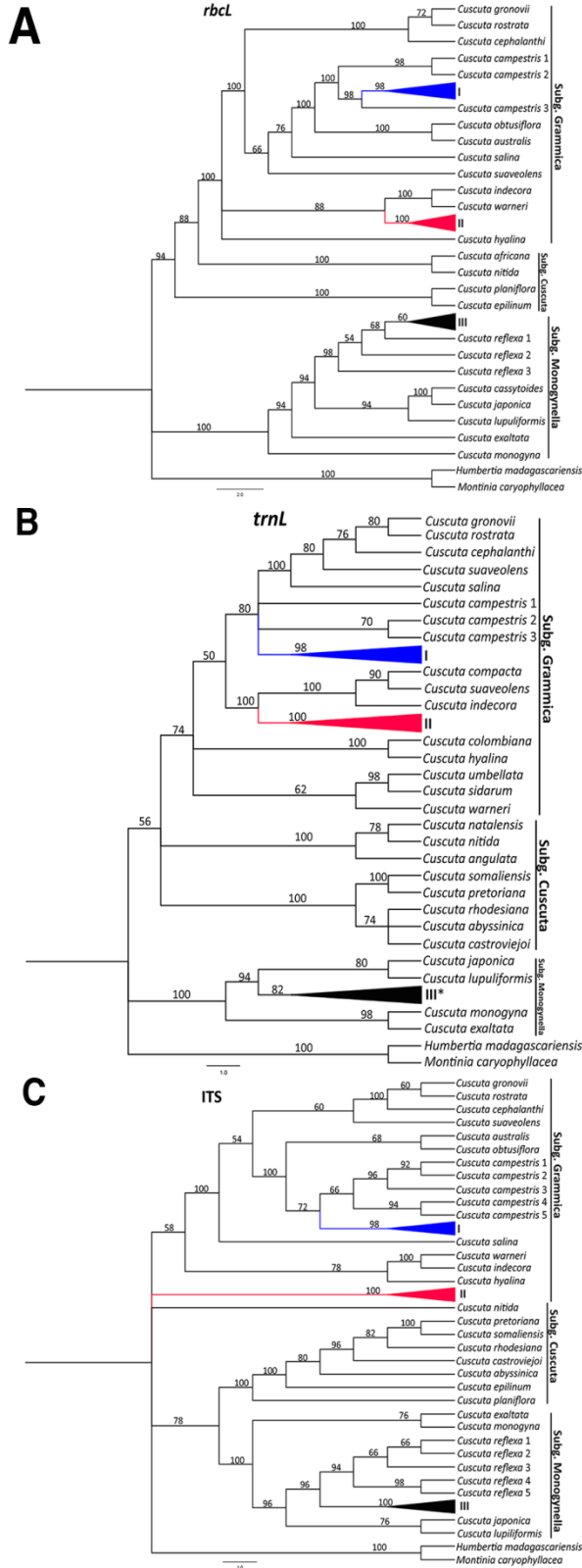


Fig. 2 Phylogenetic reconstruction of *Cuscuta* species based on *rbcL*, *trnL* and ITS regions. Maximum Parsimony bootstrap consensus trees (1000 replicates) are shown, with bootstrap supports indicated above branches. I, II and III represent *Cuscuta* taxa sequenced under this study, and denote *C. campestris*, *C. killianjari* and *C. reflexa*, respectively. The Asterisk (*) on the *trnL* tree implies that our *C. reflexa* taxa were collapsed with those from GenBank.

178 *Cuscuta* species. Fabales (20%) was the most parasitized order, followed by Lamiales

179 (16%), Malpighiales and Caryophyllales (both with 12%), whereas the rest had a single
180 species colonized by the parasite.

181 With regards to host specificity, *C. campestris* and *C. reflexa* exhibited a ‘generalist’
182 behaviour, indiscriminately parasitizing hosts across numerous orders. Among the
183 parasitized species, *Solanum incanum* and *Biancaea decapetala* were the most
184 preferred hosts for *C. campestris*, whereas *Thevetia peruviana* was the most preferred
185 host for *C. reflexa*. Conversely, *C. kilimanjari* exhibited a ‘specialist’ behaviour,
186 parasitizing host species across 2 orders only (Supplemental Table. S1).

187 We further demonstrated the parasite’s potential threat to crops by infecting tea, coffee
188 and mango with *C. reflexa*, followed by histological analysis. We focused on *C. reflexa*
189 for infections due to its invasiveness across the region, a wide host preference
190 (perennial trees and shrubs) and because it was introduced to E. Africa. In all instances
191 (100%), *Cuscuta* successfully parasitized test plants and formed haustoria within 14
192 days of infection. Cross sections, performed 4 weeks after infection, revealed
193 successful penetration of the parasite into host tissues, past the cortex and endodermis,
194 enabling successful formation of vascular bundle connections (Fig. 3). Interestingly, we
195 observed a resistance response from an infected mango plant. Specifically, the infected
196 point swelled, and exuded a sap-like substance that was deposited around the wounded
197 area. This eventually led to death of the parasite (within 4 weeks of attachment), with
198 the infected area ‘healing’ afterwards (Supplemental Fig. S3).

199 To further evaluate the imminent danger posed by these parasites to tea, we sampled
200 Kenyan locations where the ranges for tea and *C. reflexa* overlapped. As an example,
201 we highlight a site in Kakamega, Western Kenya.

202 <https://earth.google.com/web/search/0+12%272%27%27N,+34+46%2721E/@0.202444,34.77314623,1583.10168457a,0d,15y,119.88850412h,90.54106391t,0r/data=CiqiJgokCdGS14h74TRAEc6S14h74TTAGbGLz-dnrjzAlbWQBbGXbGDAlhoKFnVHbklCUWhkQ1BPdnMyZII4TTFqdFEQAq>

206 Here, we found *Markhamia lutea*, a host of *C. reflexa* was infected and growing just next
207 to a tea plantation – pointing to the definite possibility of tea infestation. A Google
208 Earth™ image (using the Street View option) taken in June 2018 showed that the tree
209 had not been infested, but by the time we visited the site in August 2019, the tree had

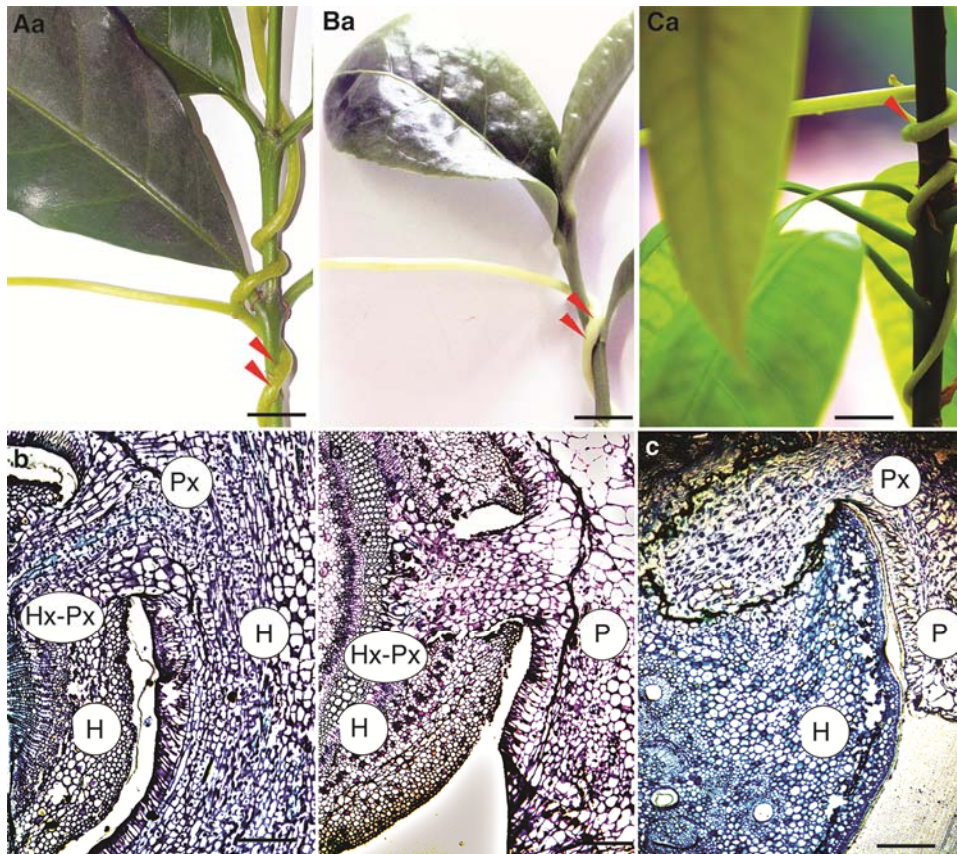


Fig. 3 *Cuscuta* parasitism and extent of ingress into host plants. The upper panel shows close up photographs of infected test plants while the lower panel are toluidine blue-stained cross sections of the host-parasite interface. Aa and Ab- coffee, Ba and Bb- tea, Ca and Cb- mango. P-parasite; H-host; HX-Host xylem; PX-Parasite xylem. Bar top panel=10 mm, bottom panel=5 mm.

210 heavy infestation that threatened to encroach the tea plantation (Fig. 4). This indicates
211 that *C. reflexa* is highly invasive with potential to rapidly infest new localities. In its native
212 ranges of Asia, *C. reflexa* has been reported to parasitize a wide range of hosts,
213 including coffee (Bhattarai *et al.*, 1989; Das, 2007). Additionally, dodder has been
214 reported on coffee in Uganda (Jennipher Bisikwa Personal Communication), and one of
215 the records at the East African Herbarium (voucher number EA16731, collected in
216 1983) indicated that one of the *C. kilimanjari* specimens parasitized coffee.

217

218 **Predicted *Cuscuta* distribution and habitat suitability**

219 Our SDMs had excellent predictive performances, with AUC values of 0.93 and 0.87 for
220 *C. reflexa* built using occurrence records from Kenya and native ranges, respectively.
221 On the other hand, models for *C. campestris* and *C. kilimanjari* had modest
222 performances, with AUC values of 0.76 and 0.72, respectively (Supplemental Figs S4-
223 S7). Precipitation of the warmest quarter (bio18=59.0%) and annual mean temperature



Fig. 4 *Cuscuta* threat on tea. **A** Google Earth™ (Street View) image of a tea plantation in western Kenya, taken in 2018. The circled bush represents *M. lutea*, a tree species commonly used as a windbreaker around plantations and later found to be a *Cuscuta* host. **B** The windbreaker infested with *C. reflexa*, one year after the first image. Arrows indicate parasitic vines threatening to encroach into the tea plantation.

224 (bio1=32.2%) were the most influential variables in the models for *C. reflexa* based on
225 occurrences in Kenya and the native range, respectively. Conversely, precipitation of
226 the driest quarter (bio17=46.2) and isothermality (bio3=47.6%) were the highest
227 contributors to the models for *C. campestris* and *C. kilimanjari*, respectively (Table 1).
228 Our models presented in Fig. 5 revealed different distribution patterns across Eastern
229 Africa, with current estimates showing that all 3 species under this study can potentially
230 colonize areas larger than the localities sampled herein.
231 Overall, high habitat suitability for *C. reflexa* (log-transformed score >0.8) is predicted in
232 Western and Central Kenya, Eastern Uganda, large parts of Rwanda and Burundi as
233 well as Central Ethiopia. Predicted habitat suitability for *C. kilimanjari* is higher than that
234 observed for *C. reflexa* across the 6 countries. Particularly, Central and Western Kenya,
235 Western Uganda, Rwanda and Burundi, as well as Central Ethiopia show high
236 suitability. Conversely, moderate habitat suitability is predicted for *C. campestris*, with
237 infestation likely to occur in Western and Central Kenya, Eastern Uganda, with pockets
238 in Ethiopia and Tanzania. Additionally, many major coffee- and tea-growing areas show
239 high habitat suitability for all species. Our collected occurrence data indicate that *C.*
240 *reflexa* seems to have already invaded many of these regions in Kenya. Projections of
241 our models to other regions suggest that *C. reflexa* could become or already may be a
242 concern in coffee- and tea-growing regions of Rwanda, eastern Uganda, and the Harar
243 coffee zone of Ethiopia.

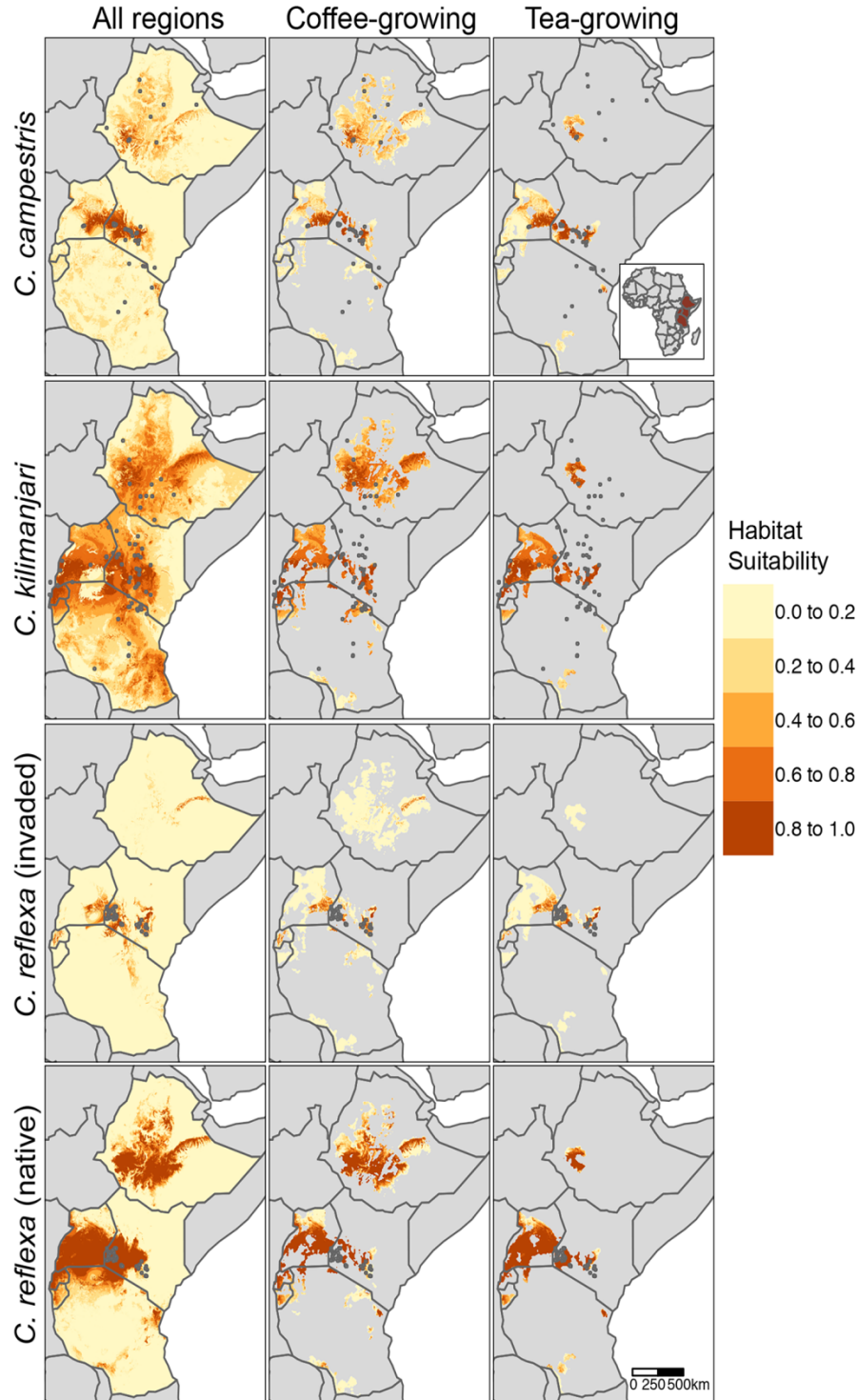


Fig. 5 Habitat suitability for *C. campestris*, *C. kilimanjari*, *C. reflexa* across Ethiopia, Kenya, Uganda, Rwanda, Burundi, and Tanzania. Dark grey points indicate locations of occurrence records. For *C. reflexa*, species distribution models were trained using occurrences from the invaded range in Kenya ($n=66$) or native range from Afghanistan to Indo-China ($n=165$), then projected to the six countries. Models for *C. campestris* and *C. kilimanjari* were constructed using a combination of occurrence records obtained from our sampling activities (in Kenya), as well as those obtained from GBIF and herbarium specimens at the East African Herbarium. Projections were masked to coffee- and tea-growing regions, estimated to produce >1 metric tons in 2017 (IFPR, 2020).

244 Noteworthy, the predicted distributions are supported by various local press describing

245 dodder infestations in the aforementioned countries including Uganda
246 ([https://www.newvision.co.ug/new_vision/news/1503872/dangerous-plant-invades-](https://www.newvision.co.ug/new_vision/news/1503872/dangerous-plant-invades-kampala-city)
247 [kampala-city](https://www.newvision.co.ug/new_vision/news/1503872/dangerous-plant-invades-kampala-city)) and Kenya ([https://www.nation.co.ke/news/Dodder-plant-poses-threat-to-](https://www.nation.co.ke/news/Dodder-plant-poses-threat-to-trees-and-crops/1056-5138904-aawhphz/index.html)
248 [trees-and-crops/1056-5138904-aawhphz/index.html](https://www.nation.co.ke/news/Dodder-plant-poses-threat-to-trees-and-crops/1056-5138904-aawhphz/index.html)).

249

250

251 Discussion

252 *Cuscuta* identification

253 Interactions among global change components, such as land use, agricultural
254 intensification and invasions by non-native species, cause substantial changes to plant
255 community composition worldwide. Consequently, plant communities that arguably play
256 the biggest role in establishing and maintaining ecosystems are deteriorating. A key
257 driver of such community change is invasion by alien plants that displace/arrest
258 development of native species, subsequently reducing habitat quality, causing
259 economic losses, and posing a serious threat to human wellbeing (Vila' *et al.*, 2011).
260 Once established, the spread of invasive plants is extremely difficult to control or
261 reverse. In African terrestrial ecosystems, a myriad of invasive plant species occurs, key
262 among them the current rapid spread of parasitic vines of the genus *Cuscuta*. To avert
263 loss to biodiversity and developed reasoned management programs for the parasites,
264 we analysed *Cuscuta*'s potential threat in Eastern Africa by describing their taxonomy,
265 host range and habitat suitability.

266 *Cuscuta* identification using morphological characters is difficult because members of
267 this genus lack roots and their leaves are reduced to minute scales (Kuijt, 1969).
268 However, diversity among floral components presents a unique opportunity for
269 distinguishing species. We adopted monographs by Engelmänn (1857) and Yuncker
270 (1932) to interpret stigma and style morphology, and consequently identified 3 *Cuscuta*
271 species, from 2 related subgenera (*Grammica* and *Monogynella*) in accessions
272 collected from Kenya. Individuals in subgenus *Grammica* had 2 separate styles, with
273 either globose or spherical stigmas, and were classified as *C. campestris* and *C.*
274 *kilimanjari*, respectively, whereas those in subgenus *Monogynella* had elongate stigmas
275 born on fused styles, typical of *C. reflexa*.

276 We validated this identification by sequencing *rbcl*, *trnL* and ITS regions from
277 representative individuals, and performed phylogenetic reconstruction alongside other
278 species from GenBank. These markers have been extensively used to infer
279 phylogenetic relationships, character evolution and biogeography across the genus
280 (Garcia and Martin, 2007; McNeal., *et al.*, 2007; Garcia *et al.*, 2014). In our case, all our
281 sequences were resolved alongside respective *C. campestris*, *C. kilimanjari* and *C.*

282 *reflexa* taxa from GenBank, indicating that they indeed belonged to these species.
283 Additionally, these phylogenetic reconstructions confirmed the monophyly of subgenus
284 Monogynella, with all members basal to subgenera *Cuscuta* and *Grammica*, consistent
285 with earlier reports (Garcia and Martin, 2007; McNeal *et al.*, 2007; Stefanović *et al.*,
286 2007; Garcia *et al.*, 2014). Apart from these 3, other *Cuscuta* species have also been
287 reported in Africa, although most of them belong to subgenus *Cuscuta* (Zerman and
288 Saghi, 1995; Garcia, 1999; Garcia and Martin, 2007).

289

290 **SDM-based distribution patterns**

291 *Cuscuta*'s damaging success and worldwide distribution is attributed to its ability to
292 colonize a wide range of hosts and survive in areas with an array of environmental
293 conditions (Parker and Riches, 1993). Additionally, most members are non-specific,
294 colonizing multiple host plants across various angiosperm families (Dawson *et al.*, 1994;
295 Lanini and Kogan, 2005; Kim and Westwood, 2015).

296 Our SDMs, combined with the observed host range and artificial infection assays,
297 provided insights into the parasite's potential distribution patterns in Eastern Africa.
298 These models showed that the species are likely to be present in additional areas not
299 covered by this study, as evidenced by areas of high habitat suitability.

300 Three climatic variables, precipitation of the warmest quarter, annual mean temperature
301 and isothermality had the highest contribution to our models, suggesting that they could
302 play a significant role in the predicted distribution. These were also found to significantly
303 contribute to habitat suitability for *C. chinensis* (Ren *et al.*, 2020).

304 With regards to land cover contribution, grass cover fraction was an important predictor
305 for SDMs in all three species, with lower habitat suitability corresponding with areas of
306 high grass cover. This finding is consistent with lower frequency of preferred *Cuscuta*
307 hosts in grasslands and parasitism on diverse herbaceous plants as well as perennial
308 shrubs and trees.

309 Additional identification of lower risk areas for *Cuscuta* invasion is critical for future
310 preparedness. For example, our models predicted relatively low habitat suitability in
311 central and western Uganda for *C. reflexa* (according to models based on occurrences
312 from a restricted sampling area in the invaded range). However, SDMs based on

313 occurrences throughout a broader set of environments in the native range suggested
314 high habitat suitability in these same regions. Although there are many limits to spatial
315 transferability of SDMs from native and introduced ranges (Liu *et al.*, 2020), these
316 findings suggest that current environments may not be an effective barrier to the spread
317 and establishment of *C. reflexa* in many East Africa regions and that active
318 management of *C. reflexa* will be needed to prevent its spread.

319

320 ***Cuscuta*'s potential threat to cash crops**

321 Results from artificial infection of *C. reflexa* on coffee, tea and mango revealed its
322 potential to parasitize these crops of economic importance. Specifically, we observed
323 attachment, haustoria and vascular bundle formation; all indicative of successful
324 parasitism. *Cuscuta* parasitism on coffee and tea could have devastating impacts on the
325 income generated by these crops in East African countries. In addition, presence of a *C.*
326 *reflexa*-infected *M. lutea* just next to a tea plantation is indicative that such an infestation
327 may be imminent. Governments in East Africa will therefore require to develop urgent
328 interventions and appropriate policies to stop such eventualities which would have
329 devastating effects to farmers in affected areas.

330 Interestingly, we observed a resistance response in the mango genotype artificially
331 infected with *C. reflexa*. Cross sections indicated ingression of parasitic haustoria into
332 the host and successful establishment of vascular bundle connections. However, this
333 success was short-lived with the host initiating wound response and chemical
334 deposition that resulted in death of the parasite and later, healing of the infected area. It
335 is possible that this resistance response goes beyond the observed wounding, although
336 this remains to be investigated. Such a phenomenon could also be key in determining
337 dodder's host preference since plants that display resistance are avoided during
338 parasitism (Kaiser *et al.*, 2015). Previous studies have described this type of resistance
339 (Albert *et al.*, 2006) among other mechanisms, including incompatibility due to
340 anatomical attributes (Dawson *et al.*, 1994), induction of defence-related stress
341 hormones (salicylic and jasmonic acid) as well as use of mechanical barriers that block
342 parasitic ingression into host vasculature (Kaiser *et al.*, 2015). Consequently, species
343 such as *Gossypium hirsutum* (Capderon *et al.*, 1985), *Solanum lycopersicum* (Albert *et*

344 *al.*, 2006; Runyon *et al.*, 2010) and some varieties of chickpea (*Cicer arietinum*)
345 (Goldwasser *et al.*, 2012) have been reported to resist dodder infection and are
346 therefore avoided during host selection.

347

348 **Conclusions and future prospects**

349 In summary, our findings reveal presence of 3 *Cuscuta* species; *C. campestris*, *C.*
350 *kilimanjari* and *C. reflexa* across various ecosystems in Kenya. The first 2, endemic to
351 or naturalized in Eastern Africa, have been documented in the Flora of Tropical East
352 Africa, alongside others such as *C. australis*, *C. suaveolens* Seringe, *C. hyalina* Roth,
353 *C. cassyoides* Engelm, *C. epilinum* and *C. planiflora* Tenore (Verdcourt, 1963).
354 However, to the best of our knowledge, this is the first report describing occurrence of
355 *C. reflexa*, a south Asian species, in continental Africa. These parasites have a broad
356 host range, and infestation on crops of economic importance may be inevitable if urgent
357 actions are not taken to stop their spread. In fact, our predictions show that many
358 regions across Eastern Africa are characterized by highly suitable habitats for *Cuscuta*
359 infestation, and may already be infested. Therefore, this work will be critical in
360 developing informed strategies for managing the parasite and averting the looming risk.
361 This may potentially involve identifying resistant plant species and genotypes to aid
362 development of cultural control and adaptation measures in agriculture and forestry
363 within the region. Additionally, unravelling the physical, biochemical and genetic factors
364 controlling the observed resistance response in mango will provide insights into
365 regulation of these resistance phenomena and guide future control strategies.

366

367 **Materials and methods**

368 **Sample collection**

369 We collected a total of 96 *Cuscuta* accessions across Kenya. In our case, an accession
370 is defined as material from an individual plant from the same species found within a
371 similar geographical area. Sampling was done between July and November 2018, with
372 at least 5 individual accessions collected per location. Dodder flowers and vines were
373 collected and immediately dried in silica gel to await morphological analysis and DNA
374 isolation. *Cuscuta*-parasitized plants were also collected and identified to the species

375 level, according to the keys of plant identification described in the Flora of Tropical East
376 Africa (Verdcourt, 1963) and Pennsylvania State University
377 (<https://extension.psu.edu/plant-identification-preparing-samples-and-using-keys>).

378

379 **Morphological *Cuscuta* identification**

380 Morphological identification was performed according to the keys of *Cuscuta*
381 monograph constructed by Engelmann, (1857) and Yuncker, (1932). Briefly, flowers
382 were either used immediately after collection or rehydrated before microscopy (for those
383 kept in silica gel). To observe different parts, we examined a single full flower (sepals,
384 petals, gynoecium and androecium) under a Leica MZ10F stereomicroscope (Leica
385 Microsystems, UK) and photographed it. Thereafter, we carefully dissected and
386 photographed it, with focus given to the gynoecia, number of parts, fusion (or lack
387 thereof) of the styles as well as the size and shape of stigmas. Ovaries were also
388 dissected, then the number, size and color of ovules observed and photographed.

389

390 **Host plant infection and histology**

391 We evaluated whether dodder could expand its host range to tree crops of agricultural
392 value, by artificially infecting tea, coffee and mango with *C. reflexa*, under controlled
393 conditions in the greenhouse. Summarily, three months-old test seedlings were
394 maintained in potted soil with regular watering then infected by winding a 30 cm long
395 piece of parasitic vine (that had at least one node) around their stems. Parasitism was
396 determined by histological analysis of the host-parasite interface, four weeks after
397 infection as previously described (Gurney *et al.*, 2003).

398 Briefly, tissues at the interface were collected and fixed using Carnoy's fixative (4:1
399 ethanol: acetic acid), dehydrated with 100% ethanol then pre-infiltrated in Technovit
400 solution (Haraeus Kulzer, GmbH). The tissues were embedded in 1.5 ml
401 microcentrifuge tube lids containing Technovit/Hardener and left to set according to the
402 manufacturer's instructions, then mounted onto histoblocks using the Technovit 3040 kit
403 (Haraeus Kulzer GmbH). Microscopic sections (5 µm thick) of the tissues were cut using
404 a microtome (Leica RM 2145), transferred onto glass slides and stained using 0.1%
405 Toluidine Blue O dye in phosphate buffer. After washing off excess dye and drying,

406 slides were covered with slips containing a drop of DPX (BDH, Poole, UK), observed
407 and photographed using a Leica microscope mounted with a Leica MC190 HD camera
408 (Leica, UK).

409

410 **DNA extraction, polymerase chain reaction (PCR) and Sequencing**

411 We sequenced representative accessions from each of the aforementioned *Cuscuta*
412 species, following morphological characterization. We could not acquire material for
413 DNA extraction from voucher specimens held at the East African Herbarium in Nairobi,
414 Kenya, owing to the destructive nature of sampling involved. DNA was extracted from
415 flowers and hanging vines, collected at least 10 cm away from the point of attachment
416 to avoid host-DNA contamination.

417 PCR amplification of the ITS region was done using ITS4 and ITS5 primers (Baldwin,
418 1992), whereas *rbcL* was amplified using *rbcL*-512F and *rbcL*-1392R primers (McNeal
419 *et al.*, 2007). Partial amplification of *trnL* was using *trnLF*- 5'
420 CGAAATCGGTAGACGCTACG 3' and *trnLR*- 5' ATTTGAACTGGTGACACGAG 3'
421 primers, designed specifically for *Cuscuta*. PCR reactions were performed in 25 µl
422 volumes using MyTaq™ DNA polymerase kit (Bioline, Meridian Biosciences) under the
423 following conditions; 95°C for 1 minute, followed by 35 cycles comprising 95°C for 15
424 seconds, each primer's respective annealing temperature for 30 seconds and a 72°C
425 extension for 1 minute. A final 10-minute extension, at 72°C, was also included. PCR
426 products were confirmed on a 1% agarose gel, cleaned using the Qiaquick™ PCR
427 purification kit (Qiagen, USA), and sequenced on the ABI platform at Macrogen
428 (Macrogen. Inc).

429

430 **Phylogenetic analysis**

431 Sequences were edited in SeqMan Pro17 in Lasergene package (DNASTAR Inc.,
432 Madison, WI, USA) to remove low quality reads, then aligned using ClustaX version 2.0
433 (Larkin *et al.*, 2007). Sequences were submitted to NCBI (Accession numbers are
434 shown at the end of the document), then used as queries to identify similar taxa using
435 the nucleotide BLAST algorithm at NCBI. Highly similar sequences across the 3
436 *Cuscuta* subgenera were retrieved for phylogenetic reconstruction and ancestry

437 inferencing, with sequences for *Montinia caryophyllacea* and *Humbertia*
438 *madagascariensis* included as outgroups. We first constructed unrooted Maximum
439 Likelihood gene trees for the accessions under this study, then generated Parsimony
440 consensus trees (with 1000 replications) for phylogenetic reconstruction of taxa from
441 our species alongside those from NCBI. All phylogenetic analyses were performed in
442 MEGAX (Kumar *et al.*, 2018), and the trees visualized in FigTree version 1.4.4
443 (Rambaut, 2009).

444

445 **Species distribution modelling**

446 **Occurrence records**

447 We combined respective occurrence records for *C. kilimanjari* and *C. campestris* from
448 our sampling efforts in Kenya with records from the Global Biodiversity Information
449 Facility (GBIF) (<https://doi.org/10.15468/dl.9kpzum>), and records for specimens held in
450 the collection at the East African Herbarium (EA). This resulted in a total of 74 and 51
451 unique locations for *C. kilimanjari* and *C. campestris*, respectively. We found no records
452 of *C. reflexa* in neither GBIF nor in the EA collection, hence all occurrence records for
453 models based on this species' current invasion range were from localities sampled as
454 part of this study ($n = 66$ unique locations across Kenya). We also built SDMs based on
455 165 unique occurrences of *C. reflexa* from its native range (Afghanistan to Indo-China)
456 that were available from GBIF ([https://www.gbif.org/occurrence/download/0074148-](https://www.gbif.org/occurrence/download/0074148-200613084148143)
457 [200613084148143](https://www.gbif.org/occurrence/download/0074148-200613084148143)). To characterize the background of the study, we randomly
458 sampled 1,000 points from a radius of 300 km from known occurrences.

459

460 **Environmental variables**

461 Species distribution models were based on five bioclimatic variables, namely annual
462 mean temperature (bio1), isothermality (bio3), precipitation seasonality (bio15),
463 precipitation of the driest quarter (bio17), and precipitation of the warmest quarter
464 (bio18), as well as three variables related to vegetation structure, namely land cover
465 fraction of grass (veg1), shrub (veg2), and tree (veg3). Four of the bioclimatic variables
466 (bio1, bio3, bio15, and bio18) were previously reported as important for species
467 distribution models for *C. chinensis* (Ren *et al.*, 2020), whereas the fifth (bio17)

468 exhibited high feature importance in our preliminary analyses. Bioclimatic data were
469 obtained from the CHELSA dataset
470 (<https://zenodo.org/record/3939050#.X3N49y2ZM8Z>) (Karger *et al.*, 2017), whereas
471 vegetation layers were from the Copernicus Global Land Service (Buchhorn *et al.*,
472 2020). These layers were based on epoch 2019 from Collection 3 of the annual, global
473 100m land cover maps, and were resampled to match resolution of the bioclimatic
474 layers (1 km) using the bilinear interpolation method of the 'resample' function from the
475 R package 'raster' (Hijmans 2019). The vegetation layers captured aspects of
476 vegetation cover, which may be important for *Cuscuta* spp. parasitism on various
477 herbaceous and woody host species. All variables had Pearson's correlation coefficients
478 less than 0.8 across background points of the study.

479

480 **Model building and prediction of suitable habitats**

481 Species distribution models were built using the Maxent algorithm (Phillips *et al.*, 2006).
482 The Models were tuned and evaluated with R version 3.6.1 with ENMeval (Muscarella
483 *et al.*, 2014) using the checkerboard2 method for partitioning occurrence data into
484 training and test sets. To determine overlap between *Cuscuta* spp. distributions with
485 major coffee- and tea-growing areas, we used crop production maps from IFPRI, (2020)
486 (<https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/FSSKBW>)
487 to mask *Cuscuta* spp. distribution models to just those areas estimated to produce at
488 least one metric ton of coffee or tea in 2017.

489

490 **Accession Numbers**

491 **rbcL**

492 ***C. campestris***; MW078922, MW078923, MW078924

493 ***C. kilimanjari***; MW078930, MW078931, MW078932

494 ***C. reflexa***; MW078927, MW078928, MW078929

495 **ITS**

496 ***C. campestris***; MT947605, MT947606, MT947607

497 ***C. kilimanjari***; MT952140, MT952141, MT952142

498 ***C. reflexa***; MW080817, MW080818, MW080819

499 ***trnL***

500 ***C. campestris***; MW086603, MW086604, MW086605

501 ***C. kilimanjari***; MW086607, MW086608, MW086609

502 ***C. reflexa***; MW115588, MW115589, MW115590

503

504 **Supplemental Data**

505 The following supplemental materials are available

506 **Fig. S1** Categories of *Cuscuta* species observed parasitizing various susceptible host
507 plants in Kenya.

508 **Fig. S2** Unrooted Maximum Likelihood trees based on *rbcL*, *trnL*, ITS and a
509 combination of the 3 regions.

510 **Fig. S3** Resistance response exhibited by a mango (*Mangifera indica*) genotype under
511 *C. reflexa* infection.

512 **Fig. S4** Area under curve (AUC) values for *C. campestris*.

513 **Fig. S5** Area under curve (AUC) values for *C. kilimanjari*.

514 **Fig. S6** Area under curve (AUC) values for *C. reflexa*

515 **Fig. S7** Area under curve (AUC) values for *C. reflexa*

516 **Supplemental Table S1** Occurrence records of *Cuscuta* species collected from Kenya

517

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520 providing occurrence records. We acknowledge Prof. Claude dePamphilis
521 (Pennsylvania State University-USA) for fruitful scientific discussions and Prof. Alistair
522 Jump (University of Stirling-UK) for thoughtful reviews.

523

524 **Table 1.** Permutation importance of bioclimatic and vegetation variables. Values
 525 represent percent (%) contributions of each variable to the model. An asterisk (*) in
 526 each column indicates the highest contributing variable

Variable	<i>C.</i> <i>campestris</i>	<i>C.</i> <i>kilimanjari</i>	<i>C. reflexa</i> (invaded)	<i>C. reflexa</i> (native)
Annual Mean Temperature (bio1)	4.4	0	0	32.2*
Isothermality (bio3)	2.5	47.6*	13.7	1.1
Precipitation Seasonality (bio15)	0	12.7	0.5	15.6
Precipitation of Driest Quarter (bio17)	46.2*	2.7	0.5	15.9
Precipitation of Warmest Quarter (bio18)	4.9	7.7	59.0*	13.2
Land Cover Fraction (Grass) (veg1)	40.1	25.8	14.9	1.7
Land Cover Fraction (Shrub) (veg2)	0.3	0	0.8	11.2
Land Cover Fraction (Tree) (veg3)	1.5	3.5	10.6	9.1

527

528

529 **Figure Legends**

530 **Fig. 1** Profiles of floral morphology among *Cuscuta* accessions collected across Kenya,
531 showing variations in gynoecia, ovule shape, size and colour across species. Aa-Ad *C.*
532 *campestris*- evidenced by small, white flowers with separate styles that bear globose
533 stigmas; Ba-Bd *C. kilimanjari*- confirmed by thick separate styles with spherical stigmas;
534 Ca-Cd *C. reflexa*- evidenced by short fused styles that bear ligulate stigmas. Bars Aa =
535 0.4 mm; Ab = 0.4 mm; Ac = 0.4 mm; Ad = 0.1 mm Ba = 0.8 mm; Bb = 0.8 mm; Bc = 1
536 mm; Bd = 1 mm; Ca = 1.2 mm; Cb = 1.2 mm; Cc = 1 mm and Cd = 0.2 mm.

537 **Fig. 2** Phylogenetic reconstruction of *Cuscuta* species based on *rbcl*, *trnL* and ITS
538 regions. Maximum Parsimony bootstrap consensus trees (1000 replicates) are shown,
539 with bootstrap supports indicated above branches. I, II and III represent *Cuscuta* taxa
540 sequenced under this study, and denote *C. campestris*, *C. kilimanjari* and *C. reflexa*,
541 respectively. The Asterisk (*) on the *trnL* tree implies that our *C. reflexa* taxa were
542 collapsed with those from GenBank.

543 **Fig. 3** *Cuscuta* parasitism and extent of ingress into host plants. The upper panel
544 shows close up photographs of infected test plants while the lower panel are toluidine
545 blue-stained cross sections of the host-parasite interface. Aa and Ab- coffee, Ba and
546 Bb- tea, Ca and Cb- mango. P-parasite; H-host; HX-Host xylem; PX-Parasite xylem. Bar
547 top panel=10 mm, bottom panel=5 mm.

548 **Fig. 4** *Cuscuta* threat on tea. **A** Google Earth™ (Street View) image of a tea plantation
549 in western Kenya, taken in 2018. The circled bush represents *M. lutea*, a tree species
550 commonly used as a windbreaker around plantations and later found to be a *Cuscuta*
551 host. **B** The windbreaker infested with *C. reflexa*, one year after the first image. Arrows
552 indicate parasitic vines threatening to encroach into the tea plantation.

553 **Fig. 5** Habitat suitability for *C. campestris*, *C. kilimanjari*, *C. reflexa* across Ethiopia,
554 Kenya, Uganda, Rwanda, Burundi, and Tanzania. Dark grey points indicate locations of
555 occurrence records. For *C. reflexa*, species distribution models were trained using
556 occurrences from the invaded range in Kenya ($n=66$) or native range from Afghanistan
557 to Indo-China ($n=165$), then projected to the six countries. Models for *C. campestris* and
558 *C. kilimanjari* were constructed using a combination of occurrence records obtained
559 from our sampling activities (in Kenya), as well as those obtained from GBIF and

560 herbarium specimens at the East African Herbarium. Projections were masked to
561 coffee- and tea-growing regions, estimated to produce >1 metric tons in 2017 (IFPR,
562 2020).

563

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