

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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23

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25 experimental work. J.M. carried out fieldwork, sequence analysis, infection assays and  
26 wrote the draft manuscript. B.N.M carried out morphological characterization. W.K  
27 performed histological analysis. P.S. curated environmental data. E.S.B. and M.W  
28 carried out species distribution modelling. R.O, M.P, A.A & P.O assisted with conceptual  
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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).

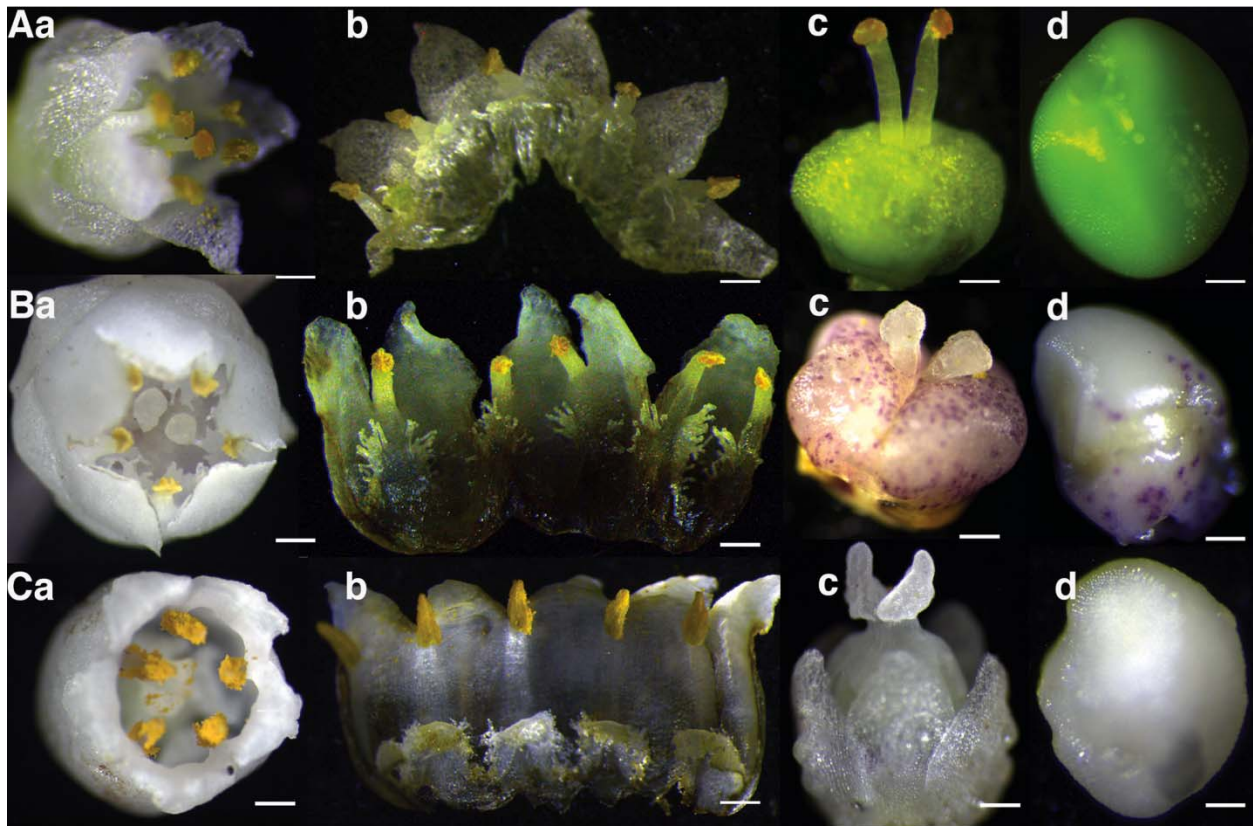
147 ***C. kilimanjari* Oliv**: accessions here had thick, coarse and purple vines, about 1 mm in  
148 diameter (Supplemental Fig. S1B). Flowers were pale white, waxy, about 4 mm wide.  
149 Both sets of calyx and corolla were obtuse, whereas stamens were shorter than the  
150 lobes, with short and 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

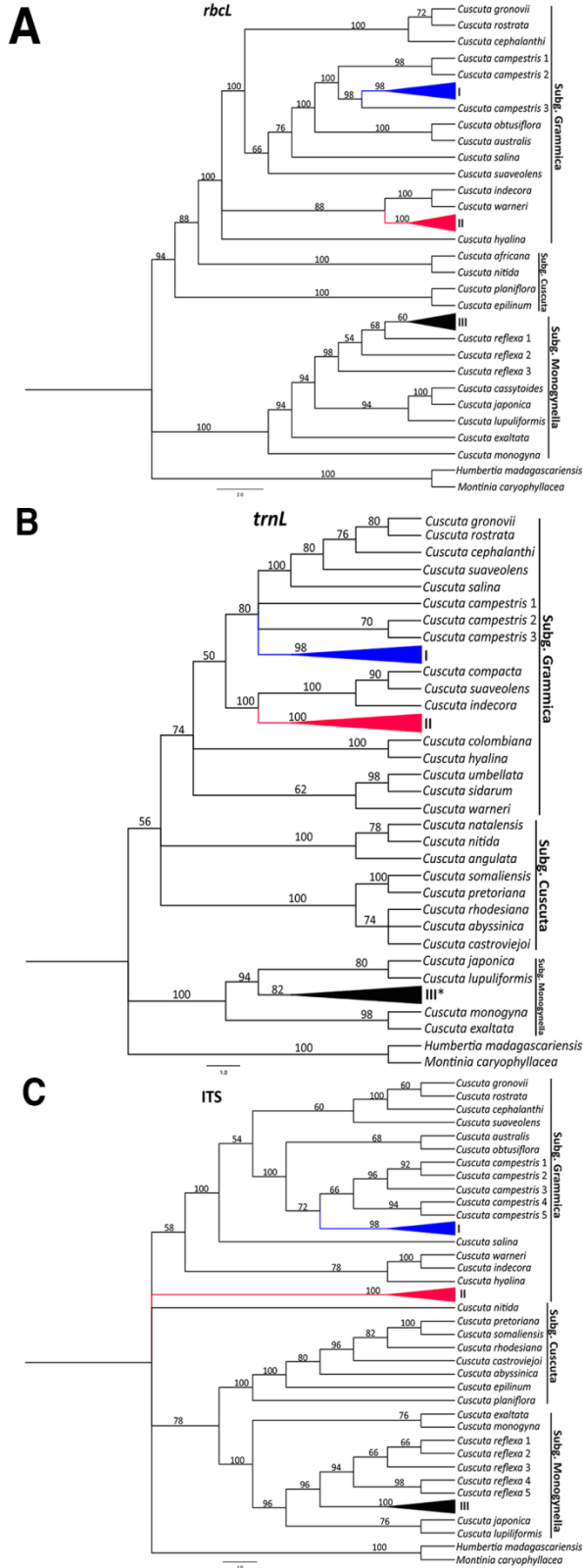


Fig. 2 Phylogenetic reconstruction of *Cuscuta* species based on *rbcL*, *trnL* and ITS regions. Maximum Parsimony bootstrap consensus trees (1000 replicates) are shown, with bootstrap supports indicated above branches. I, II and III represent *Cuscuta* taxa sequenced under this study, and denote *C. campestris*, *C. killimanjari* 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.

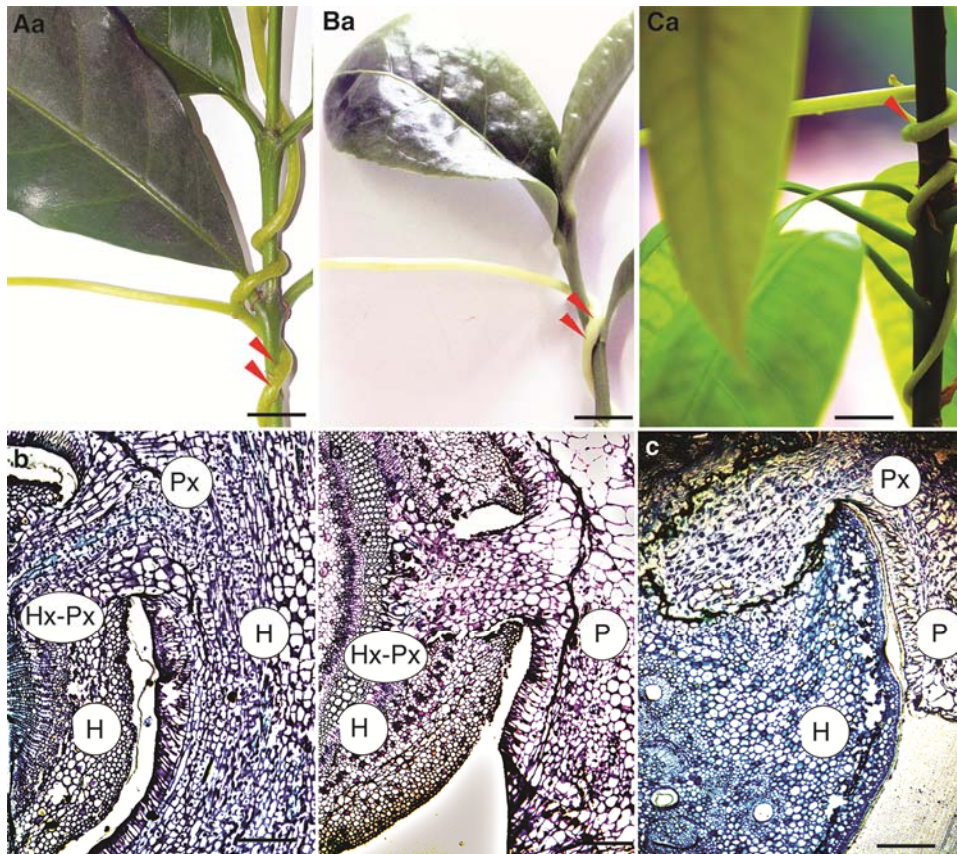
181 With regards to host specificity, *C. campestris* and *C. reflexa* exhibited a ‘generalist’  
182 behaviour, indiscriminately parasitizing hosts across numerous orders. Among the  
183 parasitized species, *Solanum incanum* and *Biancaea decapetala* were the most  
184 preferred hosts for *C. campestris*, 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-dnrjzAlbWQBbGXbGDAlhoKFnVHbkICUWhkQ1BPdnMyZII4TTFqdFEQAq>

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

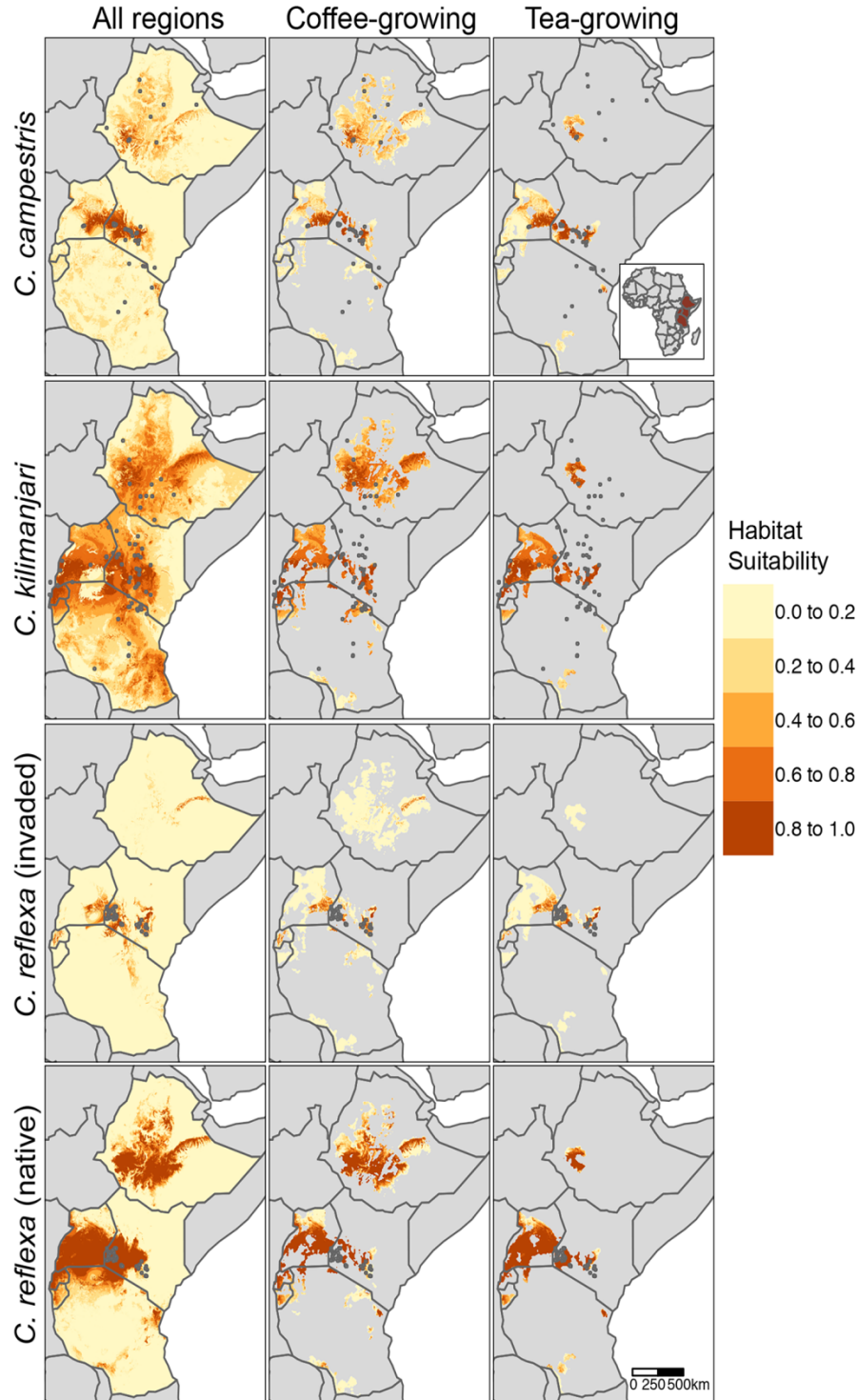
### 218 **Predicted *Cuscuta* distribution and habitat suitability**

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)).

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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

<b>Variable</b>	<b><i>C.</i></b>	<b><i>C.</i></b>	<b><i>C. reflexa</i></b>	<b><i>C. reflexa</i></b>
	<b><i>campestris</i></b>	<b><i>kilimanjari</i></b>	<b>(invaded)</b>	<b>(native)</b>
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 ingression 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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