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

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

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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

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24   **Author contributions:** S.R. conceived the study, guided fieldwork and oversaw
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
29   support and manuscript editing. All authors read and approved the final manuscript.

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Abstract

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

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

Introduction

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

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

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

Cuscuta life cycle follows a systematic pattern that begins with seed germination, attachment and penetration of a suitable host (through a specialized organ called 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 structre. 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 bisphosphate 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 screenhouse 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.

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Results

Floral morphological characters reveal 3 *Cuscuta* species

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

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

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

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

Phylogenetic analysis

Parsimony consensus trees for accessions under this study, alongside other *Cuscuta* species from GenBank, revealed consistent topologies across all 3 (*rbcL, trnL* and ITS) regions (Fig. 2). In brief, 3 major clades, corresponding to the 3 *Cuscuta* subgenera, were resolved across the datasets with good bootstrap support. Specifically, *C. campestris* accessions from the current study were resolved in the first major clade with other reported species of subgenus Grammica, sister to *C. campestris* taxa from
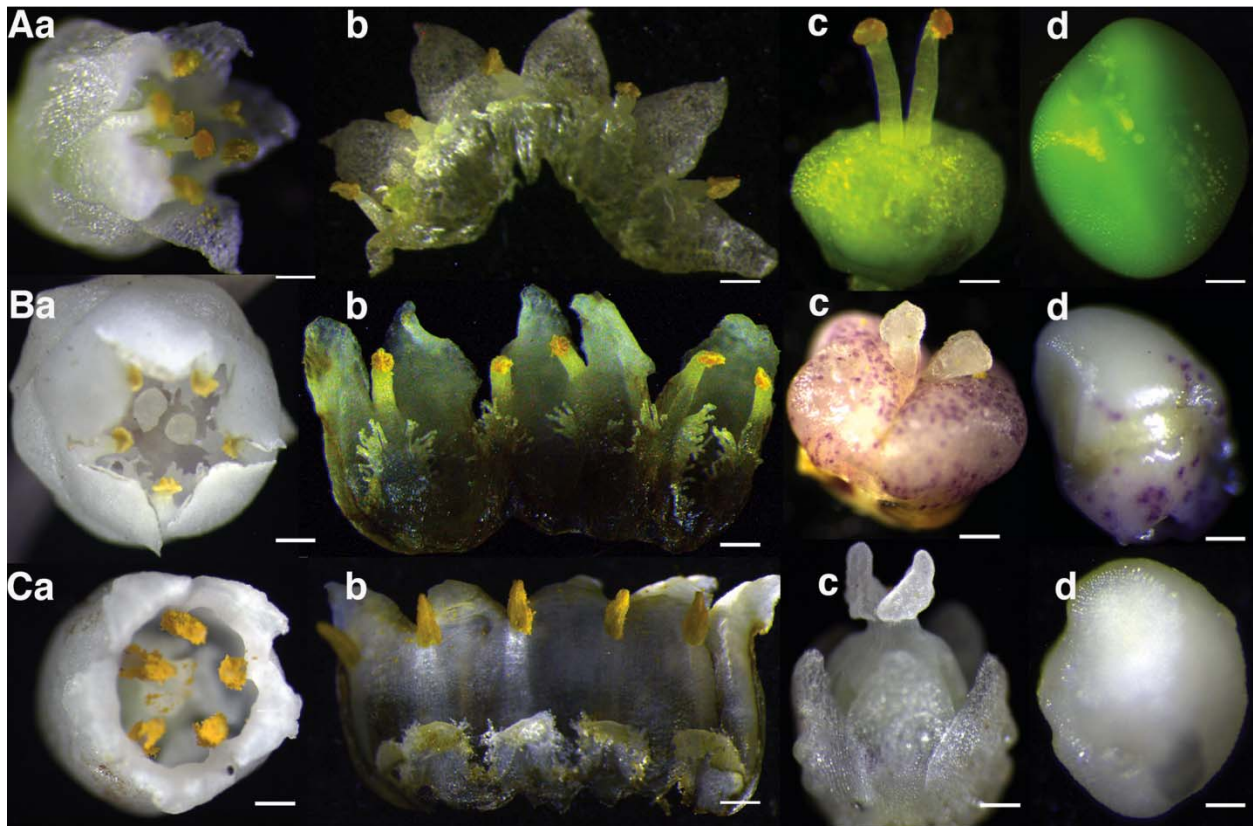
Fig. 1 Profiles of floral morphology among *Cuscuta* accessions collected across Kenya, showing variations in gynoecia, ovule shape, size and colour across species. Aa-Ad *C. campestris*- evidenced by small, white flowers with separate styles that bear globose stigmas; Ba-Bd *C. kilimanjari*- confirmed 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.

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

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

A total of twenty-six (26) host plant species across 13 angiosperm orders, comprising shrubs (40%), trees (44%) and herbs (16%) were parasitized by the aforementioned
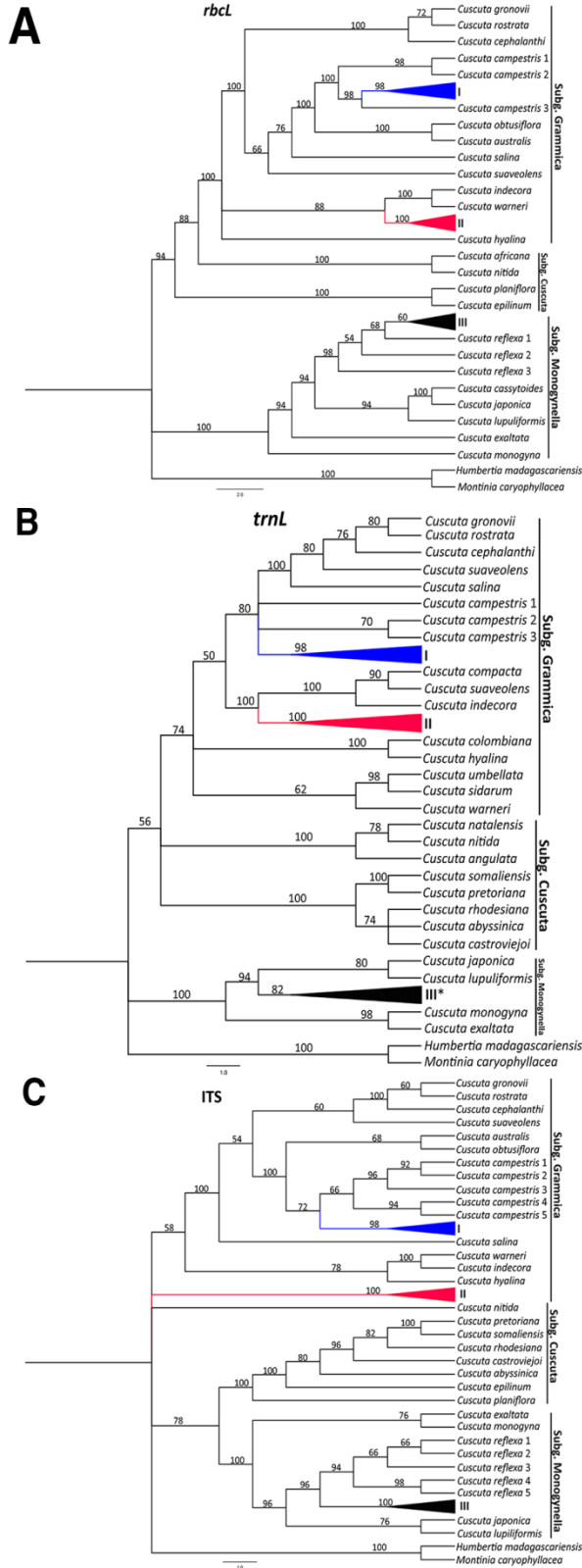
Fig. 2 Phylogenetic reconstruction of *Cuscuta* species based on *rbcL*, *trnL* and ITS regions. Maximum Parsimony bootstrap consensus trees (1000 replicates) are shown, with bootstrap supports indicated above branches. I, II and III represent *Cuscuta* taxa sequenced under this study, and denote *C. campestris*, *C. kilimanjari* 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

203   ,34.77314623,1583.10168457a,0d,15y,119.88850412h,90.54106391t,0r/data=CigiJgok

204   CdGS14h74TRAEc6S14h74TTAGbGLz-

205   dnrjzAIbWQBbGXbGDAIhoKFnVHbklCUWhkQ1BPdnMyZll4TTFqdFEQAg

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
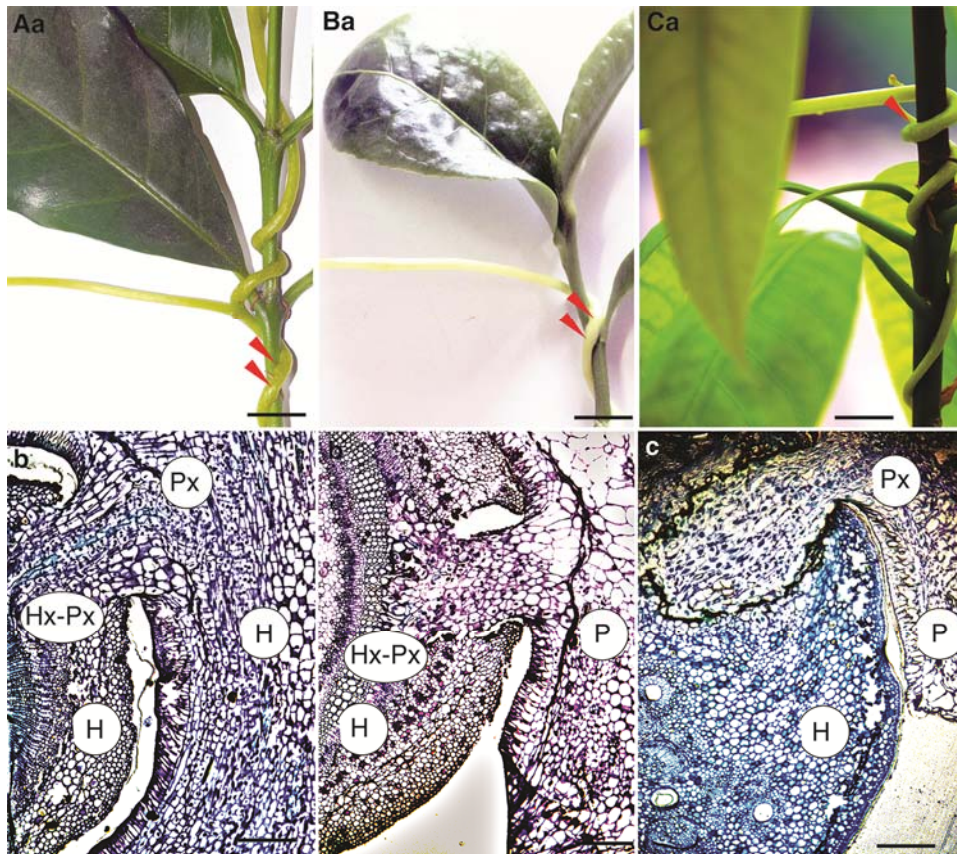
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Fig. 3 *Cuscuta* parasitism and extent of ingression into host plants. The upper panel shows close up photographs of infected test plants while the lower panel are toluidine blue-stained cross sections of the host-parasite interface. Aa and Ab- coffee, 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.
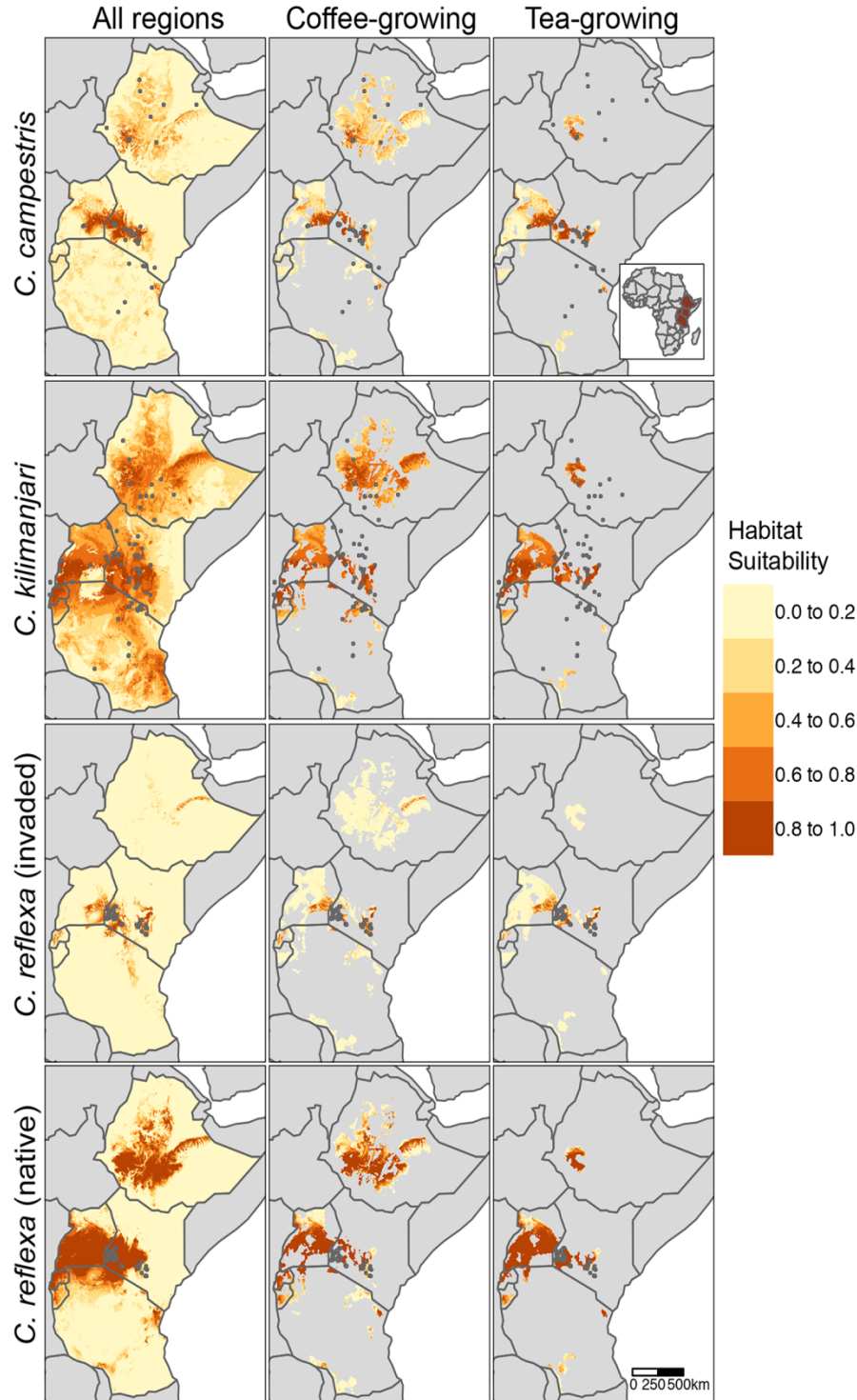
Fig. 5 Habitat suitability for *C. campestris, C. kilimanjari, C. reflexa* across Ethiopia, Kenya, Uganda, Rwanda, Burundi, and Tanzania. Dark grey points indicate locations of occurrence records. For *C. reflexa*, species distribution models were trained using occurrences from the invaded range in Kenya (*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-

247   kampala-city) and Kenya (https://www.nation.co.ke/news/Dodder-plant-poses-threat-to-

248   trees-and-crops/1056-5138904-aawhphz/index.html).

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Discussion

***Cuscuta* identification**

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

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

We validated this identification by sequencing *rbcL, trnL* and ITS regions from representative individuals, and performed phylogenetic reconstruction alongside other species from GenBank. These markers have been extensively used to infer phylogenetic relationships, character evolution and biogeography across the genus (Garcia and Martin, 2007; McNeal., *et al.*, 2007; Garcia *et al.*, 2014). In our case, all our 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*

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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. cassytoides 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

17

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

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

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

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 *trnL*F- 5'

420 CGAAATCGGTAGACGCTACG 3' and *trnL*R- 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

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-
457 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

Acknowledgements

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	*C. campestris*	*C. kilimanjari*	*C. reflexa* (invaded)	*C. reflexa* (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

Figure Legends

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.

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. kilimanjari* and *C. reflexa*, respectively. The Asterisk (*) on the *trnL* tree implies that our *C. reflexa* taxa were collapsed with those from GenBank.

Fig. 3 *Cuscuta* parasitism and extent of ingression 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.

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.

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

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

Parsed Citations

Albert M, Belastegui-Macadam XM, Bleischwitz M, Kaldenhoff R (2008) Cuscuta spp: Parasitic Plants in the Spotlight of Plant Physiology, Economy and Ecology. BT - Progress in Botany', in Lüttge U, Beyschlag W, and Murata J (eds). Berlin, Heidelberg: Springer Berlin Heidelberg 267–277
Google Scholar: Author Only Title Only Author and Title

Albert M, Belastegui-Macadam X, Kaldenhoff R, (2006) An attack of the plant parasite Cuscuta reflexa induces the expression of attAGP, an attachment protein of the host tomato. Plant J 48(4):548–556
Google Scholar: Author Only Title Only Author and Title

Baldwin BG (1992) Phylogenetic Utility of the Internal Transcribed Spacers of Nuclear Ribosomal DNA in Plants; An Example from the Compositae. Mol Phylogenet Evol 1 (1):3–16
Google Scholar: Author Only Title Only Author and Title

Bhattarai T, Bhandary H, Shrestha P (1989) Host range of Cuscuta reflexa Roxb. in the Kathmandu Valley, Nepal. Plant Protection Quarterly 4(2):78-80
Google Scholar: Author Only Title Only Author and Title

Braukmann T, Kuzmina M Stefanović S (2013) Plastid genome evolution across the genus Cuscuta (Convolvulaceae): two clades within subgenus Grammica exhibit extensive gene loss. J Exp Bot 64(4):977–989
Google Scholar: Author Only Title Only Author and Title

Buchhorn M, Lesiv M, Tsendbazar NE, Herold M, Bertels L, Smets B (2020) Copernicus Global Land Cover Layers-Collection 2. Remote Sens 12:1044
Google Scholar: Author Only Title Only Author and Title

Capderon M, Fer A, Ozenda P (1985) About an unreported system leading to the expulsion of a parasite – Cuscuta on cotton-plant (Cuscuta lupuliformis Krock on Gossypium hirsutum-L). Comptes rendus de l'Académie des Sciences 3(300):227–232
Google Scholar: Author Only Title Only Author and Title

Cotter M, Renzoandre P-L, Sauerborn J (2012) Understanding the present distribution of the parasitic weed Striga hermonthica and predicting its potential future geographic distribution in the light of climate change. In Julius-Kühn-Archiv 434:630–636
Google Scholar: Author Only Title Only Author and Title

Debabrata Das (2007) Host range diversity of Cuscuta reflexa Roxb. in South 24-Parganas District of West Bengal. Environ Ecol 25(1):106-108
Google Scholar: Author Only Title Only Author and Title

Dawson JH, Musselman LJ, Wolswinkel P, Dörr I (1994) Biology and control of Cuscuta. Reviews of Weed Sci 6:265–317
Google Scholar: Author Only Title Only Author and Title

Engelmann G (1857) Botanical notebook 23: Cuscuta. Available at: https://www.biodiversitylibrary.org/item/234938
Google Scholar: Author Only Title Only Author and Title

FAO (2017) Food and Agriculture Organization. http://www.fao.org/faostat/en/#data/QC. Accessed September 2019
Google Scholar: Author Only Title Only Author and Title

García MA (2019) Cuscuta subgenus Cuscuta (Convolvulaceae) in Ethiopia, with the description of a new species. Ann Bot Fenn 36(3):165–170
Google Scholar: Author Only Title Only Author and Title

García M A, Costea M, Kuzmina M, Stefanovic S (2014) Phylogeny, character evolution, and biogeography of Cuscuta (Dodders; Convolvulaceae) inferred from coding plastid and nuclear sequences. Am J Bot 101:670–690
Google Scholar: Author Only Title Only Author and Title

GBIF.org (07 October 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.9kpzum

Goldwasser Y, Miryamchik H, Sibony M, Rubin B (2012) Detection of resistant chickpea (Cicer arietinum) genotypes to Cuscuta campestris (field dodder). Weed Res 52(2):122–130
Google Scholar: Author Only Title Only Author and Title

Gurney AL, Grimanelli D, Kanampiu F, Hoisington D, Scholes JD, Press MC (2003) Novel sources of resistance to Striga hermonthica in Tripsacum dactyloides, a wild relative of maize. New Phytol 160:557-568
Google Scholar: Author Only Title Only Author and Title

Hijmans RJ (2019) raster: Geographic Data Analysis and Modelling. R package version 3.0-7. https://CRAN.R-project.org/package=raster
Google Scholar: Author Only Title Only Author and Title

IFPR (2020) International Food Policy Research Institute; "Spatially-Disaggregated Crop Production Statistics Data in Africa South of the Saharan for 2017" https://doi.org/10.7910/DVN/FSSKBW, Harvard Dataverse, V1

Kaiser B, Vogg G, Fürst UB, Albert M (2015) Parasitic plants of the genus Cuscuta and their interaction with susceptible and resistant host plants. Front Plant Sci 6:1–9

Google Scholar: Author Only Title Only Author and Title

Karger D, Nikol OC, Jürgen B, Tobias K, Holger K, Rodrigo WS, Niklaus E Z, Linde HP, Michael K (2017) Climatologies at High Resolution for the Earth's Land Surface Areas. Sci Data 4(1):170122

Google Scholar: Author Only Title Only Author and Title

Kim G, Westwood JH (2015) Macromolecule exchange in Cuscuta – host plant interactions. Curr Opin Plant Biol 26:20–25

Google Scholar: Author Only Title Only Author and Title

Kuijt J (1969) The biology of parasitic flowering plants. University of California Press, Berkeley.

Google Scholar: Author Only Title Only Author and Title

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Mol Biol Evol 35(6):1547-1549

Google Scholar: Author Only Title Only Author and Title

Lanini WT, Kogan M (2005) Biology and Management of Cuscuta in Crops. Ciencia e Investigación Agraria 32:165–179

Google Scholar: Author Only Title Only Author and Title

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higginset DG (2007) Clustal W and Clustal X Version 2.0. Bioinformatics 23(21):2947–48

Google Scholar: Author Only Title Only Author and Title

Liu C, Wolter C, Xian W, Jeschke JM (2020) Species Distribution Models Have Limited Spatial Transferability for Invasive Species. Ecol Lett 23:1682–1692

Google Scholar: Author Only Title Only Author and Title

McNeal JR, Arumugunathan K, Kuehl JV, Boore JL, dePamphilis CW (2007) Systematics and plastid genome evolution of the cryptically photosynthetic parasitic plant genus Cuscuta (Convolvulaceae). BMC Biol 5:1–19

Google Scholar: Author Only Title Only Author and Title

García MA (1999) Cuscuta subgenus Cuscuta (Convolvulaceae) in Ethiopia, with the description of a new species. Ann Bot Fenn 36(3):165–170

Google Scholar: Author Only Title Only Author and Title

García MA, Costea M, Kuzmina M, Stefanovic S (2014) Phylogeny, character evolution, and biogeography of Cuscuta (Dodders; Convolvulaceae) inferred from coding plastid and nuclear sequences. Am J Bot 101:670–690

Google Scholar: Author Only Title Only Author and Title

Garcia MA, Martin MP (2007) Phylogeny of Cuscuta Subgenus Cuscuta (Convolvulaceae) Based on nrDNA ITS and Chloroplast trnL Intron Sequences. Syst Bot 32(4):899–916

Google Scholar: Author Only Title Only Author and Title

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702-708

Google Scholar: Author Only Title Only Author and Title

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: An R Package for Conducting Spatially Independent Evaluations and Estimating Optimal Model Complexity for Maxent Ecological Niche Models. Methods Ecol Evol 5(11):1198–1205

Google Scholar: Author Only Title Only Author and Title

Parker C (2012) Parasitic Weeds: A World Challenge. Weed Sci 60(2):269-276.

Google Scholar: Author Only Title Only Author and Title

Parker C, Riches CR (1993). Parasitic weeds of the world: Biology and control. CAB International, Wallingford, UK: 332.

Google Scholar: Author Only Title Only Author and Title

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. Ecol Model 190:231–59

Google Scholar: Author Only Title Only Author and Title

Press MC, Phoenix GK (2005) Impacts of parasitic plants on natural communities. New Phytol 166:737–751

Google Scholar: Author Only Title Only Author and Title

Rambaut A (2009) FigTree v1.2.2. .

Google Scholar: Author Only Title Only Author and Title

Ren Z, Zagortchev L, Ma J, Yan M, Li J (2020) Predicting the potential distribution of the parasitic Cuscuta chinensis under global warming. BMC Ecol 20:28

Google Scholar: Author Only Title Only Author and Title

Runyon JB, Mescher MC, Felton GW, De Moraes CM (2010) Parasitism by Cuscuta pentagona sequentially induces JA and SA defence

pathways in tomato. Plant Cell Environ 33:290-303

Google Scholar: Author Only Title Only Author and Title

Stefanović S, Kuzmina M, Costea M (2007) Delimitation of major lineages within Cuscuta subgenus Grammica (Convolvulaceae) using plastid and nuclear DNA sequences. Am J Bot 94(4):568–589

Google Scholar: Author Only Title Only Author and Title

Verdcourt B (1963) Convolvulaceae. In Hubbard, CE, Milne-Redhead E. (eds.), Flora of tropical East Africa: 1-16. Crown Agents for Overseas Governments and Administrations, London

Google Scholar: Author Only Title Only Author and Title

Yuncker TG (1932) The Genus Cuscuta. Torrey Botanical Society, 18(2):113–331

Google Scholar: Author Only Title Only Author and Title

Zerman N, Saghir AR (1995) The genus Cuscuta in Algeria. Arab J Plant Prot 13(2):69–75

Google Scholar: Author Only Title Only Author and Title

Zhang C, Chen L, Tian CM, Li T, Wang R, Yang QQ (2016). Predicting the distribution of dwarf mistletoe (Arceuthobium sichuanense) with GARP and Maxent models. J Beijing For Univ 38(5):23–32

Google Scholar: Author Only Title Only Author and Title