Worldwide interconnections of Africa using crops as historical and cultural markers

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The historical, social, and economical importance of precolonial connections between Africa and the rest of the world has been undervalued. In the present study, we use crops as historical and social markers to analyze intercontinental connections from the perspective of Kenyan and Ugandan regions northeast of Lake Victoria. Crops were inventoried in 148 small farms from 74 localities, using successively free listing, to reveal their socio-cultural salience, and a closed list method, for a more complete picture of the agricultural, environmental and social diversity. The total sample included 75 crops (30 African, 21 Asian, 21 American, and 3 European). Among farms, crop richness varied from 6 to 32. It was higher in Uganda than in Kenya, and lowest around the Winam Gulf. The 12 American crops introduced at Renaissance were uniformly distributed, and the observed structure was mostly due to differences in African and Asian crop richness. In terms of crop frequency, exotic crops account for 74%, with 46% for American crops. The 14 most frequent crops included 10 from America, 3 from Asia, and 1 for Africa, with negligible differences among linguistic groups. Consistently, the free listing citation order demonstrated the high cultural salience of American crops. The spatial distribution of minor crops suggest differential diffusion among linguistic groups, which could be further studied using linguistic approaches on crop names.

1. Introduction

The importance of the geographical location of sub-Saharan Africa between the Atlantic and Indian oceans has not yet been revealed in the light of its past connections with other tropical continents. On the contrary, intercontinental exchanges have been undervalued in a history that has put emphasis on the 18th century slave trade or on the 19th century colonialism, suggesting that the integration of Africa in worldwide networks was conditioned by external action.

In fact, we know that the connections between Africa and the rest of the world did exist well before the European colonial conquests, and then that the continent was not as isolated as suggested by colonial historiography. However, the historical, social, and economical importance of these interconnections has not been well established.

The aim of the present contribution is to analyze (i) worldwide interconnections of Africa using crops as historical and social markers and (ii) the economic and cultural value of exotic crops. Crop diffusion has usually been considered one crop at a time (e.g. McCann 2001), or by considering those that share the same area of origin (Alpern 2008). In this study, on the contrary, we consider the contribution of exchanges, both intra- and intercontinental, to the agrobiodiversity of a whole region, the northeastern shores of Lake Victoria, covering diverse agrosystems across different ethnolinguistic groups.

The Great Lakes Region is a good place for implementing such analyses as it is characterized by high environmental and sociocultural diversity. Furthermore, it appears to be a real crossroad of agricultural traditions (Chastanet 1998), representing a kind of Africa in miniature, where diversity of crop origins reflects interconnections at different spatial and temporal scales.

Beyond the diversity of crop origins, we further paid attention to the socio-cultural value of crops, using the free listing method (Borgatti 1999) as an elicitation technique to explore and delimit a domain of knowledge. The most common form consists in asking respondents to list spontaneously items that characterize a domain. As noted by Henley (1969) and underlined by Borgatti (1999), "the order in which items are listed by individual respondents is not arbitrary." We used this technique for inventorying the crops cultivated by farmers. Farmers that were interviewed mentioned a first run of crops, one quickly following the other, followed by a visible pause, and then a new run began with different crops. The main challenge is to interpret these different runs, considering the relative position of crops on the list produced by each respondent. The hypothesis is that crops that are more central tend to be mentioned first. When crops are grouped according to their continental origin, the average position of American, African, Asian or European crops informs us about their socio-cultural value.

2. Materials and methods

2.1 Study site

This study was carried out in Kenya and Uganda along the northeastern shore of Lake Victoria in June 2016 and June 2017, among farmers practicing small-scale, low-input agriculture. As cultivating a crop at a given location depends on environmental and socioeconomical factors, our strategy was to include a wide diversity of environments and social groups in our sample. Thus, elevation varied between 1041 and 2028 m, while social diversity involved Bantu and Nilotic speakers and different political organizations, based on lineage in Kenya and kingdoms in Uganda.

Our geographical sampling strategy was based on an *a priori* homogenous spatial distribution around the northeastern shores of Lake Victoria. It involved 74 geographic sampling units (GSUs, Figure 1), with two farm interviews in each. Thus, a total of 148 farms were surveyed, 66 in Kenya and 82 in Uganda. Farms were located at a mean of 1291 m above sea level. Among the informants, 104 belonged to a Bantu group, and 44 to a Nilotic group. There was an equivalent number of women and men (76 women and 72 men); their age ranged from 22 to 87 years, with a mean of 50 years. In most cases (within 67 GSUs), the two interviews concerned farmers from the same ethnolinguistic group.

2.2 Crop inventory and analysis

During the interview, crops were inventoried in three steps. In the first one, the farmer was asked to list his crops spontaneously. This free-list task was conducted in the language of farmers. We asked the farmers to list the crops that they were cultivating during the current season. The crop citation order was recorded. The crop cultural salience was

estimated based on the frequency and rank of their mention across the free lists (Smith & Borgatti 1997; Sutrop 2001). The free listing task was completed by asking the farmer to rank the relative importance of area dedicated to each crop.

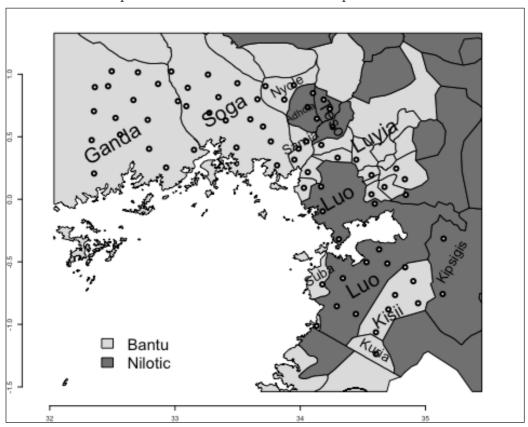


Figure 1. Localization of geographic sampling units (GSUs) and distribution of ethnolinguistic groups around Lake Victoria in western Kenya and eastern Uganda Source: World Language Mapping System, Version 19 (2016), with emends for the northern Kisii (Gusii) borderlines.

In the second step, the crop list was completed by referring to a predefined list of crops as observed in the region. Indeed, a preliminary survey had been carried out in February 2016 in Kenya to establish such a list. Thus, those crops that had not been spontaneously mentioned by farmers during the free list task (step 1) were recorded as present or absent on the farm. This closed list included 26 crops: avocado (Persea americana), cooking bananas and plantains (Musa acuminata and Musa plantain group), ripening (dessert) banana (Musa acuminata), common bean (Phaseolus vulgaris), cassava (Manihot esculenta), chili (Capsicum annuum), coconut (Cocos nucifera), coffee (Coffea arabica and C. canephora), cowpea (Vigna unguiculata), finger millet (Eleusine coracana), groundnut (Arachis hypogaea), guava (Psidium guajava), Ethiopian kale (Brassica carinata), maize (Zea mays), mango (Mangifera indica), napier grass (Pennisetum purpureum), onion (Allium cepa), papaya (Carica papaya), pearl millet (Pennisetum glaucum), pigeon pea (Cajanus cajan), rice (Oryza spp), sisal (Agave sisalana), sorghum (Sorghum bicolor), squash (Cucurbita spp.), sugar cane (Saccharum officinarum), sweet potatoes (Ipomea batatas), tea (Camellia sinensis), and taro (Colocasia esculenta).

The third step aimed at recording the names of crops that were not yet mentioned in steps 1 and 2, through open discussion with farmers and direct on-field observations. Through the three steps, a total of 75 species were inventoried. Farm crop richness and GSU crop richness were computed. Crop x farmer combinations were used as statistical units to compute proportions and estimate relative crop frequencies.

The distinction among crops has been based on very practical criteria, including farmers' perceptions, diversity of uses, diversity of species, and taxonomical difficulties, particularly for distinguishing related species from field observation or from farmers' descriptions. Indeed, crops do not always correspond to a given botanical species. For example, coffee corresponds to two species and cultivated cotton to four Gossypium species, two from the Old World and two from the New World. In such cases, the choice of one species is generally dictated by adaptation, techno-economical parameters and seed availability, just as for the choice of cultivars, so that there was no functional reason to distinguish different crops within coffee or cotton. Similarly, one species or species complex can be domesticated for different uses and thence submitted to divergent selection processes, so that farmers recognize different crops, such as in the case of African eggplants, for which they name three crops in the study area. A rarer case is that of highly diverse genera, such as Amaranthus (amaranths), Dioscorea (yams: Alpern 2008) and Cymbopogon (lemon grasses: Quattrocchi 2006) where several species may be differentiated by farmers as well as botanists, but the taxonomical complexity makes their field identification highly problematic, so the crop was only identified at the genus level. The four observations of lemon grasses were removed from our geographical dataset, because of the strong ambiguity resulting from the diversity of botanical species, uses and geographic origins.

Crop diversity was mapped using the Richness procedure of the Diva-Gis software, with the Circular Neighborhood option, which allows representing the total number of crops recorded in any GSU within a radius of ca. 20 km. In the circle around a GSU, the heterogeneity in species richness (revealed by the color code) indicates how neighbour GSUs contribute to local agrobiodiversity with additional crops.

All statistical analyses were performed using R (ver. 3.5.1, Team 2018), with the packages data.table (ver. 1.11.4) and ggplot2 (ver. 3.0) for plot and table output, as well as knitr (ver. 1.20) for reproducible research. The RStudio's Flares package (Wencélius *et al.* 2017) was used to analyze freelist data.

3. Results and discussion

3.1 The origins and distribution of regional agrobiodiversity

On average, farmers cultivated 21 species (minimum 6 and maximum 32). Table 1 lists the 75 distinct crops inventoried, the number of observations for each (number of GSUs and farms), and their continent of origin.

Figure 2 presents the distribution of the inventoried agrobiodiversity in the study area. The number of crops varies between 15 and 36 per GSU. It is globally higher in the Ugandan part, with 31-35 crops for most GSU (yellow-orange circles), than in the Kenyan Nyanza region, with 16-28 crops for most GSUs (yellow circles). Lower values for Uganda were found east and southeast of Kampala and around Jinja, where agrobiodiversity compares with that of Kenyan GSUs. Furthermore, the component of variation among GSUs is also superior in most of the Ugandan part, particularly in the Luhya, Teso, Adhola, Nyole, and Busoga regions. There, the DIVA-GIS Circular Neighborhood procedure identifies many areas where the combined agrobiodiversity that was inventoried within a radius of 20 km,

is superior to the maximal diversity found in any GSU alone (reddish orange and red areas). Within Kenya, there is a marked difference between the Luo territory (Kisumu and Homa Bay counties), where less than 25 crops are grown in most GSUs, and the Kisii and Luhya territories, where most GSUs present 25-30 crops. The Circular Neighborhood areas where the number of crops is 30-35 are all under the influence of Luhya or Kisii farms. Thus, these groups seem to cultivate a slightly wider agrobiodiversity, with more variation among GSUs.

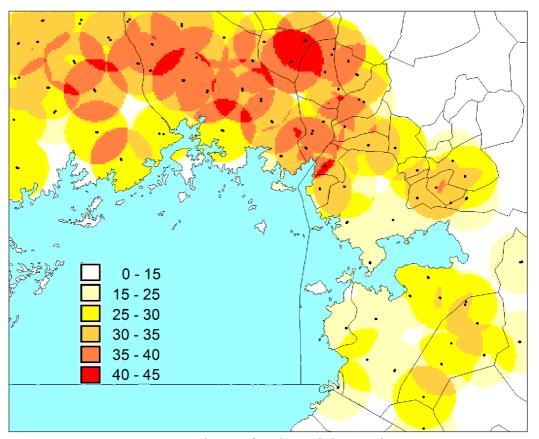


Figure 2. Distribution of total recorded crop richness. Farms are represented by dots; the color code indicates crop number within a radius of ca. 20 km.

3.1.1 African crops

Among these 75 crops, 30 are native to Africa, even though the original species may have been partly or mostly substituted by exotic close relatives: American cotton, Asian and American yams, and the Asian mustard (*Brassica juncea*) that is easily confused with the Ethiopian kale. Twenty-four of these crops can be considered native to the Great Lakes region as they have their origin in East Africa. The other six originated from West Africa: pearl millet (Manning *et al.* 2011; Cubry *et al.* 2017), bambara nut (Goli 1997), the three African eggplant crops (but *Solanum anguivi* is found as a weed in most of tropical Africa) (PROTA4U 2018), and oil palm. The latter is native in the tropical belt from western to Central Africa. Most of eastern Africa is unsuitable or marginally suitable for oil palms because it is too dry or lies at too high an altitude, or both (Corley & Tinker 2003).

Table 1. List of the 75 crops recorded in the Great Lakes Region, with their continent of origin, period of introduction, and associated references. Crops domesticated in northeastern Africa are mentioned as native; crops domesticated in western/central Africa are noted as "WA," unless the period of their introduction is known. To save space in the last column, year of publication/consultation is omitted for very common references: Alpern (2008), NRC (2008), PROTA4U (2018), Purseglove (1985 & 1987).

Crop	Species	Origin	Period	References	
Sorghum	Sorghum bicolor	Africa	Native	Winchell <i>et al.</i> 2017 PROTA4U	
Pearl millet	Pennisetum glaucum	Africa	Antiquity	Manning et al. 2011; Cubry et al. 2017	
Finger millet	Eleusine coracana	Africa	Native	Boivin & Fuller 2009	
Yam	Dioscorea spp.	Africa, Asia, America	Native	Alpern	
Bambara nut	Vigna subterranea	Africa	WA	Goli 1997	
Cowpea	Vigna unguiculata	Africa	Native	PROTA4U	
Lablab	Dolichos lablab	Africa	Native	Boivin & Fuller 2009	
Pea	Pisum sativum	Asia/Africa	Native	PROTA4U	
African eggplant (gilo)	Solanum aethiopicum gr. Gilo	Africa	WA	NRC 2008	
African eggplant (shum)	Solanum aethiopicum gr. Shum	Africa	WA	NRC 2008	
Bitter berries / pea eggplant	Solanum anguivi	Africa	WA	PROTA4U	
Okra	Abelmoschus esculentus /A. callei	Asia/Africa	Native	Joshi <i>et al.</i> 1974	
Jute mallow	Corchorus olitorius	Africa	Native	Benor et al. 2012	
Ethiopian kale	Brassica carinata	Africa	Native	PROTA4U	
African nightshade	Solanum spp. / S. nigrum / S. scabrum	Africa	Native	PROTA4U	
Cleome/ spider plant	Cleome gynandra	Africa	Native	PROTA4U	
Amaranth	Amaranthus spp.	Africa, Asia, America	Native	Alpern	
Crotalaria	Crotalaria spp. (brevidens/ochroleuca)	Africa	Native	PROTA4U	
Bottle gourd	Lagenaria siceraria	Africa	Native	Erickson <i>et al.</i> 2005; Kistler <i>et al.</i> 2014	
Oil palm	Elaeis guineensis	Africa	WA	Maley 1999	
Canarium	Canarium schweinfurthii	Africa	Native	Orwa et al. 2009	
Tamarind	Tamarindus indica	Africa	Native	Diallo <i>et al.</i> 2007; Alpern; NRC	
Mutugundo	Vangueria apiculata	Africa	Native	Katende 2000	
Watermelon	Citrullus lanatus	Africa	Native	Paris 2015	
Oysternut	Telfaira pedata	Africa	Native	PROTA4U	
Coffee	Coffea arabica / C. canephora	Africa	Native	Boivin et al. 2014	

Crop	Species	Origin	Period	References
Lemon grass	Cymbopogon spp.	Asia/Africa	Native	Quattrocchi 2006
Napier	Pennisetum purpureum	Africa	Native	
Cotton	Gossypium spp.	Africa, Asia, America	Native	Wendel et al. 2010
Kenaf	Hibiscus spp.	Africa	Native	PROTA4U
Rice	Oryza spp	Asia	Antiquity	Fuller <i>et al.</i> 2011; Boivin <i>et al.</i> 2014
Sugarcane	Saccharum officinarum	Asia	Medieval	Denham 2011; Moore <i>et al.</i> 2014
Banana / cooking	Musa acuminata / M. x paradisiaca gr. plantain	Asia	Antiquity	Perrier et al. 2018
Banana / ripening	Musa acuminata	Asia	Antiquity	Perrier et al. 2018
Taro	Colocasia esculenta	Asia	Antiquity	Diallo <i>et al.</i> 2007; Alpern; NRC
Sesame	Sesamum indicum	Asia	Antiquity	Bedigian 2003; Fuller 2003
Green gram	Vigna radiata	Asia	Antiquity	Fuller 2007; Boivin et al. 2014
Pigeon pea	Cajanus cajan	Asia	Antiquity	Khoury <i>et al.</i> 2015; Varshney <i>et al.</i> 2017
Soya bean	Glycine max	Asia	Modern	Fuller 2007; Guo <i>et al.</i> 2010; PROTA4U; Purseglove
Carrot	Daucus carota subsp. sativus	Asia	Renaissance	Alpern
Onion	Allium cepa	Asia	Antiquity	PROTA4U
Eggplant	Solanum melongena	Asia	Medieval	Ranil <i>et al.</i> 2017
Mango	Mangifera indica	Asia	Medieval	Purseglove; Russell- Wood 1998
Citrus	Citrus spp.	Asia	Medieval	Luro & Ollitrault 2001; Boivin <i>et al.</i> 2014
Coconut	Cocos nucifera	Asia	Antiquity	Gunn <i>et al.</i> 2011; Boivin <i>et al.</i> 2014
Jackfruit	Artocarpus heterophyllus	Asia	Modern	Morton 1987; Fuller 2002)
Jambolan	Syzyjium cumini	Asia	Antiquity	Morton 1987
Loquat	Eriobotrya japonica	Asia	Modern	Blasco <i>et al.</i> 2014; Wang <i>et al.</i> 2017
Turmeric	Curcuma longa	Asia	Antiquity or Medieval	Alpern; Purseglove
Ginger	Zingiber officinale	Asia	Antiquity or Medieval	Purseglove; Boivin <i>et al.</i> 2014
Tea	Camellia sinensis	Asia	Modern	Purseglove

Crop	Species	Origin	Period	References
Maize	Zea mays	America	Renaissance	McCann 2001; Van Heerwarden <i>et al.</i> 2011
Sunflower	Helianthus annuus	America	Modern	Smith 2014
Cassava	Manihot esculenta	America	Renaissance	Carter <i>et al.</i> 1993; Clement <i>et al.</i> 2010
Sweet potato	Ipomea batatas	America	Renaissance	Alpern; Roullier <i>et al.</i> 2011
Irish potato	Solanum tuberosum	America	Modern	Blench 1998
Common bean	Phaseolus vulgaris	America	Renaissance	Alpern; Blair <i>et al.</i> 2012
Groundnut	Arachis hypogaea	America	Renaissance	Alpern; Clement <i>et al.</i> 2010; Hammons 1982
Squash/pumpkin	Cucurbita spp.	America	Renaissance	Alpern; Brown <i>et al.</i> 2013; Katz 1998
Tomato	Solanum lycopersicum	America	Modern	Jenkins 1948; Alpern; Blench 1998
Chili	Capsicum annuum	America	Renaissance	Alpern; Brown <i>et al.</i> 2013; Katz 1998
Avocado	Persea americana	America	Modern	Alpern; Purseglove; Chen et al. 2009)
Cocoa	Theobroma cacao	America	Modern	Clement <i>et al.</i> 2010; Purseglove
Guava	Psidium guajava	America	Renaissance	Alpern; Clement <i>et al.</i> 2010
Papaya	Carica papaya	America	Renaissance	Coppens <i>et al.</i> 2007; Alpern; Katz 1998
Passion fruit	Passiflora spp	America	Modern	Purseglove; Yockteng <i>et al.</i> 2011
Pineapple	Ananas comosus	America	Renaissance	Coppens d'Eeckenbrugge <i>et</i> <i>al.</i> 2018
Soursop	Annona muricata	America	Renaissance	Alpern; Morton 1966
White sapote	Casimiroa edulis	America	Modern	Morton 1987
Vanilla	Vanilla spp. (V. planifolia)	America	Modern	Correll 1953
Tobacco	Nicotiana tabacum	America	Renaissance	Winter 2000
Sisal	Agave sisalana	America	Modern	Alpern; PROTA4U; Purseglove
Cabbage	Brassica oleracea var. capitata	Europe	Medieval to Renaissance	Alpern
Grapevine	Vitis vinifera	Europe	Renaissance	Pooley 2009; Reynolds 2017
Pyrethrum	Chrysanthemum spp.	Europe	Modern	Purseglove

In fact, we mostly observed isolated palms, and no palm grooves. The origin of sweet watermelon is still debated; Chomicki & Renner (2015) advocate for a West African origin from the egusi melon (*Citrullus mucosospermus*), based on a phylogenetic analysis, while Paris (2015) underlines that the sexually compatible wild north-eastern form was overlooked and sustains that it is conspecific with the cultivated form. The distribution of this putative ancestor is centered on the Nile Valley, extending from Egypt to the north, Kenya to the south, Darfur to the west, and Ethiopia to the east. In any case, the domestication and diffusion of watermelon is very ancient, as it was present in Egypt more than 4000 years ago and reached northern Africa, the Middle East and western Asia more than 3000 years ago. Wild cotton has been reported in South Africa (Wendel *et al.* 2010). We have found no information on the region of origin of the first cotton cultivated in the Great Lake Region but Walshaw (2010) underlined the importance of cotton cultivation, probably *Gossypium herbaceum*, in the 11th century in Pemba.

Based on the distribution of sorghum diversity, northeastern tropical Africa has long been associated with its domestication (PROTA4U 2018). Recent archaeobotanical evidence, involving both wild and cultivated types, from 5500 BP, point to the Middle Nile region in Sudan (Winchell *et al.* 2017). Some West African crops possibly diffused with Bantu migrations, others were introduced earlier (see below).

The African crops can be characterized first by their function and use. All three cereals are adapted to drought: sorghum, pearl millet and finger millet. Archaeobotanical remains of the latter were found in the nearby Central Rift dated ca. 1200BP, while remains of domesticated sorghum and pearl millet have been reported in Rwanda, dated c. 1600 BP, together with remains of domesticated finger millet, dated 1250-1000 BP (Giblin & Fuller 2011). In our inventory, the only African starchy tubers are yams, including the air potato that produces both tubers and aerial bulbils. The most diverse crop group is by far that of legumes and leafy vegetables, with 15 crops: bambara nut, cowpea, lablab, pea, three African eggplants, okra, jute, kale, nightshade, Cleome, amaranths, Crotalaria, and bottle gourd. At least, cowpea, lablab, pea, jute, kale, nightshade, Cleome, and Crotalaria are native. Palms, trees and fruits/nuts contribute with five crops: oil palm, Canarium, tamarind, mutugundo (Vangueria apiculata), watermelon, and oysternut. This roster is completed with coffee, napier, cotton, and kenaf. Surprisingly, several native crops are rare in our inventory, with six of them reported in only one GSU: bottle gourd, watermelon, kenaf, pea, lablab, mutugondo, and cotton (although we observed cotton cultivation areas while traveling between GSUs).

Although most of the inventoried African crops are native to East Africa, several are markers of ancient long distance exchanges between this region and South Asia. Thus, five of them, sorghum, pearl millet, finger millet, cowpea, and lablab had reached India, probably through sea trade, at least in the early fourth millennium BP, (Fuller & Boivin 2009; Boivin et al. 2009; Manning et al. 2011; Winchell et al. 2017). According to Boivin et al. (2014), mapping of archaeobotanical remains of these crops on early South Asian sites indicates that they did occur as a package, alongside already established crops. They long remained a minor component of early subsistence, increasing gradually in importance in the last two millennia. Jute mallow (Corchorus olitorius), a leafy vegetable, cultivated or collected from the wild, is another East-African crop that diffused to the whole continent and to South Asia. Indeed, the close genetic relationships of North and East African populations to Asian materials suggests the dispersal of already domesticated material

via the Mediterranean-Indian trade routes (Benor *et al.* 2011). In Asia, it is now used as an important commercial fiber plant, together with the Indian white jute (*C. capsularis*). Unfortunately, its antiquity has not been established yet, as the four-millenia old jute cloth remains found in an Harappan site (Indus Valley) do not allow distinguishing between these two species (Wright *et al.* 2012).

Tamarind, whose wild populations can be found from the Atlantic to the far edges of Central Africa and beyond (NRC 2008), is certainly very ancient in the region. Indeed, it diffused further to Asia, where Buddhist sources mentioned its existence around 650 BC (Diallo *et al.* 2007). Thus, it constitutes an additional marker of the ancient exchanges between East Africa and Asia. Its Arab name (*tamr hindi*, "date of India") has been interpreted as an argument of Indian origin, however it may just reflect its ancient diffusion, indicating only that it was well established in India when Arab travelers arrived there.

The okra crop (*Abelmoschus callei* and *A. esculentus*) is also present in both Africa and Asia, however *A. esculentus* is of uncertain origin, although its diversity is far greater in Africa than in Asia (Schippers 2002).

Arabica coffee, now pantropical, diffused first to Arabia, between 1000 and 1500 AD (Boivin *et al.* 2014). Wild robusta coffee was collected in African equatorial forests, from the west coast to Uganda. It was also grown on a small scale before colonization (Purseglove 1987).

Last but not least, bottle gourd is the most ancient contribution of the African flora to pantropical agrobiodiversity. As a domesticated plant, it was already present in Asia by 11,000 BP and in the Americas by 10,000 BP. The genetic analysis of Erickson *et al.* (2005) suggested a connection between the American and Asian gourds, and thence an introduction by early colonizers of the Americas through Beringia. Kistler *et al.* (2014) refuted this interpretation, because of the too cold climate of Beringia in the Late Pleistocene and the lack of ethnographic evidence in Siberia and Alaska. As their DNA study related the American archaeobotanical remains to African gourds, they proposed a Late Pleistocene natural ocean drift of African wild gourds through the Atlantic Ocean, followed by wide dispersal and multiple domestication events in the Americas. Their little parsimonious hypothesis fails to consider that wild gourds have so far been reported only from East Africa and never from the Americas, and that the human colonization of the Americas largely predates the last two millennia of the Pleistocene (Dillehay 1989, 1999, 2011; Roosevelt *et al.* 1996).

Figure 3 presents the distribution of the richness of African crops, showing the same trend as for total richness, with a lower diversity in the Luo territory as compared to that of the Kisii and Luhya people, and a lower diversity in the Kenyan Nyanza province as compared to the Ugandan share of the study area. However, there is no such difference among the Luhya of both countries. Again, we observe a lower diversity east of Kampala and around Jinja.

Figure 3 also presents the distribution of African cereals. Sorghum is quite ubiquitous, despite its remarkable absence in six GSUs east and northeast of Kampala. This absence is not specific to sorghum, as the second most common African cereal, finger millet, is being abandoned in Buganda, where it is absent in most GSUs. It is also absent in three Busoga and three Kenyan Luhya GSUs. Finally, pearl millet reports are sporadic and limited to the Kenyan Nyanza province, across all ethnolinguistic groups.

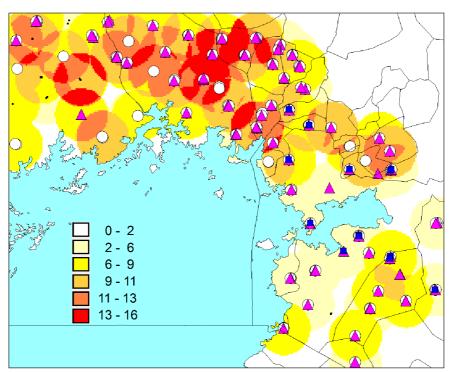


Figure 3. African crop richness (background) and distribution of African cereals in the study area: sorghum (white circles), finger millet (pink triangles), and pearl millet (blue squares).

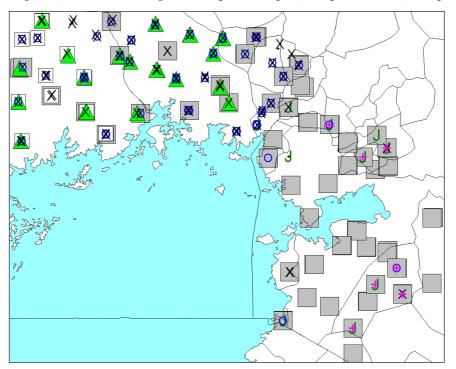


Figure 4. Distribution of seven African vegetables in the study area Ethiopian kale (grey squares); African egg plants (shum: white squares; gilo: green triangles); jute (green 'J'); Cleome (blue circles); amaranths (black 'X'); African nightshade (pink crosses).

Yam was very commonly observed in Buganda, Busoga and Nyole country (all GSUs but seven), whereas it was absent in other Ugandan and Kenyan groups, except for three of the easternmost Luhya GSUs.

Among African legumes, the most widely distributed crop was cowpea, quite ubiquitous in the Nyanza province of Kenya (all GSUs except two Kipsigi and one Kisii); in Uganda, it is ubiquitous among the Luhya, Teso, and Adhola, but absent in one of the three Nyole GSUs, and in three of the 13 Soga GSUs. As for sorghum, Buganda is distinguished by the rarefaction of cowpea, absent in 10 GSUs out of 16. Bambara nut was observed occasionally, among Kisii (one GSU), Luhya (two GSUSs), Nyole (one GSU), and Basoga (two GSUs). The unique lablab report was from a Kenyan Luhya GSU.

Figure 4 presents the distribution of seven vegetables: Ethiopian kale, amaranths, African nightshade, Cleome, jute, and African eggplants (gilo and shum). These crops present interesting contrasts between the Kenyan and Ugandan parts of the study area and between ethnolinguistic groups as well. Jute and African nightshade are not rare among Bantu people (Kisii and Luhya) farms of the Nyanza province of Kenya, whereas their presence is null or negligible on the Ugandan side. Similarly, Ethiopian kale (not shown on Figure 4) appeared quite ubiquitous in Nyanza (all GSUs but one), while it appeared only occasionally in the Ugandan sample, without obvious specificity for any ethnolinguistic group. Conversely, amaranths and Cleome are much more common in the Ugandan inventory. African eggplants present an even more specific distribution, as they appeared strictly limited to Buganda and Busoga (gilo) or to Busoga (shum). Another particular case is that of the Luo territory (Kisumu and Homa Bay counties), where only Ethiopian kale is common, the other six vegetables appearing quite rare.

Perennials also show strong distribution contrasts. Coffee was very commonly observed in Uganda, while it was confined to Kisii and Kipsigi highlands on the Kenyan side. Tamarind was mostly confined to the Ugandan part, with eight observations in Busoga, Nyole, Teso, and Adhola, against one in the westernmost Kenyan GSU (Lhuya). Canarium was found in Busoga and Buganda (two observations each). Oysternut observations are dispersed in Buganda (four GSUs), Busoga (five GSUs), and Nyole (one GSU).

3.1.2 Asian crops

Our inventory includes 21 crops from Asia, 12 of which are ancient introductions (Antiquity to early Middle Age) from Asia. Four are major staples: Asian rice (*Oriza sativa*), cooking and dessert bananas, and taro (*Colocasia esculenta*), which originated in South East Asia. Sesame and two legumes (green gram and pigeon pea) are Indian domesticates, while the third legume, soya, is of Chinese origin. Two vegetables, carrot and onion, are from Central Asia, while eggplant originated in South East Asia. The Asian contribution is particularly important for fruit trees, with mango, jackfruit and coconut, from India, citrus trees and jambolan, which originated further to the east, and loquat, from China, although loquats (three farms) and coconuts (one farm) are poorly represented in our inventory. The only coconut palm, recorded in a relatively wealthy farm, was planted from a germinated nut brought by Mombasa merchants. In fact, the presence of this species around Lake Victoria seems to depend on such sporadic imports, as only tall adult palms were observed in the landscape. The Asian crop list is completed with tea, turmeric and ginger, the latter two recorded only once.

Pigeon pea is the only Indian crop whose date of introduction into Africa, at least 4000 BP (Khoury *et al.* 2015; PROTA4U 2018), compares with that of the oldest African

domesticates into India. However, apart from the fact that East Africa is considered a secondary center of diversification for the species, we have found no data supporting its antiquity. Other poorly documented ancient introductions are those of taro and banana (see below), jambolan, turmeric, and ginger. Turmeric may have been introduced by Austronesian people into Madagascar, and it may have reached East Africa in the 8th century, while ginger would have been introduced into East Africa by the Arabs in the 13th century (Purseglove 1985). The case of onion is better documented, with a probable domestication in Central Asia, a diffusion to Mesopotamia around 4500 BP, and an introduction into Africa through Egypt around 3600 BP, followed by diffusion into tropical Africa (PROTA4U 2018).

Taro and plantains, from South-East Asia, are most often considered as part of a same crop complex whose introduction is much more ancient than those of other Asian crops. However, direct archaeobotanical evidence is scarce or too debatable. Indirect evidence involves the high diversity of banana in Africa, and linguistics for words relating to taro (Blench 2009). The discovery of very ancient archaeobotanical banana microremains, dated 4000 BP in Uganda and 2500 BP in Cameroon, has been largely challenged. According to the genetic analyses of Perrier *et al.* (2018), the strictly endemic "Eastern African Bananas" complex, linking seedy with parthenocarpic diploid as well as triploid bananas, originated in southern Indonesia. Its introduction is associated with one or several human migratory waves across the Indian Ocean. As for the West-African plantains, the wide somatic diversification suggests a long period of selection by farmers. The antiquity of banana in the region has been confirmed by linguistic studies, indicating a pre-Bantu introduction in the early first millenium and a westward diffusion to the Lake Victoria region, through the Eastern Rift obstacle, in the late first millennium (Perrier *et al.* 2018).

For most other Asian crops of our inventory, their diffusion from Asia to Africa is more recent but less well documented than in the reverse direction. It took several, direct or indirect, routes, and was much more progressive, hampering inferences on the inland development of exotic crops. The very diverse actors of these translocations include traders from ancient and Roman Egypt, Arabia, Indian as well as insular South East Asia.

Sesame (Sesamum indicum) spread very early from the Indus region: it was important in Mesopotamia by 4000 BP and present in Egypt before 3300 BP. In the 2nd century BC, it was a precious good in the trade between India and the Mediterranean, along the Arabian and Red Sea coasts, and it was probably known in the Horn of Africa (PROTA4U 2018). In this same context, archaeobotanical remains attest the presence of other Asian crops, including rice, coconut, green gram (or mung bean, Vigna radiata, domesticated in India before 3500 BP; PROTA4U 2018), and citron (Citrus medica) in Roman Egypt (Walshaw 2010; Boivin et al. 2014). For the Medieval period, lime (Citrus aurantifolia), eggplant, and cotton were reported on the Red Sea shores in the 11th century. In East Africa, rice, green gram, sesame, Citrus, and coconut appear in the Swahili Coast archaeobotanical assemblages of the last centuries of the first millennium AD; they were probably accompanied by taro (Blench 2009). In the 10th century, Al-Masudi stated that banana was as abundant in Zanzibar as in India, coconut had become a staple, and, according to Abu al-Hanifa, the finest cane sugar came from this region (Watson 1983, cited in Boivin et al. 2014). From the 11th century onwards, at least on Pemba, rice had also become a dominant staple (Walshaw 2010). Later, Ibn Battuta also observed citrus trees and important banana growing on the island of Mombasa (Boivin et al. 2014). Lime (Citrus aurantifolia) probably

diffused through sub-Saharan Africa as a result of Islamic trade (Watson 1983; cited in Boivin *et al.* 2014), as likely did ginger (from South Asia). The introduction of the eggplant (*Solanum melongena*) would also be related to the Medieval Islamic trade. The latter was relayed by Swahili and more local traders (Vernet-Habasque 2018). Thus, *Citrus* reached particular importance inland in Mozambique, from where salted lemons were exported as far as India in 1586 (dos Santos 1891).

For West Africa, Arab sources indicate that sesame and sugar cane were present in the 12th century (Burkill 1997; Alpern 2008), very probably introduced via the Mediterranean, and the presence of sour orange (*Citrus x aurantium*) was reported in the 14th and 16th centuries (Watson 1983; cited in Boivin *et al.* 2014). From the 15th century, the Portuguese also participated in sugar cane propagation. In the 14th century, both al-`Umari and Ibn Battuta saw a food resembling taro in Mali (Blench 2009). The presence of these crops in both East and West Africa suggests that overland diffusion was quite active, so that introductions were not necessarily limited to eastern coastal areas.

Purseglove (1987) suggested that mango might also have been introduced to Africa via Persia and Arabia, in the 10th century. The presence of mango trees in Mogadishu suggests Arab diffusion (Russell-Wood 1998). However, the short seed-life and the lack of grafting techniques, the diffusion of the species and its cultivars strongly limited its diffusion, and only with the arrival of the Europeans did mango gain popularity. In the 16th century, a special technique employing grafting was developed and, in the 17th century, the Portuguese planted mango in coastal areas of both East and West Africa. But acceptance was slow and spread into the interior was erratic (Yadav & Singh 2017).

In Kenya, Tanzania and Uganda, tea is a late introduction, from the early 20th century for commercial production in the 1920s and 1930s (Purseglove 1987).

Figure 5 presents the distribution of the richness of Asian crops. It shows a lower richness in the Luo and Kisii territories of the Kenyan Nyanza province as compared to the Ugandan share of the study area and the neighbouring Luhya areas. Within Uganda, we observe again a lower diversity east of Kampala and around Jinja. As compared with total richness on the whole study area, there appears to be less variation among neighbour GSUs.

The six most common Asian crops are mango, cooking and dessert bananas, taro, sugar cane and onion. Mango was absent in only four GSUs, cooking and dessert bananas in five and seven respectively, taro in ten, sugar cane in 16, and onion in 25 (Figure 5). Three of the four mango absences are explained by elevation above 1700 m, in northern Kisii and Kipsigis GSUs. No clear geographic structure appears for the five other very common crops, except for a higher frequency of banana absence among the Luo (half of the corresponding GSUs lacking at least one type) and a higher frequency of onion absence in Busoga (nine out of 14 GSUs).

The higher diversity of Asian crops in Uganda is clearly supported by the distributions of the other Asian crops. Thus, citrus trees, pigeon pea, soya bean (Figure 6) and sesame (Figure 7) are much more common in the Ugandan part than in the Kenyan one. The difference is even clearer north of Kisumu. Similarly, jackfruit (Figure 7) is mostly present on the Ugandan side, with mature to very old trees. The individuals reported beyond the border, in the Luhya GSUs of Kenya, were all much younger (30-40 cm dbh), suggesting a recent diffusion into northern Nyanza. Further from the border, but still in Luhya country, jackfruit was observed along the road, but not in the visited farms. Sixteen of the 17

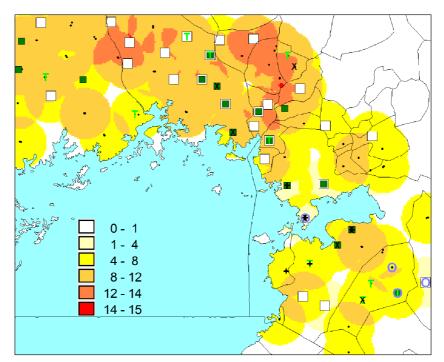


Figure 5. Asian crop richness (background) and "negative" distribution of most common Asian crops in the study area

Symbols identify GSUs where the following crops were absent: onion (white squares); sugarcane (green square); taro (green 'T'), cooking banana (black 'X');

dessert banana (black crosses); mango (blue circles).

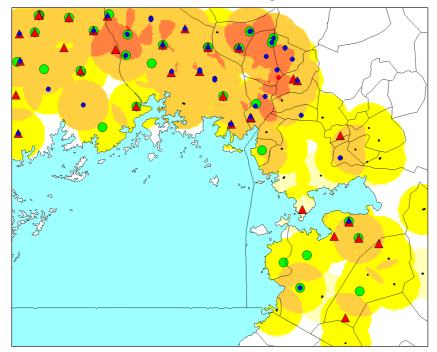


Figure 6. Asian crop richness (background) and distribution of recorded citrus trees (green circles), pigeon pea (red triangles), and soya bean (blue dots).

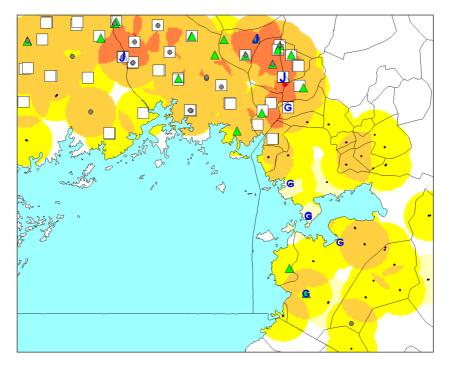


Figure 7. Asian crop richness (background) and distribution of jackfruit (white square), sesamum (green triangles), eggplant (*S. melongena*; grey dots), jambolan (blue 'J'), and green gram (blue 'G').

eggplant observations are from Uganda, with a particular frequency in Busoga, Nyole and Adhola GSUs. The three records of jambolan are exclusive to Uganda, whereas the four records of green gram are all Kenyan. Tea is the second case of a predominantly Kenyan crop in the study area, as it was cultivated at commercial scale in six GSUs in Kisii and Luhya highlands (above 1500 m), versus only one GSU in the Ugandan part, at an elevation of 1200 m.

3.1.3 American crops

Our inventory includes 21 American crops, 12 of which were introduced at Renaissance, soon after the Portuguese and Spanish voyages to the Americas, and nine in the last two centuries by colonial administrations. The species of the first group include the Mesoamerican trilogy or Three Sisters (maize, bean and squash), and two other major staples, cassava and sweet potato, all of which have become dominant in the agricultural landscape. Chili pepper is less evident, but widely present in home gardens. The presence of four fruit species reflects the particular interest of early Portuguese travelers for tropical fruits that were established in their trading posts all around tropical Africa. Papaya is the most commonly planted in home gardens, very probably because of its fast growth, year-round flowering and fructification, and high productivity. Guava is also very common, often as a semi-feral component of the vegetation in anthropized landscapes in the Nyanza province of Kenya. Pineapple is less frequent, being occasionally used as a commercial crop, at small to medium scales (from a few dozen plants to a few hectares). The rarest Renaissance introduction is soursop (isolated trees in two farms). Tobacco plants are rare too (two observations, for home consumption).

Maize, introduced in Europe by Colombus in 1493, has been cultivated in Portugal since 1500 and established very fast on the coasts of western and northern Africa. It is mentioned in São Tomé in 1534 and Cape Verde in 1540 (imported from the Antilles until 1640 and later from Brazil), on the Gold Coast in 1554, in the kingdom of Congo from 1570, in western Mozambique in 1561 and, by Portuguese growers, in Zanzibar and Pemba in 1643, from where it diffused inland by caravan trade (Bahuchet & Philippson 1998; Madeira Santos & Ferraz Torrão 1998; Mc Cann 2001; Alpern 2008; Freitas 2018). Introduced by the Turkish in Egypt in 1517, it diffused along the Nile and Southwest to Nigeria, following pilgrimage routes. It was common in Ethiopia around 1520 (Desjardin & McCarthy 2012). In sum, it was introduced to Africa in different points and times, most often by the Portuguese (Miracle 1966). Indeed, the major contributions of Brazilian coast materials and Islamic trade routes can still be recognized, particularly in the genetic makeup of West African maize (Westengen et al. 2012). By 1860, it was abundant in Uganda, as a garden plant, in most of the major state systems—Buganda, Bunyoro, Toro, Ankole, and Acholi (McCann 2001). It was then common too in Kenya, but important as a staple only in the southeastern coastal lowlands. It became a major Kenyan crop during World War I, when disease in pearl millet led to famine (Smale et al. 2006). Since then, maize cultivation has benefitted from considerable investments and, from the late 20th century, it has become the main staple in southern and eastern Africa (McCann 2001; Smale & Jayne 2003).

"Though manioc has not experienced a recent dramatic growth in cultivation as seen in the case of maize, manioc is the most widely planted crop in tropical Africa, the continent's second most important food crop, and a cherished cultural tradition despite its foreign provenance" (Holler 2007). Portuguese brought cassava to their stations on African coasts, from Ghana to Somalia. Until about 1600, it was mostly cultivated in West and Central Africa for provisioning slave ships. It diffused inland, particularly by river people trade, replacing traditional staples (millet, yam, plantains) or even maize. In East Africa, it was introduced in Mozambique (possibly in the 16th century), Sofala, Kilwa, Zanzibar, Pemba and Mombasa during the 17th century, but it reached the upper Zambezi from Angola rather than Mozambique. It diffused inland slowly, and was reported throughout the Great Lakes Region by many travelers in the mid-19th century, introduced by Arab traders. Later, its cultivation was further stimulated by colonial administrations as a famine food (Carter *et al.* 1993; Bahuchet & Philippson 1998).

The sweet potato was almost certainly observed by Columbus on his first voyage and it was transported to Africa very early, as it was present in São Tomé in 1520-1540 (Alpern 2008). It was introduced on the Indian Ocean side in relation to Portuguese trade travels, as indicated by batata-derived names for the crop in India and the East Indies (Dalgado 1913), and confirmed by the observations of Van Lischoten (1610). Before 1586, it was very cheap and abundant in Sofala (dos Santos 1891). Its very likely arrival in China around the mid-16th century (Ho 1955) gives further support to its early diffusion all around the Indian Ocean. By 1876, it was abundant in the Great Lakes region (McCann 2001).

The common bean was well established in Africa before the colonial era. Genetic diversity of the crop and its pathogens and linguistic evidence indicate that it became a major crop in Central to Eastern African highlands earlier than in other parts of the continent. In fact, the Portuguese introduced it from the 16th century through Sofala, Zanzibar and Mombasa, from where it was carried to these highlands by trading caravans and merchants (PROTA4U). In 1586, it was abundant and cheap in Sofala (dos Santos 1891). On the western side, it was reported in 1645-8 in Congo (Alpern 2008).

According to Alpern (2008), the American groundnut was reported in 1664 in Congo/Angola, or even earlier, by van den Broecke in 1608-12, in Loango. The West-African two-seeded types from Brazil (PROTA4U 2018) were certainly introduced by the Portuguese in the 16th century and got well established inland before the end of the 18th century (Katz 1998). This first introduction was very likely followed by others along the East-African coast, as (i) the root-name 'pinda', borrowed by the Portuguese from the Congolese, spread to Asia with the crop, while another name in India, meaning 'Mozambique nut', indicates an introduction from this Portuguese trade post into Goa (Dalgado 1936). A clear evidence of very early introductions by the Portuguese is the presence of the crop in China in the early half of the 16th century (Ho 1955). In addition, three-seeded groundnut types from Peru were taken by the Spaniards to the Philippines, from where they spread to Japan, China, Indonesia, Malaysia, India, Madagascar and East Africa (PROTA4U 2018). From the coast, groundnut would have been introduced in Uganda by early traders and travelers around 1862 (Okello *et al.* 2010).

Squashes and pumpkins (*Cucurbita pepo, C. moschata*, and *C. maxima*) are also early Portuguese introductions. They were reported in Guinea in 1564-65 (Alpern 2008), and in the Kongo kingdom in 1668 (Katz 1998). As for the groundnut, Indian root-names, originating from the Portuguese 'abóbora', indicate introduction via the Portuguese trade posts around Africa (Dalgado 1936). They are not only cultivated for their fruit, but also for their leaves. According to these different uses, farmers sometimes mentioned distinct vernacular crop names for the same botanical species.

Earliest reports of chili in Africa are from Gambia (1686; Alpern 2008) and Congo, also in the 17th century (Katz 1998). Vernacular names indicate that the plant was often assimilated to indigenous types of pepper, however composite names such as 'indongas-anpota', corresponding to 'nungu za mputu' (pepper from the Portuguese), are reminiscent of a Portuguese introduction. The quite common term 'pilipili' comes from the Arab 'filfil' for pepper, a term that would have diffused from the Swahili coast (Katz 1998).

Local names of tobacco and fruit crops testify remarkably to their history. Thus, many names for the pineapple have conserved the Amazonian root 'nanas' in Africa and Asia; those for papaya reflect the Brazilian and Antillean names 'papai', 'ababai', 'ambapaya'; those for tobacco are strongly reminiscent of the Antillean 'tabaco' (a smoking device), and those for guava have conserved the root 'pera', from the first Portuguese name of the fruit (Dalgado 1936).

The diffusion of the pineapple to Africa and tropical Asia is probably the best documented case of the systematic introduction of a range of crops by the Portuguese in all these regions. Within less than two decades after the official discovery of Brazil by Cabral, a couple of closely related cultivars was distributed from West Africa to China and the Philippines and there are abundant reports of pineapple cultivation from the mid-16th century (e.g. 1586 for Mozambique inland; Coppens d'Eeckenbrugge *et al.* 2018).

The Portuguese also introduced papaya to West Africa. According to Alpern (2008) and Freitas (2011), it was present in 1630 in Luanda 1647 in São Tiago (Cape Verde) and its presence was mentioned in a 1661 treaty between the English and Fetu at Cape Coast (Ghana). The Abbé Proyart (1776, cited by Katz 1998) ascertained that papaya was the most common American fruit in Congo. Three names for papaya in northern Nigeria suggest a late introduction from across the Sahara (Blench 1998; Alpern 2008). A third route for this crop involves the Spaniard, from Mexico through the Philippines and the Indian Ocean (Blench 1998).

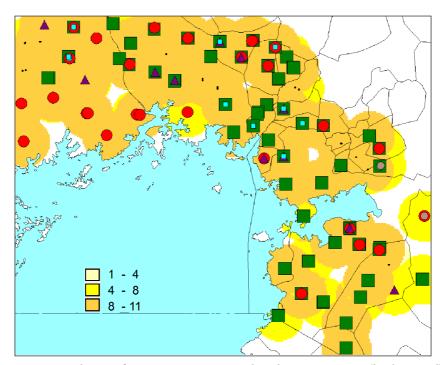


Figure 8. Richness of American crops introduced at Renaissance (background) and distribution of sisal (green squares), tomato (red circles), passion fruit (purple triangles), Irish potato (grey circles) and pineapple (light blue squares).

Guava was present in Cape Verde in 1657 and in Angola in 1686 (Alpern 2008). Its diffusion was certainly favored by its propension to be invasive in anthropized landscapes. This capacity contradicts Alpern's assertion of a much later inland diffusion, related to missionaries of the colonial period. The Portuguese also introduced guava to East Africa, India and the East Indies (Dalgado 1936), where both root-words, 'pera' and 'goiaba', are common. In the Nyanza region, many farmers pretend, with some disdain, that they do not cultivate this fruit, and some even consider it as a weed, however most of them preserve part of the many spontaneous seedlings in their home gardens and fields. This fruit is less common in Uganda where spontaneous germination seems rare.

According to Alpern (2008), the soursop was reported in Angola in 1668, and other closely related species arrived early in West Africa, consistent with an early Portuguese introduction. Soursop is still very common in Congo (Katz 1998). We have found no specific information for East Africa, nor even for India (Asouti & Fuller 2008). An alternative Spanish route from Mexico is consistent with the Philippine name 'guyabano', derived from the Spanish 'guanábana'.

Tobacco was reported in Africa in the late 16th century (Alpern 2008). According to Purseglove (1987), the Portuguese had distributed it widely in their sphere of influence.

Figure 8 shows the distribution of richness for the 12 American species introduced at Renaissance. In striking contrast with all other maps presented above, this map shows very little variation among GSUs. Thus, the highest number of species was 11, observed for the Ugandan GSU that is closer to both the lakeshore and the border with Kenya. By far, the most common values are 9 and 10 (yellow orange areas). The yellow areas correspond to neighborhoods with values of 8, except for one GSU in Luo country (with a

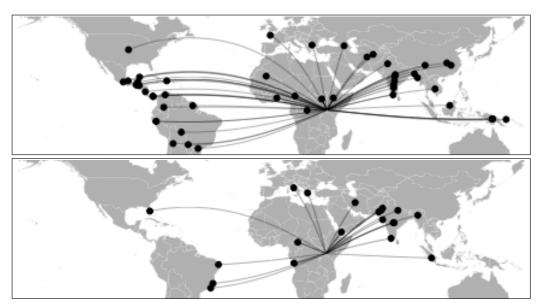


Figure 9. Intercontinental connections of East Africa, as represented by crop diffusion, both inward (upper) and outward (lower).

value of 6) and the two Kipsigi GSUs (5 and 7). This lack of geographic and ethnolinguistic structure can be explained by the very high frequency of most these crops. Indeed, only pineapple (9 GSUs), soursop (3 GSUs), and tobacco (2 GSUs) are uncommon, whereas maize and common bean are ubiquitous, sweet potato is absent in one GSU, squash in two, cassava in four, guava in five, groundnut in six, papaya in seven, chili in eight. In the highland Kisii and Kipsigi GSUs, elevation seems to play a role in the absence of tropical lowland crops such as cassava, chili, groundnut and papaya.

The eight other American inventoried plants introduced in modern times, during the colonial period are sunflower, Irish potato, tomato, avocado, cocoa, passion fruit (Passiflora edulis), white sapote (Casimiroa edulis), vanilla, and sisal. Cherry tomatoes were brought in pre-colonial times, across the desert, in the 19th century, however larger modern tomatoes diffused in colonial times (Blench 1998). The Irish potato was probably introduced into East Africa in the late 19th century (Purseglove 1987). One of the earliest dates for avocado seems to be 1824 in Senegal (Alpern 2008). In the Belgian colonies, it was introduced in the early 20th century in Mayombe, mentioned as a non-commercial fruit-tree, and later, more formally, via the colonial botanical gardens, in its three subspecific forms. For example, it arrived in Katanga in the 1930s (Van Laere & Dubois 1953), and in 1929 in Rwanda-Burundi (Alpern 2008). Sisal was smuggled into Tanganyika by a German agronomist in 1893 and it was introduced into Kenya in 1903 (Purseglove 1985). As passion fruit economic development only started in the mid-20th century (Yockteng et al. 2011), this crop was very probably introduced in the same period. According to Purseglove (1987), the Spanish and Portuguese introduced cocoa into the Gulf of Guinea in the 17th century. However, it was introduced in Uganda in 1901, from Kew.

With one observation in Kenya, (Teso), the white sapote, a little known fruit species from Central America, seems to be rare in the study area and is not mentioned among the useful trees in Uganda (Katende 2000). In the preliminary survey in Kenya, we had met a farmer who had imported white sapote plants from Ethiopia. Indeed, it seems more

common in Ethiopia (Satheesh 2015), Zimbabwe (Flora of Zimbabwe 2018) and South Africa (Morton 1987). Its introduction in Africa has probably not been documented.

Only the distribution of avocado compares with that of major American crops introduced at Renaissance, as it is present in all GSUs but three. Sisal comes second among the modern introductions, being very common in Kenya (only absent in eight GSUs) and eastern Uganda, and getting less frequent to the west (Figure 8). The reverse situation was observed for tomato, more frequent to the west, around Kampala. Records of passion fruits (essentially *P. edulis*) are scattered in the study area. Observed in two GSUs, Irish potato has only local importance, at high elevations. Cocoa, sunflower, vanilla and white sapote were recorded once each.

3.1.4 European crops

Given the poor diversity of native European crops and the difficulty to adapt temperate species to tropical conditions, their poor contribution is not surprising. Cabbage was recorded in eight GSUs, with only one case from Kenya. Grapevine and pyrethrum were recorded only once.

3.1.5 Intercontinental crop diffusion and worldwide interconnection

Figure 9 shows crop inward (Fig. 9A) as well as crop outward (Fig. 9B) worldwide connections to and from the Great Lakes Region. With the relative exception of Australia, all continents have contributed to the crop diversity recorded. The most important Australian contribution was visible in the many *Eucalyptus* and *Grevillea* plantations, which were not taken into account. In our inventory, the 30 African crops represent 40% of the total, Asian and American 28% each, and Europe 4%. The higher proportion of African crops must be tempered by the fact that we counted crops of multicontinental origins as African. In fact, three crops may have been developed from species found in Africa and Asia (okra, pea, lemon grasses), and three more were developed separately in America, Africa and Asia (yams, amaranths and cotton) from different species. A more botanical approach would probably show that the three continental contributions are roughly similar, in term of species numbers.

Despite the distance from their places of origin and their relatively late introductions (from Renaissance to modern times), the contribution of American crops is remarkable, as it compares with that of crops native to Africa and Asia, most of which have been present for much longer periods. Furthermore, we have seen that, contrary to African and Asian crops, whose distribution often indicates particular acceptance by specific ethnolinguistic groups, most American crops introduced in Renaissance times (nine crops out of twelve), as well as the more recent avocado, have become major crops, with a quite uniform presence across agricultural landscapes (see Figure 8), showing a wide acceptance across cultural groups.

3.2 Economic and cultural salience of American crops

3.2.1 Economic salience of American crops

The high proportion of exotic crops (73.65%) reveals how important were worldwide interconnections of Africa. Only 26.35% of crops that are cultivated today were from Africa. The analysis of crop frequency shows the particular salience of American crops in the Great Lakes Region. Their contribution represents almost half of the total (45.68%), far more than Asian crops (27.61%) and African crops (26.35%). European crops represent only 0.36% (Figure 10A).

The economic salience of American crops is reinforced by considering only major crops, cultivated by more than two-thirds of the farmers, i.e., 14 crops present in more than 98 of the 148 surveyed farms. Among them, ten are American (nine introduced by the Portuguese at Renaissance), three are Asian and one African (Table 2). In relative terms, major American crops present a frequency of 71.43% of the total, major Asian crops 21.43%, while the African share drops to 7.14% (Figure 10B). Conversely, the relative frequency of minor crops, cultivated by less than one-third of the farmers, is much higher for those of African origin (51.03%) or Asian origin (39.62%), while the share of American crops drops to 8.84% (Figure 10C). This contrast is consistent with the different patterns observed in the distribution of crops from America, Africa and Asia. Thus, American crops, particularly those introduced at Renaissance, tend to ubiquity, so they do not participate appreciably in the structuration of species richness at the levels of countries, ethnocultural groups, and even GSUs (Figure 8), whereas African crops, particularly vegetables, are much less uniformly distributed, often contrasting ethnocultural groups or even the Kenyan and Ugandese areas (Figures 4 and 5). The case of Asian crops (Figures 6 and 7) is intermediate but more similar to that of African crops.

Figure 11 presents a similar analysis comparing how worldwide interconnections were reflected in the crop rosters of Bantu and Nilotic farmers. Nilotic farmers tend to cultivate a smaller number of crops as compared to Bantu farmers. However, on average, farmers of both cultivated about 9.5 American crops, 5.8 Asian, and 5.5 African.

3.2.2 Cultural salience

Crop cultivated in the Great Lakes Region were mainly used for home consumption (94.6%) or for both consumption and sale (46.4%). They were rarely used for market only (1.5%). Groundnut, rice and maize are the main crops among those that are consumed and sold. We found no association between a crop continental origin and its market orientation. Concerning home consumption, 58.1% of the informants declared *ugali* as usual main dish. It is prepared from maize, an American crop.

As expected (Borgatti 1999), the citation rank, obtained in the crop free listing shows a good correlation with crop frequency (Figure 12), particularly for the most cited crops. It is even better correlated with the declared ranking of the surfaces dedicated to each crop (Figure 13).

Both correlations demonstrate the overall consistency of the free listing data. Again, these data support remarkably the popularity of American crops. Indeed, the crop citation rank shows a relationship with the crop continental origin. Thus, four of the five crops with the highest citation ranks (closest to one), are major American staples (maize, common bean, cassava, sweet potato), with the highest Smith index. These four crops also appear at the top of Table 2, where crops are listed in decreasing order of their cultivation frequency. In contrast, among the five next crops, three are African, with only two staples (coffee, sorghum, finger millet). Crops listed from positions 11 to 15 include three Asian crops (sugarcane, banana / cooking, soya bean; Table 3). Curiously, despite their very high frequency, cooking and dessert banana are not given a prominent status in the free listing data

Figure 14 presents a synthetic comparison of crop citation frequencies by continent of origin, for Nilotic and Bantu groups. In both cases, American crops are better ranked, African crops coming second, and Asian crops third.

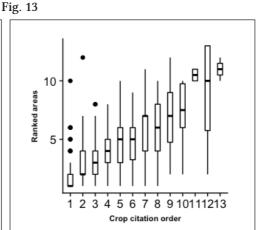


Fig. 11

Linguistic family

Bantu

Nilotic

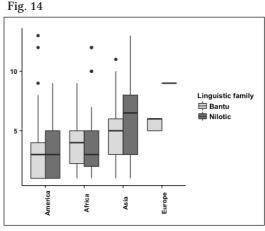


Fig. 12

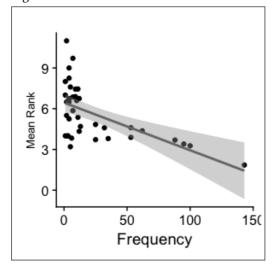


Figure 10. Crop frequencies, summed by continent of origin. A – All crops / B - major crops / C - minor crops. Major crops and minor crops correspond respectively to those found in more, or less, than two thirds of the surveyed farms.

Figure 11. Average number of species as a function of worldwide interconnections for Bantu and Nilotic farmers.

Figure 12. Mean rank of citation correlated to frequency.

Figure 13. Ranked cultivated area correlated to citation order.

Figure 14. Average citation order as a function of worldwide interconnections for Bantu and Nilotic farmers.

Table 2. List of major crops recorded in the Great Lakes Regions

Crop	Origin	Period	N
Maize	America	Renaissance	148
Common bean	America	Renaissance	144
Sweet potato	America	Renaissance	141
Cassava	America	Renaissance	133
Mango	Asia	Medieval	133
Banana / cooking	Asia	Antiquity	130
Avocado	America	Modern	128
Squash/pumpkin	America	Renaissance	126
Groundnut	America	Renaissance	123
Guava	America	Renaissance	119
Papaya	America	Renaissance	118
Banana / ripening	Asia	Antiquity	117
Sorghum	Africa	native	106
Chili	America	Renaissance	102

Table 3. Twenty most cited crops, ordered by citation frequency

Origin	Crop cited	N	Citation Frequency	Mean citation rank	Smith index
America	maize	143	0.966	1.853	0.8256
Asia	green gram	5	0.034	3.200	0.0197
America	common bean	100	0.676	3.270	0.4241
America	cassava	95	0.642	3.400	0.4044
America	sweet potato	88	0.595	3.693	0.3506
Africa	coffee	25	0.169	3.720	0.1012
Africa	sorghum	35	0.236	3.800	0.1426
Asia	tea	6	0.041	3.833	0.0267
Africa	finger millet	53	0.358	3.887	0.2027
America	pineapple	3	0.020	4.000	0.0161
Africa	bambara nuts	1	0.007	4.000	0.0017
Africa	napier	3	0.020	4.000	0.0083
Asia	sugarcane	12	0.081	4.333	0.0403
Asia	banana / cooking	62	0.419	4.371	0.2085
Asia	soya bean	32	0.216	4.594	0.1143
America	groundnut	53	0.358	4.604	0.1665
Africa	cowpea	13	0.088	4.692	0.0416
Asia	banana / ripening	25	0.169	4.840	0.0754
Africa, Asia, America	yam	4	0.027	5.250	0.0052
Africa	Ethiopian kale	11	0.074	5.364	0.0295

3.3 Historical dynamics and drivers of intercontinental crop exchanges involving Africa

In their study of the Indian Ocean food globalization, Boivin et al. (2014) presented the striking asymmetry in crop exchanges between India and Africa. On one hand, the presence of at least five African crops (sorghum, pearl and finger millet, cowpea and lablab) in western India, during the Late Harappan period (4000-3700 BP), has been interpreted as the introduction of a geographically and historically consistent package, whose absence from contemporaneous archaeobotanical assemblages on the Arabian peninsula suggests a direct sea route between two savannah agricultural systems. Then, these crops spread gradually all over India within a few centuries (Fuller & Boivin 2009). On the other hand, the diffusion and uptake of South-Asian crops into East Africa appear much slower and later. The introduction of sesame into Egypt, before 3300 BP, seems to result from a progressive overland diffusion through Mesopotamia. According to Boivin et al. (2014), the active Red Sea and Erythrean Sea trade of the early first millennium AD may explain findings of exotic crop remains, without proving local cultivation. In any case, the impact of a long regional trade history on foodways appears limited and there is little evidence for Indian food crops in the Horn of Africa, the coasts south into Tanzania, or the neighbouring Sahelian region, at least until the 11th century. Crowther et al. (2016) reported excavations in three coastal sites and five island sites of Kenya and Tanzania, dating 650-1200 AD. Their seed-crop inventory is largely dominated by pearl millet, accompanied by some sorghum, finger millet and baobab. Rare exotic seed-crop remains were found in a fourth coastal site (only one of rice and two attributed to wheat) and in two sites in Pemba and Zanzibar (a few rice remains and three green gram remains). Thus, the presence of Indian crops on the Swahili Coast only becomes discernible at the turn of the second millennium AD, although the archaeobotanical evidence is still patchy, indicating a protracted process of adoption. For example, in Pemba, rice and coconut became dominant in the 11th century (Walshaw 2010). Finally, the only Asian plant whose diffusion and adoption could be compared with "the rapid transformation of agricultural, economic and social trajectories following the species exchanges between the Old and New Worlds after 1492" (Boivin et al. 2014) may be the crop complex associated with the westward Austronesian expansion.

Contrasting the earliest seed-crop remains found in Comoros and Madagascar to those found along the Swahili Coast, Crowther *et al.* (2016) have shown that the frequency of Asian rice, mungbean and Asian cotton (*Gossypium arboreum*) provide a clear archaeological signature of the Austronesian expansion to these islands. The specificity of the association of rice and green gram was inferred from the rarity of green gram in the Near East and Arabia and its relative frequency in South and South East Asia.

Despite the clarity of the contrast observed by Crowther *et al.* (2016), banana, taro and the greater yam are better tracers of the Austronesian crop plant contribution to continental East African agriculture. Indeed, the poor preservation of cotton remains hampers the distinction between the Asian and African cotton species (Walshaw 2010; Crowther *et al.* 2014), unless DNA analyses are feasible. The same condition applies for green gram and Asian rice, two crops whose accessions from Madagascar are genetically distinct (Sangiri *et al.* 2007; Mather *et al.* 2010), opening the possibility of tracing two different introduction routes into East Africa, either directly from India or via South East Asia. Similarly, coconut could be brought by man as selected germplasm, or be native,

as the region is part of the natural distribution of the species (Sauer 1967). In contrast, although their archaeological traces are much more elusive, banana, taro and the greater yam are reliable markers because they were domesticated in South East Asia. Furthermore, the East African diploid and triploid bananas, including the AAA Mutika group typical of the Great Lake Region, are related to similar genotypes of the eastern Rift valley, Pemba, Zanzibar, and the Comoros, all of them having their origin in insular South East Asia (Perrier *et al.* 2018). Their wide somatic diversification indicates a long process of selection by East African farmers, which implies a relatively rapid inland penetration and an active adoption. Concerning the likely date of their introduction, Al-Masudi reported banana abundance in Zanzibar in the 10th century, and Ibn-Battuta described it as a staple in Mombasa (Boivin *et al.* 2014). Linguistic analyses indicate that banana cultivation started in the region in the first half of the first millennium (Perrier *et al.* 2018). This estimate is consistent with Asian crop remains dated from the eighth century in the Comoros (Crowther *et al.* 2016) and a trans-Indian Ocean migration to Madagascar around the 7th century, based on linguistics and archaeology (Allibert 2008).

To understand food globalization in the prehistoric Trans-Eurasian Exchange, Jones et al. (2011) proposed to identify drivers of food globalization in the better known Columbian Exchange, relating them to ecological opportunism (e.g. the exploitation of different types of soils), economic relations (different use and distribution of labor force, adoption of new famine crops, shorter production cycles) and cultural identity (concomitant migration of people and their crops). Only at the end of their paper do they recognize the important difference in the tempo of changes between the prehistoric and Columbian exchanges. Boivin et al. (2012) answered that Jones et al. had focused too much on ecological drivers and insisted that the diffusion processes were gradual in the Old World, whereas, "with the Columbian Exchange [...] the process began abruptly, and was complete in many respects in as little as a hundred years." After this strong statement, they reexamined the question, considering the tradable potential of agricultural products, the importance of farmers' curiosity for new plants, and the relation between power, social prestige and exotic plants and animals, with examples including a noble-savage-view of Amazonian landscape domestication and the importance of trading spices and spectacular horticultural plants in botanical gardens. Then, they focused on examples from the Trans-Eurasian exchange, insisting on the delay between introduction and economic importance and proposing a crop typology to distinguish among cash crops, spices/exotica, risk-buffering crops and staples, to describe regional crop trajectories. In conclusion, they called for softening the "ecological and caloric" approach of Jones et al. (2011) and emphasized "a role for the prestigious, cosmological and medicinal qualities of exotic plants obtained from distant regions," not limited to spices.

The examination of an extremely wide and diverse corpus of spatially, temporally and biologically heterogeneous information, often derived from indirect archaeological, linguistic and genetic evidence, is too difficult to interpret. Here, we propose to reexamine our field observations in a much more specific geographical setting, taking into account the origin and diffusion history of crops, as well as small farmers' perceptions of their economic and social importance. Thus, we limit our analysis to the crops that we have inventoried for which we have reasonably good information.

In the analysis of crop diffusion and uptake, contrary to the proposal of Jones *et al.* (2011), we distinguish long-distance crop intentional translocation across the seas from

progressive overland diffusion. The former must also be distinguished from sea trade, as we have seen that the presence of plant remains in coastal cities is not synonymous to the cultivation of the corresponding crop.

Overland progressive diffusion is a long process involving a myriad of short distance translocations followed by local adoptions. This process is not directional, and it can be submitted to ecological as well as social barriers, seed exchanges being conditioned by farmers' social organization (Leclerc & Coppens d'Eeckenbrugge 2012; Labeyrie *et al.* 2016). The need for communication through a common vocabulary between the giver and the receiver, so commonly exploited by crop linguistics, is obviously related to crop diffusion.

Most crops from West Africa (Bambara nut, African eggplants, oil palm, tamarind, baobab), West/Central Asia (carrot, onion), and South Asia (sesame, green gram, pigeon pea) arrived in East Africa through a long and erratic process of overland diffusion, as we have seen in the case of Indian crops.

The West African pearl millet must have followed the same process much earlier, well before 4000 BP, as it was further transferred directly to Gujarat, presumably by sea, together with at least four East-African crops (sorghum, finger millet, cowpea and lablab; Fuller & Boivin 2009). Whether the movements of these crops was favored by concomitant human migrations has not been ascertained. In any case, they took place under rather uniform ecoclimatic conditions corresponding to savannah agriculture.

In contrast, the Austronesian migration introduced food crops adapted to more humid conditions, as rice, the greater yam, taro, and banana. This contribution was small in number of species, but very effective in terms of adoption and subsequent dispersion overland. While rice importance is dependent on particular topography and water availability, yam, taro and banana have penetrated far inland. Bananas were soon established in abundance on the coast, as well as in highlands, and even beyond the Eastern Rift ecological obstacle, which implies an intentional overland translocation. Their adoption was such that farmers developed a specific East African banana complex with marked intraregional differentiation (Perrier *et al.* 2018). Mutika triploid bananas are ubiquitous in the Lake Victoria region. In our sample, they are absent only in farms of the very dry northern shore of the Winam Gulf.

For its tropical part, the Columbian Exchange could be termed the Portuguese Exchange as well. The first objective of the Portuguese explorations, since the early 14th century and well before their interest in inland colonies, was the control of the spice trade with Asia, imposing the establishment of coastal stopovers and fortified trading posts all around Africa. There, they systematically carried plant seeds and propagules and tested them for the survival of their small colonies and garrisons (Ferrão *et al.* 2008). After the discovery of Brazil, they continued, introducing systematically American crops in Africa and Asia, so that Lopes and Pigafetta (1591; cited by Ferrão *et al.* 2008), referring to Saint Helena Island, could write: "every ship brings some plant, fruit or garden grass." The systematic introduction of American crops in so many sites was accomplished in close interaction with African coastal populations, who often adopted the Amerindian and Portuguese crop names. The new crop then diffused inland, essentially through African networks. In this overland phase, each crop could move independently, according to differential adoption dynamics in the societies and environments along their route (see Gallagher 2016). In a few cases, as for maize, caravan trade from North Africa also played a role, involving

intentionality and accelerating diffusion. When European colonial powers entered the interior scene in the 19th century, the American crops introduced by Portuguese had been adopted and adapted by most African farmers. Colonial administrations further developed particular crops (mainly maize and cassava) and introduced a few new ones. In our regional crop sample, only the diffusion of avocado and, to a lesser extent, that of sisal can be compared with that of the Renaissance package. Later, colonial policies were relayed by the independent governments, as shown by maize development (Smale & Jayne 2003).

With the same efficiency, the Portuguese also extended the westward distribution of non-American crops, such as mango and coconut, over Africa and the New World tropics (cfr section 3.1.2). The forced migration of African slaves participated significantly to the Columbian Exchange, however this westward tropical component essentially involved West Africa.

In our sample, the American crop package introduced by the Portuguese at Renaissance is well represented, with 12 crops. Nine of them, maize, cassava, sweet potato, common bean, groundnut, squash, chili, guava and papaya, are listed among the 14 crops of major frequency (Table 2). The three others, pineapple, soursop and tobacco are much less frequent. Millenia before, the dozen Renaissance introductions had diffused in all Pre-Columbian Tropical America, satisfying the needs of a wide diversity of people and adapting to highly diverse environments, between sea level and 3000 m elevations and at all tropical latitudes. These crops were mainly collected from coastal Brazil, but they had arrived there by overland diffusion from their domestication centers in Mesoamerica lowlands and highlands (maize, sweet potato, common bean, chili, squash, papaya), the Andes (common bean, squash), the lowlands of Southern South America (ground nut, cassava, tobacco) and northern South America (sweet potato, guava, pineapple). All of them are now pantropical, and some could even adapt to temperate conditions and/ or new uses (e.g. maize, squash and common bean). The same holds true for the most frequent Asian crop, banana. Although it originated in the hot and humid environment of South East Asia, it has become pantropical, adapting to a wide range of latitudes and elevations. Thus, the success of these major exotic crops appears to be related to their intrinsic ecological adaptability and economic qualities. More specific ecological and/ or economical reasons may be invoked for particular species, but the balance between advantages and drawbacks is highly dependent on the particular context. For example, maize is very generally credited with higher yield and labor productivity and lesser susceptibility to bird predation, but much higher susceptibility to climatic hazards. In the arid conditions of the northern shore of the Winam Gulf, we could observe that susceptibility to drought had a limited weight in the farmer's decision when opposed to the governmental support and/or economical incentives. At best, they lead the farmer to keep cultivating sorghum to mitigate the climatic risk. For fruits, the crop specific qualities appear more determinant. Guava and papaya reproduce very easily and demand limited labor. In the Nyanza province of Kenya, where guava is self-propagating, it is even disdained by farmers. The case of pineapple is different. This widely diffused crop is still attractive but demanding, and its long production cycle (16-18 months) is not compatible with the cash flow of a small farm. In the region of study, it seems it has evolved to a specialty production, for small farmers who can afford reserving a commercial plot to this fruit. The observations of tobacco and soursop were limited to one or two plants in the home garden. The soursops were occasionally sold on local markets, whereas the tobacco was grown for gifts.

Most modern introductions (five out of nine) are cash crops (cocoa, sisal, passion fruit, sunflower, vanilla). Only one, the avocado, introduced in colonial times, is now a highly frequent crop that compares with those of the Renaissance package. In fact, it was probably not available on coastal Brazil in the early 16th century. Indeed, our knowledge about the diffusion of the highland subspecies from Guatemala and Mexico is limited to the presence of avocados in Andean countries, and the origin of the lowland subspecies is still mysterious (there was no Pre-Columbian "West Indian avocado" in the West Indies). Another very common American plant introduced in modern times is sisal. This dual-purpose crop (fence and fiber) was certainly more frequent in the preceding farmer generation, but it is losing ground to cheap synthetic fibers.

Our observations on the distribution of American crops from the Columbian Exchange do not shed light on social drivers of crop adoption. On the contrary, these crops have been so widely adopted that no significant geographic pattern can be deduced from their distribution (Figure 8). Furthermore, their perception by farmers is fully consistent with their high frequency in our farm sample (Tables 2 and 3). Surprisingly, the geographic pattern observed in the distribution of agrobiodiversity (Figure 2) is only related to the distribution pattern of African crops (Figures 3-4) and Asian crops (Figures 5-7). Thus, differences among social farmer groups are most visible in the distribution of the most ancient crops, which can be explained by the differential abandonment or adoption of crops.

Differential crop abandonment may also be related to economic or political factors. For example, such factors may explain the lower crop diversity around Kampala, in relation with progressive urbanization, or to the northwest margin of the surveyed area, in relation with past conflicts and tensions on land tenure. Differential adoption of crops is particularly visible in the correlation between their distribution and ethnolinguistic or political borders (see the cases of yam, jute, African nightshade, Ethiopian kale, cleome, amaranth). It is sometimes expressed by taboos and/or ignorance on a given crop in a particular ethnolinguistic group. The cases of African eggplants, which diffused from West Africa, is particularly striking: the distribution of shum is restricted to Buganda and that of gilo to Buganda and Busoga (Figure 4). The Ugandan and Kenyan groups to the east have not adopted these crops. However, African eggplants are present in northern Tanzania (Adeniji & Aloyce 2012), so their Ugandan distribution does not correspond to the end of their eastward diffusion in the region. Another particularly interesting case concerns the diffusion of the jackfruit tree from southeastern Uganda into the Nyanza province of Kenya. The distribution of young trees on the Kenyan side indicates a recent and exclusive adoption by Luhya and Teso groups, very probably from those on the Ugandan side (Figure 7). The contact between the Luhya and the adjacent Luo groups should be determinant for the continued diffusion of the jackfruit. Just as linguistic studies have brought key information on large scale crop diffusion, regional studies should be very useful in detecting preferential diffusion pathways among ethnolinguistic groups.

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Reference cited

- Adeniji OT, and Aloyce A. 2012. Farmer's knowledge of horticultural traits and participatory selection of African eggplant varieties (*Solanum aethiopicum*) in Tanzania. *Tropicultura* 30: 3, 185–191.
- Allibert C. 2008. Austronesian migration and the establishment of the Malagasy civilization: contrasted readings in linguistics, archaeology, genetics and cultural anthropology. *Diogenes* 218: 7–16.
- Alpern SB. 2008. Exotic plants of Western Africa: where they came from and when. *History in Africa* 35: 63–102.
- Asouti E, & Fuller DQ. 2008. Trees and woodlands of South India: Archaeological perspectives. Left Coast Press.
- Bahuchet S, & Philippson G. 1998. Les plantes d'origine américaine en Afrique bantoue: Une approche linguistique. In M Chastanet (Ed.): *Plantes et Paysages d'Afrique. Une Histoire à Explorer*, Karthala-CRA, Paris, 87–116.
- Bedigian D. 2003. Evolution of sesame revisited: domestication, diversity and prospects. *Genetic Resources and Crop Evolution* 50: 779–787.
- Benor S, Demissew S, Hammer K, & Blattner FR. 2012. Genetic diversity and relationships in *Corchorus olitorius* (Malvaceae s.l.) inferred from molecular and morphological data. *Genetic Resources and Crop Evolution* 59 (6): 1125–1146.
- Blair MW, Soler A, & Cortés AJ. 2012. Diversification and population structure in common beans (*Phaseolus vulgaris* L.). *PLoS ONE* 7 (11): e49488. http://doi.org/10.1371/journal.pone.0049488
- Blasco M, Mar Naval M del, Zuriaga E, & Badenes ML. 2014. Genetic variation and diversity among loquat accessions. *Tree Genetics & Genomes* 10 (5): 1387–1398.
- Blench RM. 1998. The introduction and spread of New World crops in Nigeria: a historical and linguistic investigation. In M Chastanet (Ed.): *Plantes et paysages d'Afrique. Une histoire à explorer*, Karthala-CRA, Paris, 165–210.
- Blench RM. 2009. New reconstructions of West African economic plants. In J Adelberger, & R Leger (Eds.): Language, History and Reconstructions *Frankfurter Afrikanistische Blätter* 21: 1–39. Rüdiger Köppe Verlag.
- Boivin N, & Fuller DQ. 2009. Shell middens, ships and seeds: exploring coastal subsistence, maritime trade and the dispersal of domesticates in and around the ancient Arabian Peninsula. *Journal of World Prehistory* 22 (2): 113–180.
- Boivin N, Fuller DQ, & Crowther A. 2012. Old World globalization and the Columbian exchange: comparison and contrast. *World Archaeology* 44 (3): 452–469.
- Boivin N, Crowther A, Prendergast M, & Fuller DQ. 2014. Indian Ocean food globalisation and Africa. *African Archaeological Review* 31 (4): 547–581.
- Borgatti SP. 1999. Elicitation techniques for cultural domain analysis. *Enhanced Ethnographic Methods* 3: 115–151.
- Brown CH, Clement CR, Epps P, & Wichmann S. 2013. The paleobiolinguistics of domesticated chili pepper (*Capsicum* spp.). *Ethnobiology Letters* 4: 1–11.
- Brown CH, Luedeling E, Wichmann S, & Epps P. 2013. The paleobiolinguistics of domesticated squash (*Cucurbita* spp.). In M Quinlan, & D Lepofsky (Eds): *Explorations in Ethnobiology: The Legacy of Amadeo* Rea, Society of Ethnobiology, Department of Geography, University of North Texas, 133–161.
- Carter SE, Fresco LO, Jones PG, & Fairbairn JN. 1993. *Introduction and diffusion of cassava in Africa*. Ibadan, Nigeria: IITA.
- Chastanet M. 1998. *Plantes et paysages d'Afrique: une histoire à explorer*. Karthala-CRA Éditions, Paris.

- Chen H, Morrell PL, Ashworth VETM, de la Cruz M, & Clegg MT. 2009. Tracing the geographic origins of major avocado cultivars. *Journal of Heredity* 100 (1): 56–65.
- Chomicki G, & Renner SS. 2015. Watermelon origin solved with molecular phylogenetics including Linnaean material: another example of museomics. *New Phytologist* 205 (2): 526–532.
- Clement C, De Cristo-Araújo M, Coppens d'Eeckenbrugge G, Alves Pereira A, & Picanço-Rodrigues D. 2010. Origin and domestication of native Amazonian crops. *Diversity* 2 (1): 72–106.
- Coppens d'Eeckenbrugge G, Duval M-F, & Leal F. 2018. The pineapple success story: from domestication to pantropical diffusion. In R. Ming (Ed.): *Genetics and Genomics of Pineapple*, Springer, 1–25.
- Coppens d'Eeckenbrugge G, Restrepo MT, Mora E, & Jiménez D. 2007. Morphological and isozyme characterization of common papaya in Costa Rica. *Acta Horticulturae* 740: 109–120. Corley RHV, & Tinker PB. 2003. *The oil palm*. Blackwell, Oxford.
- Correll DS. 1953. Vanilla: Its botany, history, cultivation and economic import. *Economic Botany* 7 (4): 291–358.
- Crowther A, Horton M, Kotarba-Morley A, Prendergast M, Quintana Morales E, Wood M, Shipton C, Fuller DQ, Tibesasa R, Mills W, & Boivin N. 2014. Iron Age agriculture, fishing and trade in the Mafia Archipelago, Tanzania: new evidence from Ukunju Cave. *Azania* 49 (1): 21–24.
- Crowther A, Lucas L, Helm R, Horton M, Shipton C, Wright HT, Walshaw S, Pawlowicz M, Radimilahy C, Douka K, Picornell-Gelabert L, Fuller DQ, & Boivin NL *et al.* 2016. Ancient crops provide first archaeological signature of the westward Austronesian expansion. *Proceedings of the National Academy of Sciences* 113 (24): 6635–6640.
- Cubry P, Vigouroux Y, & François O. 2017. The empirical distribution of singletons for geographic samples of DNA sequences. *Frontiers in Genetics* 8: 139.
- Dalgado SR. 1936. Portuguese vocables in Asiatic Languages. English translation of 1913 Portuguese original by Anthony Xavier Soares. Baroda: Oriental Institute.
- Denham T. 2011. Early agriculture and plant domestication in New Guinea and Island Southeast Asia. *Current Anthropology* 52 (S4): S379–S395.
- Desjardin AE, & McCarthy SA. 2012. Milho, makka, and yu mai: early journeys of *Zea mays* to Asia. USDA National Agricultural Library. https://www.nal.usda.gov/research/maize/index.shtml, accessed Feb. 4, 2019.
- Diallo BO, Joly I, McKEY D, Hossaert M, & Chevallier MH. 2007. Genetic diversity of *Tamarindus indica* populations: any clues on the origin from its current distribution? *African Journal of Biotechnology* 6 (7): 853–860.
- Dillehay TD. 1989. Monte Verde. A Late Pleistocene settlement in Chile. Vol. 1, Palaeoenvironment and site context. Smithsonian Series in Archaeological Inquiry. Smithsonian Institution Press, Washington.
- Dillehay TD. 1999. The Late Pleistocene cultures of South America. *Evolutionary Anthropology: Issues, News, and Reviews* 7 (6): 206–216.
- Dillehay TD. 2011. From foraging to farming in the Andes: New perspectives on food production and social organization. Cambridge University Press.
- Erickson DL, Smith BD, Clarke AC, Sandweiss DH, & Tuross N. 2005. An Asian origin for a 10,000-year-old domesticated plant in the Americas. *Proceedings of the National Academy of Sciences* 102 (51): 18315–18320.
- Ferrão JEM, Caixinhas ML, & Liberato MC. 2008. A ecologia, as plantas e a interculturalidade. In AT de Matos, & M Ferreira Lages (Eds): *Portugal: percursos de interculturalidade*Lisboa: Alto Comissariado para a Imigração e Diálogo Intercultural (ACIDI, I.P.), 31–223.
- Flora of Zimbabwe. 2018. *Casimiroa edulis* La Llave. https://www.zimbabweflora.co.zw/speciesdata/species.php?species_id=133100, Accessed Feb. 4, 2019.

- Freitas F. 2018. The South Atlantic Columbian Exchange. https://fredericofreitas.org/2011/05/31/ the-south-atlantic-columbian-exchange/ Accessed Feb. 4, 2019.
- Fuller DQ. 2002. Fifty years of archaeobotanical studies in India: laying a solid foundation. In S Settar, & R Korisettar (Eds.): *Indian archaeology in retrospect. Volume III. Archaeology and interactive discipline.* Indian Council for Historical Research, 247–364.
- Fuller DQ. 2003. Further evidence on the prehistory of sesame. *Asian Agri-History* 7 (2): 127–137. Fuller DQ. 2007. Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the Old World. *Annals of Botany* 100 (5): 903–924.
- Fuller DQ, & Boivin N. 2009. Crops, cattle and commensals across the Indian Ocean, *Études océan Indien*, 42–43 (2012): 2–26. http://doi.org/10.4000/oceanindien.698
- Fuller DQ, Boivin N, Hoogervorst T, & Allaby R. 2011. Across the Indian Ocean: the prehistoric movement of plants and animals. *Antiquity* 85 (328): 544–558.
- Gallagher D. 2016. American plants in Sub-Saharan Africa: a review of the archaeological evidence. *Azania* 51 (1) 24–61.
- Giblin JD, & Fuller DQ. 2011. First and second millennium AD agriculture in Rwanda: Archaeobotanical finds and radiocarbon dates from seven sites. *Vegetation History and Archaeobotany* 20 (4): 253–265.
- Goli AE. 1997. Bibliographical review. In J Heller, F Begemann, & J Mushonga (Eds.): *Bambara groundnut Vigna subterranea (L.) Verdc. Promoting the conservation and use of underutilized and neglected crops*. Institute of Plant genetics and Crop Plant Research, Gatersleben. Department of Research & Specialist Services, Harare. International Plant Genetic Resources Institute, Rome. 4–10.
- Gunn BF, Baudouin L, & Olsen KM. 2011. Independent origins of cultivated coconut (*Cocos nucifera* L.) in the Old World tropics. *Plos One* 6 (6): e21143.
- Guo J, Wang Y, Song C, Zhou J, Qiu L, Huang H, & Wang Y. 2010. A single origin and moderate bottleneck during domestication of soybean (*Glycine max*): implications from microsatellites and nucleotide sequences. *Annals of Botany* 106 (3): 505–514.
- Henley NM. 1969. A psychological study of the semantics of animal terms. *Journal of Verbal Learning and Verbal Behavior* 8 (2): 176–184.
- Ho PT. 1955. The introduction of American food plants into China. *American Anthropologist* 57 (2): 191–201.
- Holler J. 2007. American Crops, Africa. In B Thomas (Ed.): Encyclopedia of Western Colonialism since 1450. Macmillan Reference, USA, Vol 1, 38–41.
- Jenkins JA. 1948. The origin of the cultivated tomato. *Economic Botany* 2 (4): 379–392.
- Jones M, Hunt H, Lightfoot E, Lister D, Liu X, & Motuzaite-Matuzeviciute G. 2011. Food globalization in prehistory. *World Archaeology* 43 (4): 665–675,
- Joshi AB, Gadwal VR, & Hardas MW. 1974. Okra. In JB Hutchinson (Ed.): Evolutionary studies in world crops. Diversity and change in the Indian sub-continent. Cambridge University Press, London.
- Katende B. 2000. *Useful Trees and Shrubs for Uganda*. Technical handbook No 10, Identification, Propagation and Management for Agricultural and Pastoral Communities.
- Katz E. 1998. Plantes américaines au Sud Congo. In M Chastanet (Ed.): *Plantes et paysages d'Afrique: Une histoire à explorer*. Karthala-CRA, Paris, 283–322.
- Khoury CK, Castañeda-Alvarez NP, Achicanoy HA, Sosa CC, Bernau V, Kassa MT, ... Struik PC. 2015. Crop wild relatives of pigeonpea [*Cajanus cajan* (L.) Millsp.]: distributions, ex situ conservation status, and potential genetic resources for abiotic stress tolerance. *Biological Conservation* 184: 259–270.
- Kistler L, Montenegro A, Smith BD, Gifford JA, Green RE, Newsom LA, & Shapiro B. 2014. Transoceanic drift and the domestication of African bottle gourds in the Americas. *Proceedings of the National Academy of Sciences* 111 (8): 2937–2941.

- Labeyrie V, Thomas M, Muthamia ZK, & Leclerc C. 2016. Seed exchange networks, ethnicity, and sorghum diversity. *Proceedings of the National Academy of Sciences* 113 (1): 98–103.
- Leclerc C, & Coppens d'Eeckenbrugge G. 2012. Social organization of crop genetic diversity. The G × E × S interaction model. *Diversity* 4 (1): 1–32.
- Madeira Santos ME, & Ferraz Torrão MM. 1998. Entre l'Amérique et l'Afrique, les îles du Capvert et Sao Tomé: Les cheminements des milhos (mil, sorgho et maïs). In M Chastanet (Ed.): *Plantes et paysages d'Afrique. Une histoire à explorer*, Karthala-CRA, Paris, 69–83.
- Maley J. 1999. L'expansion du palmier à huile (*Elaeis guineensis*) en Afrique Centrale au cours des trois derniers millénaires: nouvelles données et interprétations. In S Bahuchet, D Bley, H. Pagezy, & N Vernazza-Licht (Eds.): *L'homme et la forêt tropicale*). Editions du Berger, Châteauneuf de Grasse, 237–254.
- Manning K, Pelling R, Higham T, Schwenniger J-L, & Fuller DQ. 2011. 4500-Year old domesticated pearl millet (*Pennisetum glaucum*) from the Tilemsi Valley, Mali: new insights into an alternative cereal domestication pathway. *Journal of Archaeological Science* 38 (2): 312–322.
- McCann J. 2001. Maize and grace: history, corn, and Africa's new landscapes, 1500–1999. *Comparative Studies in Society and History* 43 (2): 246–272.
- Mather KA, Molina J, Flowers JM, Rubinstein S, Rauh BL, Lawton-Rauh A, Caicedo AL, McNally KL, & Purugganan MD. 2010. Migration, isolation and hybridization in island crop populations: the case of Madagascar rice. *Molecular Ecology* 19 (22): 4892–4905.
- Miracle MP. 1966. *Maize in tropical Africa. Maize in Tropical Africa*. University of Wisconsin Press, Madison, Milwaukee, London.
- Moore PH, Paterson AH, & Tew T. 2014. Sugarcane: the crop, the plant, and domestication. In PH Moore & FC Botha (Eds.): *Sugarcane: Physiology, Biochemistry, and Functional Biology*): John Wiley & Sons Ltd., Chichester, UK, 1–17.
- Morton JF. 1966. The soursop, or guanabana (*Annona muricata* Linn.). *Proceedings of the Florida State Horticultural Society* 12: 355–366.
- Morton JF. 1987. *Fruits of warm climates*. JF Morton. https://hort.purdue.edu/newcrop/morton/index.html, accessed Feb. 4, 2019.
- NRC. 2008. Lost Crops of Africa: Volume III: Fruits. Washington, D.C.: National Academies Press.
- Okello DK, Biruma M, & Deom CM. 2010. Overview of groundnuts research in Uganda: past, present and future. *African Journal of Biotechnology* 9 (39): 6448–6459.
- Orwa C, Mutua A, Kindt R, Jamnadass R, & Simons AB. 2009. Agroforestree database: a tree reference and selection guide version 4.0. World Agroforestry Centre, Kenya.
- Paris HS. 2015. Origin and emergence of the sweet dessert watermelon, *Citrullus lanatus*. *Annals of Botany* 116 (2): 133–148.
- Perrier X, Jenny C, Bakry F, Karamura D, Kitavi M, Dubois C, Hervouet C, Philippson G, & De Langhe E. 2018. East African diploid and triploid bananas: a genetic complex transported from South-East Asia. *Annals of Botany* XX: 1–18.
- Pooley S. 2009. Jan van Riebeeck as pioneering explorer and conservator of natural resources at the Cape of Good Hope (1652–62). *Environment and History* 15 (1): 3–33.
- PROTA4U. 2018. Plant Resources of Tropical Africa. *Ressources végétales de l'Afrique tropicale*. https://www.prota4u.org/database/.
- Purseglove, JW. 1985. *Tropical crops. Monocotyledons*. Longman Scientific & Technical, Harlow, England.
- Purseglove, JW. 1987. *Tropical crops. Dicotyledons*. Longman Scientific & Technical, Harlow, England.
- Quattrocchi U. 2006. CRC World dictionary of grasses: common names, scientific names, eponyms, synonyms, and etymology 3 Volume Set: V. 2. (1st ed.). Boca Ratón, Florida: CRC Press.

- Ranil RHG, Prohens J, Aubriot X, Niran HML, Plazas M, Fonseka RM, Vilanova S, Fonseka HH, Gramazio P, & Knapp S. 2017. *Solanum insanum* L. (subgenus *Leptostemonum* Bitter, Solanaceae), the neglected wild progenitor of eggplant (*S. melongena* L.): a review of taxonomy, characteristics and uses aimed at its enhancement for improved eggplant breeding. *Genetic Resources and Crop Evolution* 64 (7): 1707–1722.
- Reynolds AG. 2017. The grapevine, viticulture, and winemaking: a brief introduction. In B Meng, GP Martelli, DA Golino, & M Fuchs (Eds.): *Grapevine Viruses: Molecular Biology, Diagnostics and Management*), Springer International Publishing, 3–29.
- Roosevelt AC, da Costa ML, Lopes Machado C, Michab M, Mercier N, Valladas H, Feathers J Barnett W, Imazio da Silveira M, Henderson A, Sliva J, Chernoff B, D. Reese S, Holman JA, Toth N, & Schick K. 1996. Paleoindian cave dwellers in the Amazon: the peopling of the Americas. *Science* 272 (5260): 373–384.
- Roullier C, Rossel G, Tay D, Mckey D, & Lebot V. 2011. Combining chloroplast and nuclear microsatellites to investigate origin and dispersal of New World sweet potato landraces. *Molecular Ecology* 20 (19): 3963–3977.
- Russell-Wood AJR. 1998. The Portuguese empire, 1415–1808: a world on the move. JHU Press. Sangiri C, Kaga A,C, Tomooka N, Vaughan D, & Srinives P. 2007. Genetic diversity of the mungbean (Vigna radiata, Leguminosae) genepool on the basis of microsatellite analysis. Australian Journal of Botany 55: 837–847.
- dos Santos J. 1891. Ethiopia Oriental. Bibliotheca de Classicos Portuguezes, Lisbon.
- Sathees N. 2015. Review on Distribution, Nutritional and Medicinal Values of Casimiroa edulus Llave- An Underutilized Fruit in Ethiopia. *American-Eurasian Journal of Agricultural and Environmental Sciences* 15 (8): 1574–1583.
- Sauer JD. 1967. Plants and Man on the Seychelles coast. A study in historical biogeography. University of Wisconsin Press, Madison, Milwaukee, London.
- Smale M, & Jayne T. 2003. *Maize in Eastern and Southern Africa: "seeds" of success in retrospect*. International Food Policy Research Institute, ETPD Discussion paper n° 97.
- Smale M, De Groote H, & Owuor G. 2006. Biodiversity of maize on farms in Kenya. Brief 25: 1–4. https://www.bioversityinternational.org/e-library/publications/detail/biodiversity-of-maize-on-farms-in-kenya/
- Smith BD. 2014. The domestication of *Helianthus annuus* L. (sunflower). *Vegetation History and Archaeobotany* 23 (1): 57–74.
- Smith JJ, & Borgatti SP. 1997. Salience counts—and so does accuracy: correcting and updating a measure for free-list-item salience. *Journal of Linguistic Anthropology* 7 (2): 208–209.
- Sutrop U. 2001. List task and a cognitive salience index. Field Methods 13 (3): 263-276.
- Team RC. 2018. R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. 2013.
- Van Laere R, & Dubois L. 1953. L'avocatier. Son introduction et sa culture au Congo Belge et au Ruanda-Urundi. Direction de l'Agriculture, de l'Élevage et de la Colonisation, Ministère des Colonies.
- Van Linschoten JH. 1610. *Histoire de la navigation de Jean Hughes de Linscot Hollandois et de son voyage en Indes Orientales*. Imprimerie de Théodore Pierre, Amsterdam.
- Varshney RK, Saxena RK, Upadhyaya HD, Khan AW, Yu Y, Kim C, Rathore A, Kim D, Kim J, An S, Kumar V, Anuradha G, Narasimhan Yamini K, Zhang W, Muniswamy S, Kim JS, Varma Penmetsa R, von Wettberg E, & Datta SK. 2017. Whole-genome resequencing of 292 pigeonpea accessions identifies genomic regions associated with domestication and agronomic traits. *Nature Genetics* 49 (7): 1082–1088.
- Vernet-Habasque T. 2018. Reconsidering long-distance connections between the East African coast and the hinterland ca.1550–1800. New evidence from historical sources, communication

- presented at ANR « GlobAfrica » IFRA JOOUST Workshop, Dissemination of American Plants and Historical Changes in the African Great Lakes Region, Nairobi, November 13-15, 2018.
- Walshaw SC. 2010. Converting to rice: urbanization, islamization and crops on Pemba Island, Tanzania, AD 700–1500. *World Archaeology* 42 (1): 137–154.
- Wang Y, Shahid MQ, Lin S, Chen C, & Hu C. 2017. Footprints of domestication revealed by RAD-tag resequencing in loquat: SNP data reveals a non-significant domestication bottleneck and a single domestication event. *BMC Genomics* 18 (1): 354.
- Watson AM. 1983. Agricultural innovation in the early Islamic world; the diffusion of crops and farming techniques, 700–1100, Cambridge University Press.
- Wencélius J, Garine E, & Raimond C. 2017. FLARES.
- Wendel JF, Brubaker CL, & Seelanan T. 2010. The origin and evolution of *Gossypium*. In JM Stewart, DM Oosterhuis, JJ Heitholt, & JR Mauney (Eds.): *Physiology of Cotton*. Springer Netherlands, Dordrecht, 1–18.
- Winchell F, Stevens CJ, Murphy C, Champion L, & Fuller D. 2017. Evidence for sorghum domestication in fourth millennium BC Eastern Sudan: spikelet morphology from ceramic impressions of the Butana group. *Current Anthropology* 58 (5): 673–683.
- Winter JC. 2000. *Tobacco use by Native North Americans: sacred smoke and silent killer*. (Vol. 236). University of Oklahoma Press.
- Wright RP, Lentz DL, Beaubien HF, & Kimbrough CK. 2012. New evidence for jute (*Corchorus capsularis* L.) in the Indus civilization. *Archaeological and Anthropological Sciences* 4 (2): 137–143.
- Yadav D, & Singh S. 2017. Mango: history origin and distribution. *Journal of Pharmacognosy and Phytochemistry* 6 (6): 1257–1262.
- Yockteng R, Coppens d'Eeckenbrugge G, & Souza-Chies TT. 2011. *Passiflora*. In C Kole (Ed.): *Wild Crop Relatives: Genomic and Breeding Resources*. Springer, 129–171.