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Elaeis oleifera (Kunth) Cortés: A neglected palm from the Ecuadorian Amazon

Elaeis oleifera (Kunth) Cortés: una palma olvidada de la Amazonía ecuatoriana

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ABSTRACT.- Ecuador has an outstanding diversity of palm species, some of which have been well studied, certain others remain an enigma, however. A particular case is the American oil palm, *Elaeis oleifera* (Kunth) Cortés, first recorded in Ecuador in 1986. The genus *Elaeis* has a trans-Atlantic (Africa-America) distribution, with *E. oleifera* from the Neotropics, and *E. guineensis* Jacq. from Africa. It has been hypothesized that *E. oleifera* derives from populations of *E. guineensis*, which diverged 15 million years ago. At the local level, the populations of *E. oleifera* have a disjunct distribution, with isolated populations in Central America, the Amazonia basin, the Guianas, Chocó and the Caribbean Cost of Colombia and Venezuela, frequently associated with human or archaeological settlements. Despite the spatial and historical separation between the two species, there are no reproductive barriers to the generation of fertile hybrids. This important reproductive characteristic has allowed *E. oleifera* to become a major source of genetic variation for the improvement and adaptability of commercial populations of *E. guineensis* throughout the tropics. The Ecuadorian populations of *E. oleifera* from Taisha, with morphological, reproductive and agronomically important biochemical characteristics, have been used for the creation of commercial hybrids, which today are planted in many tropical regions.

KEYWORDS: Ecuador, *Elaeis guineensis*, fruit abscission, oil palm, palms.

RESUMEN. - El conocimiento sobre la biología de las palmas ecuatorianas es todavía limitado. Un caso particular constituye la palmera aceitera americana, *Elaeis oleifera* (Kunth) Cortés descrita para Ecuador en el año 1986. El género *Elaeis* tiene una distribución trans-Atlántica (África-América), con *E. oleifera* proveniente del Neotrópico y *E. guineensis* Jacq. del África. Se ha sugerido como hipótesis que *E. oleifera* deriva de poblaciones de *E. guineensis*, las cuales divergieron hace 15 millones de años. A nivel local, las poblaciones de *E. oleifera* presentan una distribución disyunta, con poblaciones aisladas a lo largo de la América Central, Amazonía, Guyanas, el Chocó y la costa caribeña de Colombia y Venezuela. Están frecuentemente asociadas a asentamientos humanos o arqueológicos. A pesar de la separación espacial e histórica entre ambas especies, no existen barreras reproductivas para la generación de híbridos fértiles. Esta importante característica reproductiva ha permitido que *E. oleifera* constituya actualmente la principal fuente de información genética para el mejoramiento y adaptabilidad de las poblaciones comerciales de *E. guineensis* a lo largo del planeta. Las poblaciones ecuatorianas de *E. oleifera* provenientes de Taisha (Provincia de Morona Santiago) –con características morfológicas, reproductivas y bioquímicas agronómicamente importantes– han sido utilizadas para la creación de híbridos comerciales que, actualmente, se siembran en las regiones tropicales.

PALABRAS CLAVES: abscisión del fruto, Ecuador, palma aceitera, *Elaeis guineensis*.

INTRODUCTION

Ecuador harbors one of the highest palm species diversities in the world, with more than 136 species (Valencia and Montúfar 2013). In spite of this extraordinary diversity, and the multitude of uses of many palm species, much knowledge remains to be acquired about the natural history. One example is the little-studied species *Elaeis oleifera* (Kunth) Cortés (e.g. the American oil palm) which has a high potential for the oleaginous industry. The objective of this paper is to review the literature available on the Ecuadorian populations of *E. oleifera.* As information is limited, this paper represents progress towards increasing our knowledge about the natural history, distribution and characteristics of this intriguing yet poorly studied tropical native Ecuadorian palm.

The genus *Elaeis*.- The genus *Elaeis* (subfamily Cocoseae, subtribe *Elaeidinae;* Dransfield et al. 2008) of the palm family (Arecaceae) is present in the tropical regions of Africa and in Central and South America. *Elaeis* is a small palm genus comprised of two species: *E. oleifera,* from the Americas, and its sister species *Elaeis guineensis* Jacq., from Africa, which us commonly known as the African oil palm. *Elaeis guineensis* is widely cultivated throughout the tropical regions for its fruit, which yields palm oil, and is globally considered the most important source of edible vegetable oil in both production and trade, accounting for one-third of worldwide vegetable oil production in 2009 (Murphy 2014; Vijay et al. 2016). In recent decades, scientific interest has led to research being focused on the physiology, genetics and genomics of *E. guineensis;* in particular the agronomic characteristics related to yield, and the remarkable capacity to synthesize and store lipids in both the fruit mesocarp (palm oil) and the kernel (kernel oil) tissues (Murphy 2006; Murphy 2009; Bourgis et al. 2011; Tranbarger et al. 2011; Dussert et al. 2013; Singh et al. 2013a; b; Corley and Tinker 2016; Guerin et al. 2016). Furthermore, there is a high quality draft of the *E. guineensis* genome, and "omic" technologies, bioinformatics, marker assisted selection (MAS) and transgenic technologies have been and continue to be developed in order to accelerate genetic improvements (Singh et al. 2013; Murphy 2014).

The biogeography of the *Elaeis* genus is still a puzzle. Most palm genera are strictly endemic and have evolved within the context of a specific continental area (Henderson et al. 1995); however, the genus *Elaeis* displays a trans-Atlantic disjunction given its presence on the African and American continents (Renner 2004). It has been inferred that American *E. oleifera* populations are derived from ancient *Elaeis* populations which dispersed from Africa via sea currents before the end of the Miocene (Renner 2004; Dransfield et al. 2008). Based on two different estimates, one on a dated molecular phylogeny of the palm family, and the other on *Elaeis* genome sequences, these species diverged from 15–20, or 51 million years ago, respectively (Baker and Couvreur 2013; Singh et al. 2013). The species that we now know as *Elaeis* oleifera was originally described with collections from Cartagena, Colombia, as *Alfonsia oleifera* by Kunth (1815). It was later transferred to *Elaeis* by Cortés as *Elaeis oleifera* (Kunth) Cortés (1897), and still later it was recombined as *Corozo oleifera* (Kunth) Bailey (1933). In parallel, another species was described from Brasil, *Elaeis* melanococca Mart. (1824), but that name is now treated as a synonym of *Elaeis oleifera.*

Elaeis oleifera has disjunct populations located in Central America (Honduras to Panama), the Amazonia basin, the Guianas, the Chocó and the Caribbean coast of Colombia and Venezuela, growing naturally in the tropical forest at 0–500 meters above sea level (masl), with optimal temperatures of 23–30 ºC and an optimal annual rainfall of 1400–2500 mm (Ecocrop 2007). Despite their evolutionary distance, *E. oleifera* can be crossed with *E. guineensis* to form interspecific hybrids (O x G hybrids) which can be fertile (Singh et al. 2013b; Corley and Tinker 2016). *E. oleifera* is thus used as the female parent source for genetic variation that can be useful in breeding programs that target the creation of improved commercial varieties of *E. guineensis* (Barcelos et al. 2015).

At the morphological level, while the two species are fairly similar in general appearance, there are clear differences in their vegetative and reproductive structures, between *E. oleifera* and *E. guineensis* which reflect their trans-Atlantic disjunction (Corley and Tinker 2016; Table 1). Firstly, *E. oleifera* is shorter, which may be the result of a slower annual height increase as compared with *E. guineensis,* and *E. oleifera* can display procumbent trunk growth. While root development is similar to *E. guineensis,* adventitious roots can develop along the entire length of the procumbent trunk. The leaf structure of *E. oleifera* is markedly different from *E. guineensis*, in that the leaflets of *E. oleifera* lie in a single plane, while the leaflets of *E. guineensis* are arranged in groups and project in different planes. Another striking difference is the fibrous spathe that covers the female inflorescence of *E. oleifera*, which remains until the fruit have ripened. *Elaeis oleifera* fruit are smaller and are often found to be parthenocarpic, while the fruit bunches typically display a conical shape, pointed at the top (Dranfield et al. 2008; Balslev 1987; Corley and Tinker 2016). *Elaeis oleifera* is often found in damp, swampy areas, near riverbanks or in pastureland. It is shade tolerant in comparison with

E. guineensis, which can be considered a pioneer species and is intolerant of shade. A more detailed list of the reported differences between *E. oleifera* and *E. guineensis* is found in Table 1.

***Elaeis* in Ecuador,-** The history of *Elaeis* in Ecuador is heavily influenced by the introduction of the African oil palm, *E. guineensis,* as a crop for oil production. The first reported introduction of *Elaeis guineensis* to Ecuador was in 1940 at the tropical experimental station of the Instituto Nacional de Investigaciones Agropecuarias (INIAP, Los Ríos Province) in Pichilingue; and in 1959 it was introduced to the Estación Agroforestal de San Lorenzo (Esmeraldas Province, Acosta-Solís 1971). *Elaeis guineensis* is currently cultivated in four main areas in Ecuador: Quinindé (Esmeraldas), San Lorenzo (Esmeraldas), the Southern Coast (El Oro, Guayas) and the Amazonia (Estimations of Asociación Nacional de Cultivadores de Palma Africana del Ecuador, ANCUPA in 2005 and in Danec S.A. 2018). According to current estimates, oil palm plantations constitute approximately 300 kha of total area harvested in the four zones, making Ecuador the third largest producer (following Colombia and Guatemala) of palm and kernel oil in the Americas, with 620 000 MT produced in 2016 (FAOSTAT 2018; IndexMundi 2018; United States Department of Agriculture - USDA 2018; Table 2). However, as elsewhere in the tropics, the development of the Ecuadorian oil palm industry has been controversial; mainly due to the conversion of tropical rain forest into areas for oil palm cultivation, resulting in a loss of biodiversity along with potential negative socio-economic consequences (Vijay et al. 2016; Marin-Burgos and Clancy 2017).

By 1965, a 39 ha experimental plantation of *E. oleifera* —apparently planted with seeds imported from outside of Ecuador— was established at the experimental INIAP (Instituto Nacional de Investigaciones Agropecuarias) station in Santo Domingo de los Tsáchilas (Borgtoft Pedersen and Balslev 1993). The first botanical report of native *E. oleifera* in Ecuador dates from 1986 (Balslev and Henderson 1986; Balslev 1987). The botanists Henrik Balslev (Aarhus University, Denmark) and Andrew Henderson (New York Botanical Garden) described the first native *E. oleifera* population of 10 individuals in the locality of Taisha (450 masl) in the province of Morona Santiago (Ecuadorian Amazon). Later, wild *E. oleifera* populations were also discovered in the Pastaza (Figure 1; AAU Herbarium Database 1990, 2011) and Orellana provinces (Nuevo Rocafuerte, Barba et al. 2014). The Danec S.A. Company, with French partners CIRAD/PalmElit SAS, conducted their own prospection in 2003 in the Taisha area and planted sample populations of this *E. oleifera*-Taisha material in Quinindé and in Shushufindi, Sucumbíos (Figure 2). INIAP maintains a seed bank co-

Table 1. Morphological differences between *Elaeis oleifera* (Kunth) Cortés and *E. guineensis.*

Characteristic	*E. oleifera*	*E. guineensis*
Habitat	-damp or swampy areas; near or on the riverbank; pasture land; tolerant of shade	-disturbed areas; can act as a pioneer species; difficult to assess natural habitat because often associated with human habitation; intolerant of shade
Dispersal vector	-humans, undocumented	-animals (including humans) some bird species
Stem	-short and prostrate; only the terminal portion with the leaves is erect. -1-6m tall, 40 cm diameter (trunks lying on the soil for a distance of over 3-7 m)	-erect -10 m tall, 30-50 cm diameter
Leaf /blade	-20-50 leaves -sheath 20-40 cm long -petiole 1.5-3 m long covered by short and thick spines on margins, no basal swellings on the petiole -rachis 2.9-6 m long -blade 3 to 6 m long and 2.5 m wide	-40-60 leaves -sheath 5 m long -petiole > 1.2 m long covered by short lateral spines -rachis *c.a.* 8 m
Pinnae (leaflets)	-30-90 linear and acuminate pinnae per side, middle ones up to 1 (1.2) m long, 4-6 cm wide -regularly distributed along rachis and spreading in one plane	- >100 linear and acuminate pinnae per side, middle up to 1.3 m long, 6 cm wide -arranged in groups (2 to 4) and spreading in different planes
Roots	-roots develop along whole length of procumbent trunk	-no procumbent trunk growth
Fruit	-ellipsoid-oblong, 2.5-3 cm long, 1.8-2 cm diam. -weight range from 1.7 – 5.0 g in Colombia, 5-13 g in Brazil -yellowish orange to red. -prominent apical stigmatic residue -commonly parthenocarpic fruit (up to 90%)	-spherical to ovoid, 2-5 cm long - weight range from 6 to 20 g -red to black
Fruit Bunch	-conical bunches 8 to 12 (30) kg -max. number of fertile fruits reported was 5000	-ovoid bunches up to 100kg -500 to 4000 fruit per bunch reported
Male inflorescence	-100 to 200 spikelets, 5 to 15 cm -smaller with shorter anthers -long peduncle	-long, finger-like, cilindrical spikelets, 10-20 cm lenght
Female inflorescence	-persistent spathe -long penducle -flowers sunk in the body of the spikelet -period of anthesis is erratic and may last for 3 or 4 weeks or have two peaks -long peduncle	-flowers subtended by a long bract -period of anthesis in 36 to 48 hours to 1 week.
Pollinator	-*Grasidius hybridus* O'Brien and Beserra	-*Elaeidobius kamerunicus* Faust
Pollen	-elliptical shaped	-triangular shaped
Abscission Zone	-simple, multiple abscission zone cell layers with aligned nuclei not observed -vascular tissue appears to be lignified in abscission zone.	-complex, multiple abscission zone cell layers characterized by aligned nuclei -vascular tissue not lignified in abscission zone.

Compiled from the following references: Zeven 1964; Borgtoft Pedersen and Balslev 1993; Henderson 1995; Smith 2015; Corley and Tinker 2016; Fooyontphanich et al. 2016; Auffray et al. 2017; http://www.fao.ors/faostat

Table 2. Estimation of cultivated area of *E. guineensis* and *E. oleifera* x *E. guineensis* hybrids in Ecuador. Estimations from Asociación Nacional de Cultivadores de Palma Aceitera del Ecuador ANCUPA and Danec S.A. in 2018.

Zone	Area Total (ha)	*E. guineensis* (ha)	Hybrids Total (ha)	Hybrids Coari[1] (ha)	Hybrids Taisha[2] (ha)	Hybrids others (ha)
Quinindé	210 000	203 500	6 500	5 000	1 000	500
San Lorenzo	25 000	2 500	22 500	19 500	2 500	500
Southern Coast	30 000	30 000	0			
Amazonia	30 000	15 000	15 000	11 800	3 000	200
TOTAL	**295 000**	**251 000**	**44 000**	**36 300**	**6 500**	**1 200**

[1] Coarí is an *E. oleifera* accession from Brazil. [2] Taisha is an *E. oleifera* accession from Ecuador.

llection of *E. oleifera* from different Ecuadorian provinces, but very little information about this collection has been made public (Ortega Cedillo et al. 2016). Beyond these initial reports, no comprehensive description of the wild *E. oleifera* populations present in Ecuador has been made. Thus far, individual samples in Ecuador have been reported in the eastern lowlands, mainly in the Morona Santiago (Taisha, 450 masl) and Pastaza (500 masl) provinces, on poorly drained soil and in fluvial plains (Borchsenius et al. 1998). The disjointed local distribution of *E. oleifera* in the Amazon has been explained by the anthropogenic influence on the palm's dispersal (Balée 1989).

Genetic and phenotypic diversity of *Elaeis* in Ecuador.- Several studies have used genetic markers to describe the genetic and phenotypic diversity of *E. oleifera;* however, these studies have examined only (i) seed accessions from regional gene banks, or (ii) individuals cultivated ex situ. To the best of our knowledge, no studies of natural populations in situ have been reported. Nevertheless, a study of ex situ individuals from different countries with Simple Sequence Repeats (SSRs) markers revealed that *E. oleifera* from Taisha (Morona Santiago) are, surprisingly, more genetically similar to populations from Pacific Colombia (Valley of Sinú, Antioquia) than the geographically adjacent populations from the Peruvian Amazonia (Arias et al. 2015). At the phenotypic level, while yield components (FFB-fresh fruit bunches, kg per palm year^{-1}; BN-number of bunches, palm year^{-1}; MBW-mean bunch weight, kg) were lower for Taisha individuals, other unique qualitative traits were different in comparison with populations from Colombia, Peru, and Brazil, including: (i) 14–21% higher Mesocarp/Fruit (M/F) ratio (63%); (ii) higher Fruit/Bunch (F/B) ratio for parthenocarpic

Figure 1 Wild population of *E. oleifera* from Pastaza Province, Ecuador. **(A)** An adult individual in the primary forest; **(B)** Male inflorescence at early stage of development; **(C)** Spines along of the base of the petiole. Source: Henrik Balslev (#Balslev, H. 8512), AAU Herbarium Data Base.

fruit; (iii) the absence of peduncular bracts; (iv) green immature fruits; and (v) longer spikelet stalks (Arias et al. 2015). In Ecuador, the genetic diversity of 40 individuals from the germplasm bank of INIAP in Santo Domingo was analyzed with microsatellites markers, and a low endogamy and high genetic variability was shown (Ortega Cedillo et al. 2016).

Pollination of *E. oleifera*.- While there have been a number of studies on the pollination process of *E. guineensis*, the pollination of *E. oleifera* is poorly understood (Corley and Tinker 2016; Auffray et al. 2017). Evidence shows that the genus *Elaeidobius* of the Coleoptera order, in particular *Elaeidobius kamerunicus*, is the natural pollinator of *E. guineensis.* For *E. oleifera,* the derelomine weevil, *Grasidius hybridus* (Coleoptera: Curculionidae) was collected in a natural population of *E. oleifera* in Taisha and is apparently a natural pollinator of this species (Auffray et al. 2017). In addition, *G. hybridus* was reported as a crepuscular pollinator, while *E. kamerunicus* was actively present in the morning on ex situ populations of *E. oleifera*-Taisha cultivated in the Ecuadorean Amazonia. In South America, O x G hybrids must be pollinated manually with *E. guineensis* pollen, due to the poor viability of hybrid pollen, and the hybrid inflorescences are less attractive to *E. kamerunicus*. Therefore, research on the pollination process of *E. oleifera* and O x G hybrids is an important area of study (Meléndez and Ponce 2016).

Ethnobotanical Uses of *E. oleifera*.- In Ecuador, the only indigenous name reported in the literature comes from the Achuar communities, where it is known as *Yunchik* (Borchsenius et al. 1998). No ethnobotanical uses have been formally reported from Ecuadorean populations of *E. oleifera.* However, there is a limited amount of information from other countries about traditional uses, which include folk remedies, beverages, insect-repellents and cooking (Smith 2015). Interestingly, both *E. oleifera* and *E. guineensis* are typically closely associated with human settlements and movement (Smith 2015).

Genetic breeding programs and *E. oleifera* traits of interest.- The introgression of genetic information from *E. oleifera* to the widely cultivated *E. guineensis* through the creation of O x G hybrids is a major objective of the oil palm industry, mainly due to the resistance of *E. oleifera* to lethal bud rot or fatal yellowing disease (Pudrición del Cogollo, PC; Corley and Tinker 2016; Barcelos et al. 2015). Oil palm breeders have been successful in selecting O x G hybrids with tolerance to lethal bud rot, and which have yield components comparable to the average of *E. guineensis* crosses. In addition, there is much interest in transferring the higher oleic acid content of *E. oleifera* to *E. guineensis*. Recently, a study with *E. oleifera*-Taisha showed the results of an 8-year evaluation of O x G hybrids (*E. oleifera*-Taisha x *E. guineensis*-Avros). This study revealed the outstanding potential of Ecuadorean populations of *E. oleifera* from Taisha. For example, some of these O x G hybrids showed tolerance to PC and to other diseases, had low annual growth rates, uniform anthesis, very few spathes that cover the inflorescence, and a long peduncle that makes for easier harvest (Barba and Baquero 2013). Additionally, oil derived from the fruits of hybrids had a higher concentration of oleic acid, which is attractive to the vegetable oil industry. In another article it was found that *E. oleifera*-Taisha and an intraspecific *E. oleifera* hybrid "Manaos/Taisha" had total fruit weights in the range of the *E. guineensis* (Lieb et al. 2017).

A recent study found *E. oleifera*-Taisha individuals planted ex situ in Quinindé, (Ecuador) do not drop their fruit from the bunch, which normally occurs naturally through the fruit abscission process (Fooyontphanich et al. 2016). In addition, the abscission zone of *E. oleifera* was markedly different from that of *E. guineensis* (Table 1). Fruit abscission is an important agronomic characteristic whose control is of interest to oil palm breeders in order to facilitate harvest and reduce the impact of oil acidification due to lipase activity induced in damaged abscised fruit (Morcillo et al. 2013). A recent survey of the *E. oleifera*-Taisha population in Quinindé confirmed the non-shedding character of certain individuals. In particular, one individual was found to have seedlings that develop from fruit still attached to the bunch (Figure 2E). Furthermore, an in vitro phenotype test of abscission revealed that no separation in the abscission zone took place after a 24-hour test period (Figure 2F; Fooyontphanich et al. 2016). This *E. oleifera*-Taisha individual provides genetic material important for understanding the abscission process in flowering plants, in addition to the possible introgression of genetic information to modify the abscission process in *E. guineensis.*

These limited examples show the importance of describing and conserving the local biodiversity of *E. oleifera*-Taisha, which is represented by a single locality in the Ecuadorian Amazonia. A more complete exploration of the Ecuadorian diversity of *E. oleifera* and the implementation of a national program to protect these natural populations as a source for traits and genes that could be beneficial to a sustainable oil palm industry is thus of great importance.

Conservation of *E. oleifera*.- *Elaeis oleifera* was not assessed for the International Union for Conservation of Nature (UICN) red list of Ecuador (Montúfar et al. 2011)

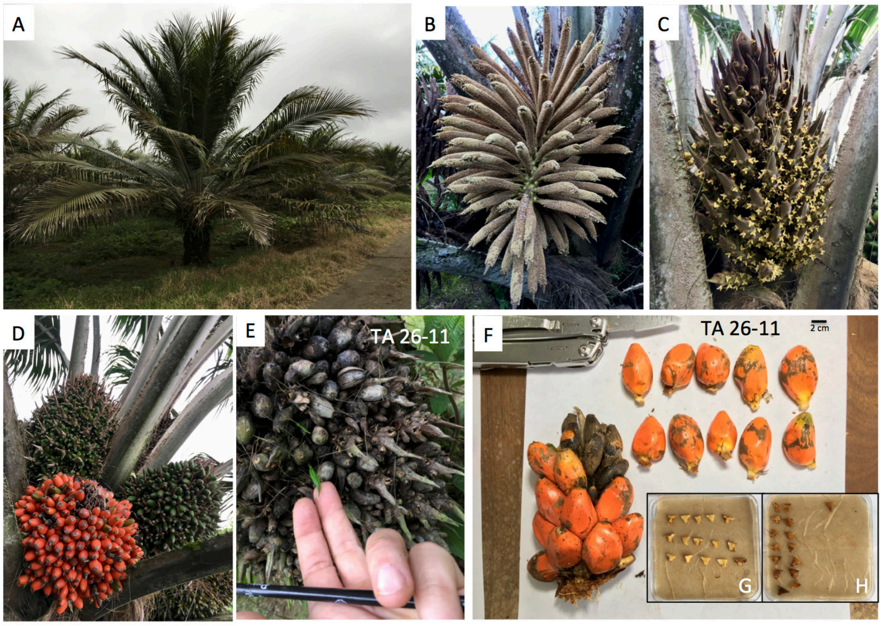

Figure 2 Examples of cultivated *E. oleifera*-Taisha material planted by Danec S.A. and partners in Quinindé, Ecuador. (A) An adult individual; (B) Male inflorescence at later stage of development; (C) Female inflorescence; (D) Fruit bunches at different ripening stages; (E) *E. oleifera*-Taisha individual TA26-11 does not abscise its fruit and eventually seedlings emerge from fruit that are still attached to the fruit bunch; (F) Fruit spikelets and fruit used for phenotype test of tree TA26-11; (G) Phenotypic test with fruit bases from tree TA26-11 before and (H) after test that shows that only one out of 15 fruit bases partially separated in the abscission zone after 24 hours. Phenotype test was performed as described previously (Fooyontphanich et al. 2016).

because this inventory was focused on endemic species. However, due to its limited known distribution, the few botanical collections reported, and its economic importance as a source of genetic material for the oleaginous industry, this species could be considered endangered and should therefore be included into the National Agenda of Research of Biodiversity (INABIO 2017).

In conclusion, the cultivation of oil palm in industrial plantations is controversial in tropical countries, including in Ecuador. However, it is clear one objective, and a major worldwide challenge, is how to develop more productive, sustainable genetic material and cultivation practices that will reduce the pressure on native tropical rain forests. *E. oleifera* clearly could have a positive impact on both biodiversity conservation and the genetic improvement of the oil palm. In addition to the well documented importance of the disease resistance traits of *E. oleifera* —such as resistance to lethal bud rot—, if new *O* x *G* hybrids could be developed to improve production per ha, this could help reduce the pressure to convert biodiversity-rich tropical rainforest into oil palm plantations. Additionally, if the introgression of the genetic traits of *E. oleifera* to *E. guineensis* could produce oils of better quality (e.g., higher oleic acid content) this could improve the quality of oil consumed in Ecuador and respond to demand for unsaturated oleic rich palm oil. Despite how little is known about Ecuadorian *E. oleifera*, from this review it is clear that individuals possess interesting agronomic traits, which are of importance to oil palm breeders for the improvement of *E. guineensis.* However, very little is known about the biodiversity of the Ecuadorian *E. oleifera* populations and about what additional genetic traits of interest could be discovered. Questions that remain include whether other populations of *E. oleifera* exist in Ecuador? What other agronomic traits of interest are stored in the few populations that are known in Ecuador? What are the origins of the isolated disjointed populations in Ecuador? What we do know is that *E. oleifera* is one of the most fascinating palms, in particular due to its procumbent trunk, which gives the impression that it moves in search of the best ecological conditions in the forest. Unfortunately, in spite of the economic importance and potential of Ecuadorian *E. oleifera,* very little is known about this neglected palm species.

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