

On the reinstatement of *R. samoensis* and *R. brevistyla* in East Pacific red mangroves (*Rhizophora*, *Rhizophoraceae*)

Xavier Cornejo¹, Carmita Bonifaz¹

¹Herbario GUAY, Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Av. Raúl Gómez Lince s.n. y Av. Juan Tanga Marengo (campus Mapasingue), Guayaquil, Ecuador. Orcid: 0000-0002-4081-4047

Recibido 01 agosto 2023, aceptado 11 de noviembre 2023, en línea 14 de diciembre 2023.

Abstract

On the basis of previously presented molecular studies, *Rhizophora samoensis* (Hochr.) Salvoza and *R. brevistyla* Salvoza (*Rhizophoraceae*) are here reinstated as valid names for the Eastern Pacific red mangroves. The identical meaning of vernacular names of *R. samoensis* from Samoa and coastal Ecuador is here reported for first time. The lectotype of the basionym *Rhizophora mangle* var. *samoensis* is designated.

Keywords: Lectotype; mangal; Pacific Ocean, transoceanic; vernacular names.

Resumen

Con base en estudios moleculares previamente presentados, se reestablece *Rhizophora samoensis* (Hochr.) Salvoza y *R. brevistyla* Salvoza como nombres válidos de mangles rojos para el Pacífico Este. Se reporta por primera vez el idéntico significado de los nombres vernáculos de *R. samoensis* en Samoa y costa de Ecuador. Se designa el lectotipo del basónimo *Rhizophora mangle* var. *samoensis*.

Palabras claves: Lectotipo; manglar; nombres vernáculos; océano Pacífico; transoceánico.

Introduction

Rhizophora L. (*Rhizophoraceae*) is the emblematic and most conspicuous Pantropical genus of mangroves; it is characterized by aerial prop roots, decussate branches and evergreen simple leaves, a pair of deciduous narrowly-lanceolate stipules in a conical-terminal arrangement, cymose-axillary inflorescences, berry-like fruits that develop piercing-pendulous outer embryos termed hypocotyls, propagules or radicles (Salvoza, 1936; Hou, 1960; Tomlinson, 1986; Duke, 2010; Cornejo, 2014; Cerón-Souza et al., 2010; Prance, 2018). The genus comprises six species and hybrids commonly known as red mangroves which for thousands of years have provided many goods and services to countless human groups that have settled and flourished along seacoasts mostly in tropical and also in subtropical belts between latitudes of around 32°N and 38°S (Stothert, 2011; Lo et al., 2014; Prance, 2018).

Currently, the species of *Rhizophora* are grouped into two biogeographically disjunct and isolated realms, whose genetic divergence using cpDNA has been estimated to have occurred approximately 10.6 MA (5.4 to 16.3 MA), when the Tethys Sea closed

(Takayama et al. 2021). Each of those *Rhizophora* realms are floristically dissimilar and having a particular composition, namely the Indo-West Pacific (IWP) and Atlantic-East Pacific (AEP) (Salvoza, 1936; Tomlinson, 1986; Duke, 2010; Takayama et al., 2021), the AEP group is the focus of this paper. Two species and a hybrid are formally recognized to occur broadly along both coasts of the American continents: *R. mangle* L. (1753, the nomenclatural generic type), *R. racemosa* G. Mey (1818) and *R. x harrisonii* Leech. (1918; Cerón-Souza et al., 2010; Cornejo, 2013; Prance, 2018).

Rhizophora has been monographed by Salvoza (1936), Hou (1960) and Prance (2018); however, recent molecular studies (Takayama et al., 2013, 2021; Francisco et al., 2018; Mori et al., 2021) are challenging the traditional taxonomy and nomenclature on this genus for AEP, that since Linnaeus' time has been mostly based on morphology. The genetic studies (op. cit.) suggest that the strong similarity in nuclear and chloroplast markers and the identical haplotype and alleles does not allow genetic differentiation between the Polynesian *R. samoensis* (Hochr.) Salvoza lineage, the only species of *Rhizophora* in Samoa (Whistler, 1992; Fig. 1: A, B) and most of the eastern Pacific populations (Fig. 2: A, B), the latter traditionally

* Correspondencia del autor:

E-mail: xcornejoguay@gmail.com



Esta obra está bajo una licencia de creative commons: atribución-NoComercial-SinDerivadas 4.0. Los autores mantienen los derechos sobre los artículos y por tanto son libres de compartir, copiar, distribuir, ejecutar y comunicar públicamente la obra.

identified as *R. mangle*, coupled to the absence of clear-cut morphological characters, indicates that both names of indistinguishable transpacific populations refer to a single genetic taxonomic entity (Duke, 2002; Takayama et al., 2013, 2021; Mori et al., 2021). Furthermore, due to the apparently absence of sharp morphological characters to separate the populations of *R. mangle* from the Pacific and Atlantic coasts and following the principle of priority, Art. 11 of ICBN (Turland et al., 2018), *R. samoensis* has been synonymized and treated in a very broad sense as *R. mangle* (Linnaeus, 1753; Guppy, 1906; Hou, 1960; Prance, 2018), the older name for a species genetically distinct and originally described from the West Indies.

Conversely, recent studies based on molecular markers have revealed a diphyly and different genetic structure of *R. mangle* and *R. racemosa* on the oceanic basins of either side of the American continent, which plays the role of a barrier to gene flow within the genus, and that *R. racemosa* from the Atlantic basin is more genetically similar to *R. mangle* from the same basin than to *R. racemosa* trees from the Pacific coast (Mori et al., 2021; Cerón-Souza com. pers.). The distinct genealogical lineages present two conspicuous allopatric patterns of distribution, each of those belonging and restricted to highly distinctive separate biogeographic units that started to differentiate from each other at least 3.1 to 3.5 MYA ago; they have been isolated since the closure of the Isthmus of Panama, an event occurred ca. 2.8 MYA, and are independently and parallel-evolving (Takayama, 2013; O'Dea et al., 2016; Cerón-Souza, unpublished). Consequently, the molecular results exhibit a case of "taxonomic inconsistency" and notorious limitation of "current morphology-based species designations" that is impractical for a precise definition of biological lineages, yielding a lack of accuracy for conservation and management purposes on East Pacific red mangroves (Mori et al., 2021). It is worthy mentioning that in the East Pacific, the endemic flora and fauna of the Galapagos Islands are a well-known case of allopatric evolution and speciation in isolated environments that in terms of periods of time is comparable to that of the *Rhizophora* in the same Pacific basin. The major islands of the Galapagos emerged between 4 to 0.07 MYA (Geist et al., 2014), allowing during this relatively short time span or even posteriorly to less than 50.000 YBP, the subsequent evolutionary formation of the conspicuous endemic taxa, e.g. the woody genus *Scaevola* (Darwin's giant daisies, Asteraceae), which comprises 15 species (1.4 MYA to 24.000 YBP), the pink iguana *Conolophus marthae* (1.5 MYA), the Galapagos' marine iguana *Amblyrhynchus cristatus* (less than 50.000 YBP), etc... (MacLeod et al., 2015; Hedrick, 2019; Fernández-Mazuecos et al., 2020), all of those within similar dates as or even younger than the red mangroves divergence on the same Pacific basin. Furthermore, must be considered that the fossil evidence suggests that during Eocene the Extra-Andean cordilleras in Northwestern South America (e.g. Chongón-Colonche)

were shallowly sumersed as a reef within an open marine environment (Moreira, 2019), and that those initially emerged as isolated islands as a consequence of a collision of coastal Ecuador against the western Andean margin most likely during or posteriorly to the latest Oligocene-Miocene (ca. 28.1 to 20.4 MY) (Jaillard et al., 1995), having a similar path of evolution that involved the colonization by prehistoric mangroves (Cornejo & Lombardi, 2021) in proto Northwestern South America, at least 10 MY before the emergence and formation of present Galapagos islands and the closure of isthmus of Panama (op. cit.).

Currently, the proven natural lineages correlate with well-defined biogeographical patterns and provide valuable insights for delimiting species (Fujita et al., 2012). Therefore, the Red Mangroves species deserve to have their own names, and a re-evaluation and reshaping of the nomenclature of East Pacific *Rhizophora* is presented here. The accurate nomenclatural perspective of mangrove diversity allows the East Pacific taxa to be regarded as separate conservation and management units, as previously suggested (Takayama et al., 2013).

Whether a genetical-biogeographic or a morphological base is chosen for the recognition of biological entities, this is an open viewpoint that is not in conflict with ICN for species and names (Turland et al., 2018). Consequently, although there is a marked tendency of different length of (dry) sepals between *R. mangle* s.s. (11-15 mm long) versus *R. samoensis* (7-11 mm long), and different length of pistils and leaf shape between *R. racemosa* s.s. (pistils up to 7 mm long and blades mostly oblanceolate to oblanceolate-elliptic or narrowly elliptic) versus *R. brevistyla* Salvoza (pistils 3-5 mm long and blades usually lanceolate or ovate to elliptic-oblong or broadly-elliptic to obovate) (Gregory; 1958; Cornejo, 2014), the recognition of separate taxa of *Rhizophora* for East Pacific is mostly based on unequivocal genetical and biogeographical evidence rather than sharply phenotypic-morphological differentiation. Therefore, as *R. mangle*, *R. racemosa* and *R. x harrisonii* are the earliest red mangroves in AEP, discovered and typified from the West Indies and Guianas, respectively (Linnaeus, 1753; Hou, 1960; Prance, 2018), those names remain attached to the Atlantic basin taxa, and consequently, changes in the nomenclature are needed for the East Pacific red mangroves. Reviewing the nomenclatural history of the East Pacific *Rhizophora*, which fortunately is well-documented, Salvoza (1936) formally recognized *R. samoensis* at specific rank and established *R. brevistyla* as a new species, both regarded as the American Pacific counterpart for the Atlantic *R. mangle* and *R. racemosa*; those are the unique names for red mangroves in the East Pacific region that must be followed according to ICN (Turland et al., 2018). Salvoza's nomenclatural proposal was accepted in Flora of Panama (Gregory, 1958), but due to the apparently slight morphological differences ended up relegated to the synonymy of the Atlantic *R. mangle*

and *R. x harrisonii* (Hou, 1960, as *R. harrisonii*), respectively; and this nomenclatural conclusion on East Pacific taxa has been broadly accepted to the present day (Cornejo, 2013, 2014; Prance, 2018). In the latter, the synonymization of *R. brevistyla* as *R. x harrisonii* was effected without any other option because Hou (op. cit.) thought that *R. harrisonii* was the only species in the genus with multiflorous inflorescences on the west coasts of the Americas, regarding *R. racemosa* as restricted to the Atlantic basin. *Rhizophora brevistyla* has been cited as a hybrid for EAP (Duke, 2017; Saenger et al., 2019), however, that name it is not regarded as valid because the hybrid status has not been formally presented following Art. 41.1, and 41.5 of ICBN (Turland et al., 2018).

Conversely, supported by the recently discovered genetic lineages on the East Pacific, the names proposed by Salvoza are here reinstated, and the populations of red mangroves traditionally identified as *R. mangle* s.l. and *R. racemosa* s.l. on the Pacific coasts of America are here recognized as *R. samoensis* and *R. brevistyla*, respectively, two genetically porous species that have experienced ancient and steady hybridization and introgression (Cerón-Souza, 2010); however, the latter species need further explanations. According to Hou (1960:629), the contracted or rather loose architecture of inflorescences is the first character to separate *R. racemosa* from *R. x harrisonii*; however, molecular results (Mori et al., 2021, fig. 4, 5; Cerón-Souza et al., unpublished) demonstrate that in the East Pacific *Rhizophora*, the individuals that have inflorescences that could be rather contracted (typical of *R. racemosa*) or somewhat elongate, slender and loose (what though to be *R. x harrisonii*), do not have a genetic differentiation among them and that the apparently morphological differences neither suggest a hybrid origin. The molecular evidence (Mori et al., 2021 fig. 4, 5; Cerón-Souza et al., unpublished) reveals that both names are a same genetic entity that can express phenotypic plasticity exhibiting contracted or slender and loose inflorescences without taxonomic value. This unexpected new information demonstrates that the traditionally used morphological character cannot separate the species and the hybrid, respectively. Consequently, opposite to Hou (1960) and Prance (2018), the Pacific *R. brevistyla* cannot be synonymized under the Atlantic *R. x harrisonii* because: i) is an allopatric different genetic lineage that has been independently originated and separately maintained on the other side of the American continent (Mori et al., 2021), ii) the rather contracted vs. loose structure of inflorescences do not correlate to a hybrid, but to a genetically consistent single species; and, iii) *R. brevistyla* has no natural dispersal capacity for reaching even the Galapagos islands that are located 500 to 650 M west off the coast of continental Ecuador, therefore, the notorious shorter capacity of dispersal, whether caused by a lower tolerance to sea salinity and/or to high Equatorial solar irradiance intensity in open sea or due to any other limiting factor, must

be regarded as a distinctive physiological-ecological difference if compared *R. brevistyla* against to the also Equatorial but trans-Atlantic populations of *R. x harrisonii* s.s. or *R. racemosa* s.s., that have a conspicuously greater dispersal range -in a higher sea surface salinity- exhibiting an average disjunction of ca. 2,500 to 3,500 M-(Breteler 1969, 1977; Tomlinson, 1986; Lo et al., 2014; Jones and Cessi, 2017; Craig et al., 2017). Therefore, the populations identified as *R. racemosa* s.l. and *R. x harrisonii* s.l. in East Pacific both are here recognized as one species under the name of *R. brevistyla*. A nomenclatural hybrid between *R. samoensis* and *R. brevistyla* is expected to be formally recognized pending further additional molecular studies.

Regarding to the morphology, the isotype of *Rhizophora mangle* var. *samoensis* Hochr., the basionym of *Rhizophora samoensis* that is held on G Herbarium, exhibit an inflorescence with 6 flowers (Fig. 1: A), that trait has been confirmed by recent field exploration in mangroves of Samoa (photos sent to senior author by Yero Kuethe), where *R. samoensis* produce inflorescences with 6 to 7 flowers (Fig. 1: B), and matches the description for this species (Salvoza, 1936). On the eastern Pacific, the populations of *R. samoensis* (currently known as *R. mangle*) often have inflorescences with 2 to 4 flowers, and sometimes 5 to 7 flowers (Fig. 2: A, B). Molecular studies (Takayama et al., 2013, 2021; Mori et al., 2021), have demonstrated that the 2 to 7 flowers per inflorescence in the transpacific populations of *R. samoensis* is the result of phenotypical plasticity within a same genetic entity. As the main character of *R. samoensis* (as *R. mangle* from E Pacific) has been stated and believed to be 2 to 4 flowers per inflorescence (e.g., Hou, 1960; Cornejo, 2014; Prance, 2018), the circumscription of this species must be broadened including the number of flowers per inflorescence that present the overlooked G isotype, therefore, an updated key to the species is provided.

Taxonomy

1. ***Rhizophora samoensis*** (Hochr.) Salvoza, Nat. Appl. Sci. Bull. Philipp. 5(3): 220, fig. 6. 1936. (Fig. 1: A, B; 2: A, B).

Basionym: *Rhizophora mangle* var. *samoensis* Hochr., Candollea 2: 447. 1925. TYPE: SAMOA. île d'Upolu, Apia, mangrove, 26 Mar 1905 (fl), B. P. G. Hochreutiner 3423 (Lectotype, designated here: G-00446757 [image!]; isotype: G [image!]).

Two mounted type specimens of *Rhizophora mangle* var. *samoensis* are hold in G herbarium, both with the same collector, number of collections, locality, and date, that with the printed label and barcode is here selected as lectotype.

Usually identified as: *Rhizophora mangle* L. *sensu lato*.

Habitat and distribution: In the east Pacific from Baja California to northwestern Peru, also in the Galapagos and trans-Pacific disjunct to the Indo West Pacific in Western Polynesia: Tonga

and Samoa; South Melanesia: New Caledonia, Vanuatu, and Fiji (Salvoza, 1936; Gregory, 1958; Duke, 2010).

For a full description and additional comments see Cornejo 2014:234 (as *R. mangle*).

2. *Rhizophora brevistyla* Salvoza, Nat. Appl. Sci. Bull. Philipp. 5(3): 211, fig. 2. 1936. (Fig. 2: C, D).

TYPE: PANAMA. Panama, along the Pacific coast, Bella Vista, 10 Sep 1929 (fl), F. M. Salvoza 1007 (Holotype: A-55199 [image!]; isotypes: L-9919 (fragm.), S-04-1961[image!]).

Usually identified as: *Rhizophora racemosa* G. Mey., *sensu lato*; *R. harrisonii* Leechm., *sensu lato*; *R. x harrisonii* Leechm., *sensu lato*.

Habitat and distribution: In the east Pacific from El Salvador to northwestern Peru (Salvoza, 1936; Gregory, 1958).

For a full description and additional comments see Cornejo 2014:238 (as *R. racemosa*).

Key To The East Pacific Species Of *Rhizophora*

1a. Inflorescences pauciflorous, 1-2-branched, geminate, cymose or true cymes with

2 to 7 flowers; ovules always cream; fully developed hypocotyls 13-30 cm long.....

Rhizophora samoensis

1b. Inflorescences multiflorous, 3-5(-6?)-branched, cymose, with 8-64 (or more?) flowers; ovules sometimes pink or reddish to crimson-red; fully developed hypocotyls 20-52 cm long.....*Rhizophora brevistyla*

Meaning of vernacular names of *rhizophora samoensis* in samoa and coastal ecuador

It is interesting to note the identical meaning of vernacular names in different languages and similar perspectives of *R. samoensis* regarding other species of mangroves from Samoa and coastal Ecuador (Acosta-Solís, 1961:79; Dinaf-Clirsen,1991; Cornejo, 2014; Whistler, 2000; Iakopo, 2006). *Rhizophora samoensis* in Samoan is known as “Togo tane” that means male mangrove (Whistler, 2000; Iakopo, 2006), whereas in coastal Ecuador the same species is known among several other Spanish vernacular names as “mangle macho” and “mangle caballero”, both also meaning male mangrove (Acosta-Solís, 1961:79;

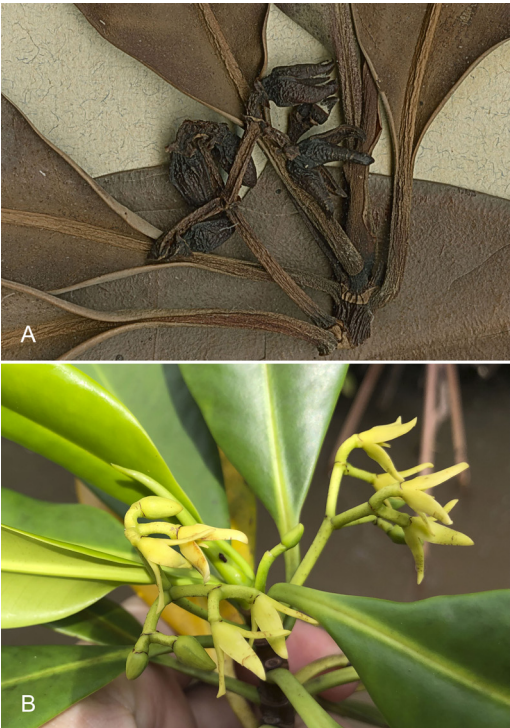


Fig. 1. *Rhizophora samoensis*, terminal leafy branches and inflorescences holding 6 to 7 flowers, from Upolu island, Samoa. A. Close up from G Isotype. B. Fresh material.— A Courtesy of G Herbarium. B. Courtesy of YERO KUETHE.

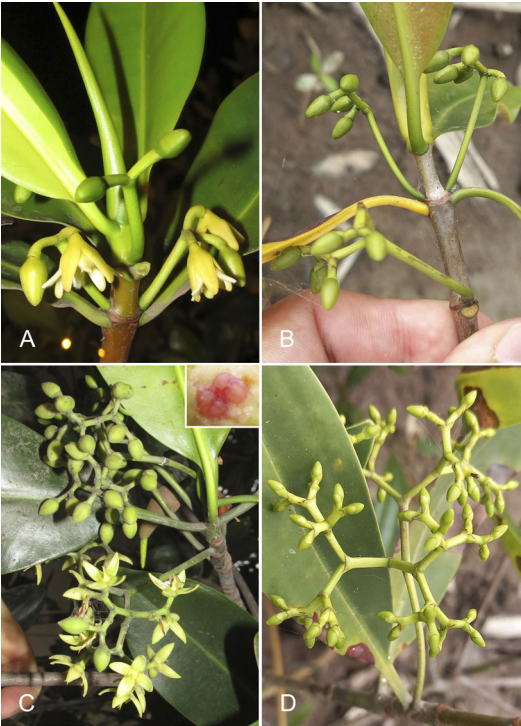


Fig. 2. *Rhizophora samoensis*, terminal leafy branches and inflorescences holding 2 to 6 flowers, from Ecuador. A. From San Cristobal, Galápagos islands. B. From Nuevo Porvenir, province of Guayas, continental Ecuador. C. From University of Guayaquil, province of Guayas. D. From Nuevo Porvenir, province of Guayas. A-D Photos by XAVIER CORNEJO.

Dinaf-Clirsen, 1991; Cornejo, 2014). In the latter region the “macho” word when applied to plants strictly means male (obs. pers.), and because of the taller height that *R. samoensis* can achieve, it is used to differentiate it from shorter species of mangroves, regarded and named as female mangroves, that is *Hilairanthus germinans* (L.) Cornejo (syn. *Avicennia germinans*, Acanthaceae) in coastal Ecuador as well as *Bruguiera gymnorhiza* the Samoan “Togo fafine” that translated is female mangrove in Samoa (Acosta-Solís, 1961:79; Whistler, 2000; Iakopo, 2006:15). The same meaning of vernacular names of the remarkable trans-Oceanic disjunct populations of *R. samoensis* on eastern and western Pacific exhibits a case of random coincidence or perhaps the evidence of some transoceanic connection (Gilmore, 1930; Heyerdahl, 1952; MacDougall, 2003; Warren, 2016; Ioannidis et al., 2020) that suggests that “mangle macho” may have been a translation to Spanish inherited from a lost pre-Hispanic autochthonous language (Galeote, 1997; Herrero-López, 2016), that was the putative ancestral origin of the mentioned vernacular names of *R. samoensis* in coastal Ecuador (Figure 1 y 2).

Acknowledgements

Thanks to herbaria A, G, GOET, and K for sharing digital images of the types of *Rhizophora brevistyla*, *R. samoensis*, *R. racemosa*, and *R. x harrisonii*, respectively. The first author visited the following herbaria: AAU, COL, GB, GUAY, INB, L, MO, NY, S, SEL, US, WIS. The revision of *Rhizophora* by Salvoza was provided by the Missouri Botanical Garden Interlibrary Loan. Ivania Cerón-Souza, Gustavo Mori and Hanno Schaefer provided useful comments on the interpretation of genetic structure of Pacific *Rhizophora*. Yero Kuethe shared with the first author his field images of *Rhizophora samoensis* from Samoa, and provided permission for publication of one of those (Fig. 1: B). Michael Nee and Gustavo Mori, reviewed and commented the manuscript.

Funding: No funding was received for this work.

Conflict of Interest: The authors declare that they have no conflict of interest.

Ethical approval: No animal testing was performed during this study.

Sampling and field studies: The study does not contain sampling material or data from field studies. Observational permit for field studies are not required in Ecuador.

Data Availability Statement: Data sharing not applicable to this article as no datasets were generated or analyzed during the current study. The herbaria A, G, GOET, and K shared digital images of the types of *Rhizophora brevistyla*, *R. samoensis*, *R. racemosa*, and *R. x harrisonii*, respectively. The first author visited the following herbaria: AAU, COL, GB, GUAY, INB, L, MO, NY, S, SEL, US, WIS.

Author Contribution Statement: XC designed research and wrote most of the manuscript. CB conceived research and wrote some parts of the manuscript. All authors read and approved the manuscript.

Literature cited

- Acosta-Solís, M. (1961) Los Manglares del Ecuador. *Revista Geográfica* 54: 69-88.
- Breteler, F. J. (1969) The Atlantic species of *Rhizophora*. *Acta Botanica Neerlandica* 18: 434-441.
- Breteler, F. J. (1977) America's Pacific species of *Rhizophora*. *Acta Botanica Neerlandica* 26: 225-230.
- Cerón-Souza, I., E. Rivera-Ocasio, E. Medina, J. A. Jiménez, W. O. McMillan, and E. Bermingham (2010) Hybridization and introgression in New World red mangroves, *Rhizophora* (Rhizophoraceae). *American Journal of Botany* 97: 945-957.
- Cornejo, X. (2013) Lectotypification and a new status for *Rhizophora x harrisonii* (Rhizophoraceae), a natural hybrid between *R. mangle* and *R. racemosa*. *Harvard Papers in Botany* 18: 37.
- Cornejo, X. (2014) *Plants of the South American Pacific Mangrove Swamps (Colombia, Ecuador, Peru)*. Edu Quil, Ed. Universidad de Guayaquil, Ecuador.
- Cornejo, X. and J. Lombardi (2021) *Salacia juradoi* (Celastraceae), a new species from coastal Ecuador. *Phytotaxa* 154: 125-130.
- Craig, P. M., D. Ferreira, and J. Methven (2017) The contrast between Atlantic and Pacific surface water fluxes. *Tellus A: Dynamic Meteorology and Oceanography* 69, 1330454. Available from: <http://centaur.reading.ac.uk/68486/8/The%20contrast%20between%20Atlantic%20and%20Pacific%20surface%20water%20fluxes.pdf>
- Dinaf-Clirsen (1991) *Inventario de manglares del Ecuador continental*. CLIRSEN y Dirección Nacional Forestal del Ministerio de Agricultura y Ganadería. Quito, Ecuador: 1-438.
- Duke, N. C. (2010) Overlap of eastern and western mangroves in the south-western Pacific: hybridization of all three *Rhizophora* (Rhizophoraceae) combinations in New Caledonia. *Blumea* 55: 171-188.
- Duke, N. C. (2017) *Mangrove floristics and biogeography revisited: further deductions from biodiversity hot spots, ancestral discontinuities, and common evolutionary processes*. In: Rivera-Monroy, V. H., V. H. Lee, S. Y. Kristensen, and R. Twilley, Eds., *Mangrove Ecosystems: A Global Biogeographic Perspective*. Springer International Publishing, Cham, pp. 17-53. https://doi.org/10.1007/978-3-319-62206-4_2.
- Duke, N. C., E. Lo, and M. Sun (2002). Global distribution and genetic discontinuities of mangroves-emerging patterns in the evolution of *Rhizophora*. *Trees* 16: 65-79.
- Fernández-Mazuecos, M., P. Vargas, R. A. McCauley, D. Monjas, A. Otero, J. A. Chaves, J. A. Guevara-Andino, and G. Rivas-Torres (2020) The Radiation of Darwin's Giant Daisies in the Galápagos Islands. *Current Biology* 30 <https://doi.org/10.1016/j.cub.2020.09.019>
- Francisco, P. M., G. M. Mori, F. M. Alves, E.V. Tambarussi, and A. P. de Souza. (2018) Population, genetic structure, introgression, and hybridization in the genus *Rhizophora* along the Brazilian coast. *Ecology and Evolution* 8: 3491-3504.
- Fujita, M. K., A. D. Leaché, F. T. Burbrink, J. A. McGuire, and C. Moritz (2012) Coalescent-based species delimitation in an integrative taxonomy. *Trends in Ecology and Evolution* 27: 480-488.
- Galeote, M. (1997). Nombres indígenas de plantas americanas en los tratados científicos de fray Agustín Farfán. *Boletín*

- de *Filología* 36: 119-161.
- Geist, D. J., H. Snell, H. Snell, C. Gooddard, and M. D. Kurz (2014) A paleogeographic model of the Galapagos Islands and biogeographical and evolutionary implications. In: K. S. Harpp, E. Mittelstaedt, N. d'Ozouville, and D. W. Graham, Eds., *The Galapagos: a Natural Laboratory for the Earth Sciences*. Wiley, Hoboken NJ. Pp. 145-166.
- Gilmore, M. R. (1930) Dispersal by Indians a factor in the extension of discontinuous distribution of certain species of native plants. *Papers of the Michigan Academy of Science, Arts and Letters* 13: 89-94.
- Gregory, D. P. (1958) Rhizophoraceae. In R. E. Woodson, Jr., R. W. Schery and collaborators, Eds., *Flora of Panama*, Part VII, Fascicle 2. Annals of the Missouri Botanical Garden 45: 136-142.
- Guppy, H. B. (1906) *Observations of a naturalist in the Pacific between 1896 and 1899*. Plant Dispersal, Vol. II. Macmillan, London.
- Hedrick, P. W. (2019) Galapagos Islands Endemic Vertebrates: A Population Genetics perspective. *Journal of Heredity* 110(2): 137-157.
- Heyerdahl, T. (1952) *American Indians in the Pacific: The Theory Behind the Kon-Tiki Expedition*. Allen and Unwin, London.
- Herrero-López, I. (2016) The literary translation into Spanish of Native American proper names: A perspective on the transcultural construction of identity. *Meta* 61: 534-552.
- Hou, D. (1960) A review of the genus *Rhizophora* with special reference to the Pacific species. *Blumea - Biodiversity, Evolution and Biogeography of Plants* 10: 625-634.
- Iakopo, M. (2006) *Mangroves of Samoa: Status and conservation*. Ministry of Natural Resources, Environment and Meteorology. Samoa, 40 pp.
- Ioannidis, A. G., J. Blanco-Portillo, K. Sandoval, E. Hagelberg, J. F. Miquel-Poblete, J. V. Moreno-Mayar, J. E. Rodríguez-Rodríguez, C. D. Quinto-Cortés, K. Auckland, T. Pars, and K. Robson (2020) Native American gene flow into Polynesia predating Easter Island settlement. *Nature* 583(7817): 572-577.
- Jaillard, É., M. Ordóñez, S. Benítez, G. Berrones, N. Jiménez, G. Montenegro, and I. Zambrano (1995) Basin development in an Accretionary, Oceanic-floored Fore-Arc Setting: Southern Coastal Ecuador during Late Cretaceous-Late Eocene Time. In A. J. Tankard, R. Suárez S., and H. J. Welsink (Eds.), *Petroleum Basins of South America*, *American Association of Petroleum Geologist Memoir* 62: 615-631.
- Jones, C. S. and P. Cessi (2017) Another reason why the Atlantic is saltier than the Pacific. *Journal of Physical Oceanography* 47: 2843-2859.
- Leechman, A. (1918) II. The genus *Rhizophora* in British Guiana. *Bulletin of Miscellaneous Information*, Royal Gardens, Kew 1918(1): 4-8.
- Linnaeus, C. (1753) *Species Plantarum*, Vol. 1, Salvius. Stockholm.
- Lo, E. Y. Y., N. C. Duke, and M. Sun (2014) Phylogeographic pattern of *Rhizophora* (Rhizophoraceae) reveals the importance of both vicariance and long-distance oceanic dispersal to modern mangrove distribution. *BMC Evolutionary Biology* 14: 83. Available from: <https://bmcevolbiol.biomedcentral.com/articles/10.1186/1471-2148-14-83>
- MacDougall, A. (2003) Did native Americans influence the northward migration of plants during the Holocene? *Journal of Biogeography* 30: 633-647.
- MacLeod, A., A. Rodríguez, M. Vences, P. Orozco-terWengel, C. García, F. Trillmich, G. Gentile, A. Caccione, G. Quezada, and S. Steinfartz (2015) Hybridization masks speciation in the evolutionary history of the Galápagos marine iguana. *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1809 (2015): 20150425.
- Meyer, G. F. W. (1818) *Primitiae Florae Essequiboensis adjectis descriptionibus centum circiter stirpium novarum, observationibusque criticis*. Göttingen: Heinrich Dieterich.
- Moreira, R. C. (2019) Bioestratigrafía y ambiente sedimentario de deposición de las calizas de la formación San Eduardo (Eoceno) al sur del Bosque Protector Cerro Blanco, Provincia del Guayas. Trabajo de titulación previo a la obtención del grado académico de Ingeniero Geólogo. Facultad de Ciencias Naturales, Universidad de Guayaquil, 97 pp.
- Mori, G. M., A. G. Madeira, M. Vargas-Cruz, Y. Tsuda, K. Takayama, Y. Matsuki, Y. Suyama, T. Iwasaki, A. Pereira de Souza, M. I. Zucchi, and T. Kajita (2021) Testing species hypothesis in the mangrove genus *Rhizophora* from the Western hemisphere and South Pacific islands. *Estuarine, Coastal and Shelf Science*. 248: <https://doi.org/10.1016/j.eccs.2020.106948>
- O'Dea, A., H. A. Lessios, A.G. Coates, R. I. Eytan, S. A. Restrepo-Moreno, A. L. Cione, L. S. Collins, A. de Queiroz, D. W. Farris, R. D. Norris, R. F. Stallard, M. O. Woodburne, O. Aguilera, M. P. Aubry, W. A. Berggren, A. F. Budd, M. A. Cozzuol, S. E. Coppard, H. Duque-Caro, S. Finnegan, G. M. Gasparini, E. L. Grossmann, K. G. Johnson, L. D. Keigwin, N. Knowlton, E. G. Leigh, J. S. Leonard-Pinguel, P. B. Marko, N. D. Pyenson, P. G. Rachello-Dolmen, E. Soibelzon, L. Soibelzon, J. A. Tood, G. J. Vermeij, and J. B. C. Jackson (2016) Formation of the Isthmus of Panama. *Science Advances* 2(8): e1600883. Available from: <https://doi.org/10.1126/sciadv.1600883>
- Prance, G. T. (2018) *Rhizophoraceae*. In: Kelly, L. and W. Thomas, Eds., *Flora Neotropica*. 120: 1-63. Published by the Organization for Flora Neotropica by the New York Botanical Garden Press, New York.
- Saenger, P., P. Ragavan, C.-R. Sheue, J. López-Portillo, J. W. H. Yong., and T. Mageswaran (2019) Mangrove biography of the Indo-Pacific. In: Gul, B., B. Böer, M. A. Khan, M. Clüsener-Godt and A. Hameed, Eds., *Sabkha Ecosystems*, Task for Vegetation Science-49 VI: Asia/Pacific: 379-400. Springer.
- Salvoza, F. M. (1936) *Rhizophora*. *Natural and Applied Science Bulletin* 5: 179-237.
- Stothert, K. E. (2011) Coastal resources and the Early Holocene Las Vegas Adaptation of Ecuador. In: Bicho, N. F., J. A. Haws, and L. G. Davis (Eds.), *Trekking the shore: Changing coastlines and the Antiquity of Coastal Settlement: Interdisciplinary contributions to Archaeology*. Springer, New York, Pp. 355-382.
- Takayama, K., M. Tamura, Y. Tateishi, E. L. Webb, and T. Kajita (2013) Strong genetic structure over the American continents and transoceanic dispersal in the mangrove genus *Rhizophora* (Rhizophoraceae) revealed by broad-scale nuclear and chloroplast DNA analysis. *American Journal of Botany* 100: 1191-1201.
- Takayama, K., Y. Tateishi, and T. Kajita (2021) Global Phylogeography of Pantropical mangrove *Rhizophora*. *Scientific Reports* 11: 117228
- Tomlinson, P. B. (1986) *The Botany of Mangroves*. Cambridge University Press, Cambridge, England, UK.
- Turland, N. J., J. H. Wiersma, F. R. Barrie, W. Greuter, D. L. Haksworth, P. S. Herendeen, S. Knapp, W. H. Kusber, D. Z. Li, K. Marhold, and T. W. May (2018) *International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code)*. Adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July (2017) Koeltz Botanical Books, Königstein.
- Warren, R. J (2016) Ghosts of Cultivation Past - Native American Dispersal Legacy Persists in Tree Distribution. *PLoS ONE* 11(3): e0150707. doi:10.1371/journal.pone.0150707
- Whistler, W. A. (1992) Vegetation of Samoa and Tonga. *Pacific Science* 46: 159-178.
- Whistler, W. A. (2000) *Plants in Samoan Culture: The Ethnobotany of Samoa*. Honolulu: Isle Botanica.