

# Diversity, Ecology and Ethnobotany of the Palms of the Yasuní National Park (Ecuador)

ROMMEL MONTÚFAR  
*Facultad de Ciencias Exactas y  
Naturales, Pontificia  
Universidad Católica del  
Ecuador, Av. 12 de Octubre  
1076 y Roca, Quito, Ecuador  
rjmontufar@puce.edu.ec*

THOMAS L.P. COUVREUR  
*UMR DIADE, Institut de  
Recherche pour le  
Développement, Université de  
Montpellier, Montpellier, France*

SANTIAGO ESPINOSA  
*Facultad de Ciencias,  
Universidad Autónoma de San  
Luis Potosí, San Luis Potosí  
México; Facultad de Ciencias  
Exactas y Naturales, Pontificia  
Universidad Católica del  
Ecuador, Quito, Ecuador*

SEBASTIÁN ESCOBAR  
*Ecinformatics and Biodiversity,  
Department of Bioscience,  
Aarhus University,  
Aarhus, Denmark*

TIMOTHY JOHN TRANBARGER  
*Facultad de Ciencias Exactas y  
Naturales, Pontificia  
Universidad Católica del  
Ecuador  
UMR DIADE, Institut de  
Recherche pour le  
Développement, Université de  
Montpellier, Montpellier, France*

AND

STUDENTS OF THE NATURAL  
HISTORY OF PALMS COURSE, 2018

Research and conservation of palm species relies on training new generations of palm biologists, especially in tropical countries. Such trainings pave the way to answer new questions related to palm biology, sustainable management, the cultural and economic links between humans and palms, and build conservation strategies through education and civil empowerment.

Ecuador is home to a vast amount of plant biodiversity (Jørgensen & León-Yáñez 1999). Palms, with 134 native species in 30 genera (Pintaud et al. 2008), represent an important part of this biodiversity occurring from sea level to 3000 m (Borchsenius et al. 1998). A large array of palm species also plays vital roles throughout the country as a food source, for construction and crafts, and for medicine. As such, palms are iconic across the country and attract much attention from researchers and students. However, to date, an active course on palm biology has not been part of the local teaching curricula in major universities. In this context the Pontifical Catholic University of Ecuador (PUCE), with the support of French National Institute for Research for Sustainable Development (IRD) and the International Palm Society (IPS), the International Mixed Laboratory BioInca (LMI BioInca) and the Universidad Autónoma de San Luis Potosí-México (UASLP), joined efforts to host the first “Natural History of Palms” course held in

Ecuador, August 3–12, 2018. The scope of this course was to train students from different universities and institutions in Ecuador, Peru and Colombia, under the concept of “talking, learning and doing science with palms.” The 22 participants mostly came from eight Ecuadorian institutions, but also two from Colombia (Universidad de Los Andes), two from Perú (Universidad Nacional Mayor de San Marcos, IIAP), in addition to two European students from Switzerland and Poland.

The course started with a two-day introduction to palms at the PUCE campus in Quito. Several talks were given about the morphology, anatomy, systematics and ethnobotany of palms. The second day was based at the PUCE herbarium (QCA), which contains one of the largest and best-conserved collections of Ecuadorian palms. Here, students learned to identify and study the morphology and classification of palms. The day ended with a walk through the PUCE campus where we were able to observe several palm species such as the



1. The Yasuní Scientific Station-PUCE. Top: Drone photo of the Station, next to the Tiputini river. Bottom: The station by night on a full moon. Photos: Rubén Jarrín.



Andean native *Parajubaea cocoides*, the planted *Phoenix canariensis*, *P. roebelenii* and an old and impressive *Jubaea chilensis*.

The next part of the course took place in the world-famous Yasuní National Park (YNP), one of the most biodiverse places on Earth (Bass et al. 2010). We departed by bus at the crack of dawn on a Monday. Getting an early start out of Quito is important to avoid the start-of-the-week rush hour. Quito is nested at 2900 m above sea level in the Andean cordillera, and the trip down to the Amazon basin is a fantastic experience for any naturalist. We crossed the cold and misty Andes and descended into the warm and humid eastern Andean slopes down to 250 m elevation, driving through a panoply of vegetation types including paramo, montane forests and tropical rainforests. As we progressed down into the Amazon, palms started to appear here and there, first high elevation species such as *Ceroxylon ventricosum*, *Dictyocaryum lamarckianum*, *Geonoma undata* and then more common species such as *Iriartea deltoidea* and *Wettinia maynensis*. Below 800 m palms become the most conspicuous plants of the scenery. After an 8-hour trip on the twisting roads, we arrived at the majestic and wide Río Napo river, a tributary of the Amazon. At this point we embarked in motorized canoes to the entry of YNP. Just after we crossed the Río Napo, a huge tropical storm whooshed up the river lifting waves and crashing thunder, a kindly reminder that we had arrived at the largest tropical rainforest in the world. From there onwards we continued into YNP and drove another hour to reach the PUCE Yasuní Research Station (YRS).

Yasuní National Park is located deep in the tropical rain forest of eastern Ecuador that is part of Western Amazonia (Fig. 1). It covers an area of ca. 1,022,736 ha and is adjacent to the Waorani Ethnic Reserve (WER) of ca. 900.000 ha. Yasuní was declared a National Park in 1979, and in 1989 YNP and WER were both incorporated into the World Network of Biosphere Reserves as Yasuní Biosphere Reserve (YBR). Yasuní is one of the most biodiverse areas of the planet with the world record of species richness per area for trees, amphibians, reptiles, birds and fishes (Bass et al. 2010).

The YRS is located on the southern bank of the Tiputini River (Fig. 1), within YNP. It is an internationally recognized research center where several long-term research programs on tropical rain forest ecology have been implemented, such as the Yasuní Forest



2. Top: R. Montúfar (with the hat) explaining the taxonomy of the genus *Geonoma* to part of the students, here *Geonoma deversa*. Middle: S. Espinosa (black shirt) taking georeferenced data for camera traps. Bottom: T. Couvreur teaching students how to take measurements for a good botanical collection of *Ammandra decasperma*. Photos: Thomas L.P. Couvreur, Anna Woyciechowska.

Dynamics plot (Valencia et al. 2004). YRS is surrounded by several terrestrial habitats such as *tierra firme* forest, seasonally flooded forest and swamps, as well as by lagoons and whitewater and blackwater streams. Finally, three Waorani communities are settled near the YRS, which allows the interaction of researchers and students with this Amazonian culture.

We spent six days in YNP. During the day we walked through the different ecosystems (Fig.



3. A sample of the different *Geonoma* species seen in Yasuni. Top left: The understory palm *Geonoma brongniartii*, note the spicate inflorescence and reddish young leaf. Top right: The understory palm *Geonoma stricta*, with bifid leaves and short robust and spicate inflorescences. Bottom left: The mid-sized clustering *Geonoma maxima*, with highly divided leaves. It is the tallest species of *Geonoma* in Yasuní. Bottom right: The single stemmed *Geonoma triglochin*, with its bifid or little divided leaves. Photos: Thomas L.P. Couvreur.



4. A sample of different palm flowers and fruits seen in Yasuni. Top left: Male flowers of *Geonoma macrostachys*, note the jointed connectives. Top right: Male flowers of *Geonoma brongniartii*, note the bifid connectives. Bottom left: The spectacular male inflorescence of *Ammandra decasperma*. Bottom right: Erect infructescence of *Astrocaryum murumuru*, note the old male rachillae above the fruits. Photos: Thomas L.P. Couvreur.

2), discussing the ecology and systematics of the species we encountered. We divided the course into four palm research themes, based on the expertise of the teachers: Systematics, diversity, seed dispersal ecology and ethnobotany. For the first three days of the course and for each theme, students were introduced to the field, the methodology and analytical tools. Thus, students learned how to make palm herbarium specimens as well as anatomical and physiological samples, set camera traps, do transects, and undertake ethnobotanical surveys. For the last two days, five or six students were assigned a small project related to one of the four themes and the following questions: How diverse is the Yasuní palm flora, and how can we identify the major genera? What are the ecological preferences of palms across different landscapes? What animals disperse palms? Which palm species are used most by the local community?

Here we present the results based on these short projects undertaken by the students. The results provide interesting insights into the palms of Yasuní that we deemed important to report.

#### How diverse is the Yasuni palm flora?

During the course, students collected a total of 36 herbarium specimens (Table 1; vouchers listed as CP2018 numbers). In some cases, a species was seen but was not collected. We also made herbarium collections of seedlings, and taught students to identify species based on seedlings, an important component for diversity studies (see below). In total, we observed 18 genera and 34 identifiable species (Table 1), representing 60% of genera in Ecuador and over 78% of genera reported for the Ecuadorian Amazon. As always, a couple of *Bactris* and *Geonoma* (Figs. 3 & 4) species remain undetermined and put our knowledge of palm taxonomy to the test.

By far the most species rich habitat is *tierra firme* (Table 1) with 13 genera observed. Where we walked away from the research station and arrived into the hilly part of the reserve, the understory is dominated in places by the phytelephantoid species *Ammandra decasperma* (Fig. 5), an acaulescent palm with spectacular, strong-scented, male inflorescences. Less common is the other phytelephantoid palm *Aphandra natalia*, recognizable by its visible stem and silvery indumentums on the leaflet undersides. We were lucky to have seen the only liana palm genus of the Neotropics,

*Desmoncus*. Because of its climbing habitat, it is quite hard to spot, but given we had 30 pairs of palm-refined eyes, we were able to see it not once but several times! Encountering *Desmoncus* always leads to interesting discussions about liana evolution and morphology in palms (Couvreur et al. 2015).

Omnipresent across the understory are numerous species of *Geonoma* (Fig. 3), which provide the ideal opportunity to discuss species complexity and diversification in tropical rain forests. Some *Geonoma* species are truly wonderful understory palms, such as *G. trigloch* (Fig. 3) with its single thick stem topped by several bifid leaves, *G. macrostachys* (Fig. 4) an acaulescent species with large bifid leaves and a spicate inflorescence or *G. maxima*, the tallest *Geonoma* of the Amazon basin, with several clustering stems that reach 5 m tall and finely pinnate leaves (Fig. 3). Among the large canopy palms, the *tierra firme* of Yasuní is dominated by species such as *Iriartea deltoidea* (Fig. 5) and *Socratea exorrhiza* with their amazing and characteristic stilt roots. *Oenocarpus bataua* with its white-silvery leaflet undersurfaces and *Attalea maripa* with its razor-sharp petiole margins are also very common.

Yasuní consists of an intricate mix between *tierra firme* and periodically inundated forests or internal valleys, each with its distinctive community of palm species (see below). Inundated areas near the station are dominated by *Geonoma brongniartii* (Fig. 3), a species that replaces the *tierra firme* *G. macrostachys*. We also encountered *Prestoea schultzeana*, a smallish understory palm with amazingly bright red rachillae and *Wettinia maynensis*, which has strange-looking, sausage-like infructescences.

Swampy areas can be found scattered across the Yasuní landscape. The dominant and most characteristic palm in this habitat is by far *Mauritia flexuosa*, one of the most abundant species in the Amazon (ter Steege et al. 2013). From above, it appears as a monodominant vegetation including only *Mauritia*. However, once you penetrate the swamp, armed with your best boots, of course, you discover a large diversity of species growing in the swampy understory, several of them also found in periodically inundated soils. To the students' delight, we visited one swamp near the station. Swampy habitats provide the opportunity to spot the "real" field botanists – those willing to get their feet wet. A number of palm species



5. Other palm species seen in Yasuni. Top left: The acaulescent *Attalea insignis*, note the erect inflorescence arising from within the leaves. Top right: The riparian *Bactris riparia*, forming very dense impenetrable colonies along rivers. Bottom left: The arborescent and very spiny *Astrocaryum chambira*. Bottom right: The arborescent and very common *Iriartea deltoidea*. Photos: Thomas L.P. Couvreur.



6. A sample of the different palm uses within the Waorani Guiyero community. Top left: A traditional Waorani house made using *Attalea butyracea* and *Geonoma macrostachys* leaves. Middle left: Handicrafts made by Waorani women with *Astrocaryum chambira* fibers. Top right: Detail of the weaving of *Geonoma macrostachys* leaves for thatching. Bottom left: Basket made by Isabel Ahua using *Oenocarpus bataua* leaves and used to carry forest fruits or animals. Bottom right: A sample of different palm products used by the Waorani Guiyero community: forefront: *Mauritia flexuosa* fruits, one of the most edible palm fruits in the Amazon; background: the *O. bataua* basket made by Isabel Ahua; left: *A. chambira* fibers with its natural color (yellow) or tinted into purple using a natural dye. Left photos: Rommel Montúfar; right photos: Thomas L.P. Couvreur.



Students of Natural History of Palms course, 2018. Top row, from left to right: Kenny Moreno, Ángel Rodríguez, Josué Sanmiguel, Karol Echeverría, Sebastián Escobar, Jhonny Jiménez, Fernanda Landeta, Héctor Reyes, Daniel Franco, Mariana Duque, Jaime Gavidia, Marinoli Rivas, Angel Cajas, Gwendolyn Peyre, Agnieszka Wojciechowska. Bottom row, from left to right: Mathew Tello, Ivonne Jalca, Daniela Pasquel, Hakim Schepis, Esteban Messa, Francisco Sánchez, Paolo Vallejo, Alvaro Rivera, Kabir Montesinos, Rommel Montúfar, Thomas Couvreur, Tim Tranbarger, Santiago Espinosa. Photo: Rubén Jarrín.

grow happily here, such as the acaulescent *Attalea insignis* (Fig. 5), *Astrocaryum chambira*, *Geonoma macrostachys* var. *acaulis*, several species of *Bactris*, such as *B. maraja*, and *Euterpe edulis*. Another swamp species is *Mauritiella armata*. Although it is present in YNP, we did not see this species in the swamps we visited; however, we did observe it on the roadside just before arriving to the park. Finally, we also encountered *Bactris riparia* (Fig. 5), a riparian species forming dense stands along the margin of the lagoons close to the Tiputini river. One species we did not encounter was *Chelyocarpus ulei*, the only Coryphoideae in Ecuador. While populations are known in Yasuní, they were too far to reach on our daily walks.

#### What are the densities of palms across different landscapes?

The students established three transects where all palm individuals were registered in order to explore the density and the ecological preferences. Two transects of 100 × 5 m were placed on a *tierra firme* forest and one transect of 80 × 5 m was set on a mixed forest (*tierra firme* and internal valley). The inclination of transects varied from zero to 45 degrees.

The mixed transect (0.04 ha) reported 95 individuals representing 19 species composed of typically *tierra firme* palms such as *Iriartea deltoidea*, *Ammandra decasperma*, *Geonoma macrostachys* and *Geonoma stricta*, but also several species characteristic of floodplains such as *Euterpe precatoria*, *Astrocaryum murumuru*, *Geonoma brongniartii*, *Attalea insignis* and *Wettinia maynensis*. Transects on *tierra firme* (0.05 ha) contained 127 and 99 individuals of eight and 14 species, respectively. *G. macrostachys*, *Phytelephas tenuicaulis*, *Prestoea schultzeana* and *I. deltoidea* were the most abundant palms. Other typically *tierra firme* palms were *Aiphanes ulei*, *Hyospathe elegans*, *Aphandra natalia*, *Chamaedorea pauciflora* and *Hyospathe elegans*. Based on the analyses of these transect data, the students suggested that topography had a strong influence over the abundance of palm species given that an increment in inclination decreased species abundance in the transects.

#### Which animals disperse palms?

It is well known that palms produce nutrient-rich fruits that are widely consumed by animals, especially birds and mammals,

**Table 1. List of species collected and identified during the Natural History of Palms at Yasuní Scientific Station.**

genus	epithet	collection number	habitat
<i>Aiphanes</i>	<i>ulei</i>	CP2018-17	<i>tierra firme</i>
<i>Ammandra</i>	<i>decasperma</i>	CP2018-18	<i>tierra firme</i>
<i>Aphandra</i>	<i>nathalia</i>	no collection	<i>tierra firme</i>
<i>Astrocaryum</i>	<i>chambira</i>	CP2018-19	inundated forest
<i>Astrocaryum</i>	<i>murumuru</i>	CP2018-14	inundated forest
<i>Attalea</i>	<i>butyracea</i> <sup>a</sup>	no collection	<i>tierra firme</i>
<i>Attalea</i>	<i>insignis</i>	CP2018-9	swamp/inundated forest
<i>Attalea</i>	<i>maripa</i> <sup>a</sup>	CP2018-22/23	<i>tierra firme</i>
<i>Bactris</i>	<i>concinna</i>	CP2018-3	inundated forest
<i>Bactris</i>	<i>corossilla</i>	CP2018-13	inundated forest
<i>Bactris</i>	<i>maraja</i>	CP2018-11	inundated forest
<i>Bactris</i>	<i>riparia</i>	CP2018-4	riparian forest
<i>Bactris</i>	<i>schultesii</i>	CP2018-036	inundated forest
<i>Bactris</i>	<i>simplicifrons</i>	CP2018-037	inundated forest
<i>Chamaedorea</i>	<i>pauciflora</i>	no collection	<i>tierra firme</i>
<i>Desmoncus</i>	<i>giganteus</i>	CP2018-23/27	<i>tierra firme</i>
<i>Euterpe</i>	<i>precatoria</i>	no collection	swamp/ inundated forest
<i>Geonoma</i>	<i>camana</i>	no collection	<i>tierra firme</i>
<i>Geonoma</i>	<i>brongniartii</i>	CP2018-2	inundated forest
<i>Geonoma</i>	<i>deversa</i>	CP2018-7	<i>tierra firme</i>
<i>Geonoma</i>	<i>macrostachys</i>	CP2018-5/34	<i>tierra firme</i>
<i>Geonoma</i>	<i>maxima</i>	CP2018-6	<i>tierra firme</i>
<i>Geonoma</i>	<i>sp.</i>	CP2018-25	inundated forest
<i>Geonoma</i>	<i>sp.</i>	CP2018-26	<i>tierra firme</i>
<i>Geonoma</i>	<i>stricta</i>	no collection	<i>tierra firme</i>
<i>Geonoma</i>	<i>triglochis</i>	CP2018-8	<i>tierra firme</i>
<i>Hyospathe</i>	<i>elegans</i>	CP2018-16	<i>tierra firme</i>
<i>Iriarte</i>	<i>deltoidea</i>	CP2018-31	<i>tierra firme</i>
<i>Mauritia</i>	<i>flexuosa</i>	CP2018-10/30	swamp
<i>Mauritiella</i>	<i>armata</i>	no collection	swamp
<i>Oenocarpus</i>	<i>bataua</i>	CP2018-20/32	<i>tierra firme</i>
<i>Oenocarpus</i>	<i>mapora</i>	CP2018-12	<i>tierra firme</i>
<i>Pholidostachys</i>	<i>synthera</i>	CP2018-15	<i>tierra firme</i>
<i>Prestoea</i>	<i>schultzeana</i>	CP2018-1/28	inundated forest
<i>Socratea</i>	<i>exorrhiza</i>	CP2018-24	<i>tierra firme</i>
<i>Wettinia</i>	<i>maynensis</i>	CP2018-21/29	inundated forest

<sup>a</sup> Recent advances in *Attalea* taxonomy suggest new identifications (Pintaud et al. 2016): *A. butyracea* reported from Yasuní corresponds to *A. bassleriana* and *A. maripa* to *A. tessmannii*. However, these taxonomic changes need to be better explored.

including humans (Howe & Smallwood 1982). These interspecific interactions are essential for palm dispersal and, therefore, the effect of forest defaunation can have negative consequences on the recruitment and survival of palm species. For our course we intended to show participants some principles and techniques to study plant-animal interactions, with an emphasis on fruit dispersal by terrestrial vertebrates. We focused on two important species: *Oenocarpus bataua* and *Mauritia flexuosa*. The ecology of these two species is very different: *M. flexuosa* inhabits swampy areas and forms monospecific aggregations or “*moretales*,” whereas *O. bataua* grows in *tierra firme* forests and does not form such aggregations. We looked for palms of these two species that had dropped fruits on the ground. After searching in *tierra firme* and a swampy *moretal*, we selected four individuals of *O. bataua* and three individuals of *M. flexuosa*. We used two camera traps to survey each palm and placed them on trunks of nearby trees, at a distance of 2–3 m from the target palm. Cameras faced the fruits on the ground and trunk of the palm and were programmed to work continuously, day and night, for three days.

Even though this time period is too short to register the animal community that could visit palms, we were able to capture some animals interacting with these palm species. We photographed two large rodents that are important dispersers of palm seeds: agouti (*Dasyprocta fuliginosa*) and paca (*Cuniculus paca*), which were feeding on fruits of *O. bataua* and *M. flexuosa*, respectively. We also photographed nine-banded armadillos that may have been looking for insects on rotten fruits. Likely due to the short time cameras were in the field, we were not able to photograph large mammals that live in Yasuní, such as tapir (*Tapirus terrestris*), deer (*Mazama zamora* and *M. murelia*) and peccaries (*Pecari tajacu* and *Tayassu pecari*), which are also important for seed dispersal. However, we were able to observe tracks of those large mammals by the sites where we placed our cameras, an indication that they were there, also looking for the sweet palm fruit.

### Which palm species are the most used by the local Waorani community?

The Waorani community of Guiyero, located 20 min by car from the research station, is where we headed to undertake our survey.

Given time limitations, we restricted ourselves to ask two main questions to 16 people (8 male, 8 female): which are the most useful palm species and what are their uses? The palm uses were grouped into seven general categories: medicinal, cultural (handicrafts, social, ludic, ritual), hunting supplies, household utensils, building, food, and cosmetics.

A staggering 18 useful palm species were named, about half of the total palm diversity we observed (Table 1, Fig. 6). The most important palms for this community were *Oenocarpus bataua*, *Iriartea deltoidea*, *Mauritia flexuosa*, *Astrocaryum chambira* and *Bactris gasipaes* var. *gasipaes*. All of them are arborescent and widespread across the Amazon basin (Henderson et al. 1995). This brief ethnobotanical exploration showed that the main use categories for palms were housing, food and hunting supplies, while to a lesser extent, household utensils, cultural, medicinal and cosmetics. Taking into consideration their uses, the most mentioned species were *M. flexuosa* and *B. gasipaes* for food, *M. flexuosa* for household utensils, *I. deltoidea* for hunting utensils, *O. bataua* and *I. deltoidea* for building, *Astrocaryum chambira* for cultural uses and *O. bataua* for medicine.

Interestingly, the perception of importance varied between gender. *Astrocaryum chambira* and *O. bataua*, used as a source of fibers and medicine, were considered the most useful palms by women, while *O. bataua* and *I. deltoidea* used for construction were mentioned as the most useful palm species by men. In addition, *Chamaedorea pauciflora*, used as a perfume, was mentioned only by women, whereas *Attalea maripa*, *Geonoma macrostachys* and *Bactris gasipaes*, used for thatching, were cited only by men.

The last day, we decided to treat our students to a surprise, and rented a motorized canoe to travel down the Tiputini river. These outings are important as we can see the palms from far in all their splendor, which changes from the understory view we generally have. We saw large river bank areas covered with *Bactris riparia*, majestic *Attalea butyracea*, and *Phytelephas tenuicaulis*. All along the river we also saw the usual suspects, such as *Iriartea deltoidea*, *Socratea exorrhiza* and *Euterpe precatoria*. However, the highlight of our river trip was not palms – students almost tipped over the canoe, when, in the blink of an eye, we spotted a small family of pink river dolphins (*Inia geoffrensis*). The mother and her

calf seemed amused by our boat and followed us, popping up now and then to the sound of camera shutters.

Finally, after six days of teaching, we left the calm hot and humid YRS and drove back up into the Andes to the noisy dry and cool city of Quito. Overall this was a great experience both for the students and teachers (Fig. 7). Focusing on different scientific disciplines centered around palms allowed a dynamic learning environment, in which students learned about the wide range of palm related research. We hope this course inspired several students to follow in the foot paths of some of the most eminent Latin American palm biologists.

### Acknowledgments

This field course was made possible by an International Palm Society grant to R. Montúfar. Additional funding was secured from the Pontifical Catholic University of Ecuador (PUCE), the support of French National Institute for Research for Sustainable Development (IRD), the International Mixed Laboratory Bio\_INCA (LMI\_Bio\_INCA) and the Universidad Autónoma de San Luis Potosí-México (UASLP). We thank the Guiyero community, who kindly allowed us to learn more about the Waorani culture, particularly Bolívar Enomenga, Isabel Ahua and Tepeña Ahua who accompanied us during our walks in the forest. We are so grateful to the authorities of YRS and its staff. We thank Esteban Baus, Rubén Jarrín and Alfredo Salazar, for video-recording the whole teaching experience, and R. Valencia for his suggestions to the text.

### LITERATURE CITED

BASS, M.S., M. FINER, C.N. JENKINS, H. KREFT, D.F. CISNEROS-HEREDIA, S.F. MCCracken, N. PITMAN, P.H. ENGLISH, K. SWING, G. VILLA, A.D. FIORE, C.C. VOIGT AND T.H. KUNZ. 2010. Global conservation significance of Ecuador's Yasuní National Park. PLOS ONE, 5, e8767.

COUVREUR, T.L.P., D. KISSLING, F.L. CONDAMINE, J.C. SVENNING, N.P. ROWE AND W.J. BAKER. 2015. Global diversification of a tropical plant growth form: environmental correlates and historical contingencies in climbing palms. *Frontiers in Genetics* 5: 452. <https://doi.org/10.3389/fgene.2014.00452>.

HENDERSON, A., G. GALEANO AND R. BERNAL. 1995. *Field Guide to the Palms of the Americas*. Princeton University Press.

HOWE, H. F. AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

JØRGENSEN, P.M. AND S. LEÓN-YÁNEZ. 1999. Catalogue of the vascular plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* 75: i–viii, 1–1182.

PINTAUD, J.-C., G. GALEANO, H. BALSLEV, R. BERNAL, F. BORCHSENIUS, E. FERREIRA, J.-J. DE GRANVILLE, K. MEJÍA, B. MILLÁN, M. MORAES, L. NOBLICK, F. STAUFFER AND F. KAHN. 2008. The palms of South America: diversity, distribution and evolutionary history. *Revista Peruana de Biología* 15: 7–29.

PINTAUD, J.-C., A. RODRÍGUEZ DEL CASTILLO, E.J.L. FERREIRA, M. MORAES AND K. MEJÍA. 2016. Towards a Revision of *Attalea* in Western Amazonia. *Palms* 60: 57–77.

TER STEEGE, H., N. PITMAN, D. SABATIER, C. BARALOTO, R.P. SALOMÃO, J.E. GUEVARA ET AL. 2013. Hyperdominance in the Amazonian tree flora. *Science* 342(6156), 1243092. <https://doi.org/10.1126/science.1243092>.

VALENCIA, R., R. CONDIT, R.B. FOSTER, K. ROMOLEROUX, G. VILLA MUNOZ, J.-C. SVENNING, E. MAGARD, M. BASS, E.C. LOSOS AND H. BALSLEV. 2004. Yasuní forest dynamics plot, Ecuador. Pp. 609–620, in LOSOS, E. AND E.G.J. LEIGH (eds.). *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. University of Chicago Press, Chicago.