



The palm *Mauritia flexuosa*, a keystone plant resource on multiple fronts

Yntze van der Hoek¹ · Sara Álvarez Solas¹ · María Cristina Peñuela¹

Received: 6 May 2018 / Revised: 29 October 2018 / Accepted: 20 December 2018 /
Published online: 4 January 2019
© Springer Nature B.V. 2019

Abstract

Keystone species are organisms, usually animals of higher trophic levels, that have large ecological impacts relative to their abundance. A recent extension of this concept recognizes hyperkeystone species, such as humans, which affect other keystone species and often play a key role in multiple ecosystem dynamics. Following a systematic review, we propose that the Neotropical palm species *Mauritia flexuosa*, though abundant locally, plays a role resembling that of a hyperkeystone species. First, it provides multiple types of key plant resources (food, nest sites, habitat) to a wide variety of species (at least 940 vertebrate species). Of vertebrates that directly use this palm as a food or nest resource (at least 74), at least 8 highly dependent on it for survival, 28 are threatened species, and at least 19 are keystone species themselves. This implies that a change in the abundance or distribution of *Mauritia flexuosa* is likely to have multiple cascading effects on Neotropical ecosystems. In addition, we highlight that this palm is also important for many invertebrates and other organisms and provides multiple ecosystem services, such as carbon sequestration. This vast ecological role of *M. flexuosa*, combined with its provision of a host of products to people, makes the species unique and worth prioritizing in conservation and plans for sustainable management across the Neotropics.

Keywords Keystone species · Neotropical palm · Conservation priority · Seed dispersal · Ecosystem services

Introduction

Worm and Paine (2016) recently put forward the concept of hyperkeystone species, which refers to species that ‘drive complex interaction chains by affecting other keystone actors across different habitats’. This builds on the traditional view of keystone

Communicated by Daniel Sanchez Mata.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10531-018-01686-4>) contains supplementary material, which is available to authorized users.

✉ Yntze van der Hoek
yntzevanderhoek@gmail.com

¹ Universidad Regional Amazónica Ikiam, Tena, Ecuador

species, which are those that have a larger impact on the stability and composition of communities and ecosystems than can be expected from their relative abundance (Paine 1969). As a result, we usually think of keystone species as large animals of higher trophic levels, such as marine top predators (Heithaus et al. 2008) or vegetation-altering herbivores (Waller and Altverson 1997). However, over the last four decades, the utility and applicability of the concept of keystone species has been extensively debated (e.g. Mills et al. 1993), refined (Paine 1995), redefined (Davic 2003), and expanded upon (Mouquet et al. 2013).

We now see that the label ‘keystone’ is being applied to an increasing number of animals (Mills et al. 1993), and even returns—though given an adapted definition—to describe ecological processes (Bednarz et al. 2004), habitats (Bonnet et al. 2009), and structures (Manning et al. 2006). In addition, we now recognize that many plant species perform keystone functions (‘keystone plant resources’, sensu (Terborgh 1986)), as they provide essential nutritional resources for animals (Nason et al. 1998; Peres 2000; Stevenson 2005; De Gredade 2013; Diaz-Martin et al. 2014), form structural elements important to a host of ecological functions (e.g. formation of microclimates or provision of nest substrates (Manning et al. 2006; Gibbons et al. 2008; Stagoll et al. 2012)), and are important sources of products used by local communities (Horn et al. 2012).

Mauritia flexuosa, a Neotropical dioecious palm species found across a large and heterogeneous range from closed *terra firme* lowland rainforests across the Amazon basin to more open savanna-like landscapes in the countries such as Brazil (where found in palm swamps called *veredas* (Tubelis 2009)) and Venezuela [where palm swamps are known as *morichales* (Ramirez and Brito 1990)]. Although it occurs even in solitary form across this vast region (Ter Steege et al. 2013) it is predominantly found in swamps or temporarily flooded terrain. *M. flexuosa* is often regarded as a keystone plant resource, across most of its range, for the many animals that nest in it (e.g. Brightsmith 2005) or that feed on its fruits (e.g., Lasso et al. 2016). Recognition for its disproportionately large impact on ecosystems includes early accounts by Von Humboldt and Bonpland (1853). They described the importance of this palm’s fruits for frugivorous birds in an environment with a scarce availability of food resources, the relatively open landscapes of the *Llanos* in Venezuela.

However, the importance of *M. flexuosa* for Neotropical ecosystems and biota is not limited to its role as a food or nesting resource. For people, *M. flexuosa* produces many other products including oils, fibers, and construction materials (Gilmore et al. 2013; Koolen et al. 2013). Moreover, *M. flexuosa* may be considered an ecosystem engineer—a species that interacts with other species through its capacity to physically alter environmental characteristics (sensu de Visser et al. 2013)—or even a foundation species that may be locally abundant (e.g. in swamps) and creates environmental conditions beneficial to other species (sensu Ellison et al. 2005), though this hypothesis seems to go largely untested for the moment being.

Many key plant resources also tend to be rather abundant at a given location—at least with respect to carnivores or herbivores. As such, even though a plant might provide keystone resources or functions, it would not necessarily be considered to have ‘disproportionate’ or ‘unexpected’ effects on the wider ecosystem (its biodiversity, processes or functioning), and thus qualify as a (hyper)keystone species (Worm and Paine 2016). *M. flexuosa* is also a relatively abundant species across its range and can be hyperdominant at certain locations (Ter Steege et al. 2013). Nevertheless, we propose that *M. flexuosa* exerts such a vast influence on its surrounding ecosystem, keystone vertebrate species included, that it approaches the definition of a species that plays multiple key roles in a range of ecological dynamics.

It is impossible to quantify the various ecological roles of *M. flexuosa* plays across all its heterogeneous and large range and to all associated organisms. For example, we still have little knowledge of its interactions with invertebrates, such as those beetles and bees that visit its flowers but do not seem to play a role in pollination (Khorsand Rosa and Koptur 2013). Similarly, its function in the creation and maintenance of palm swamps (and associated carbon sequestration) is still an underexplored topic of study (but see e.g., Vegas-Vilarrubia et al. 2010).

Given the difficulties quantifying the overall role of *M. flexuosa* in the ecosystems where it is found, but still avid to illustrate the importance of *M. flexuosa*, we opted to especially focus on the role of *M. flexuosa* as a key plant resource for vertebrates. First, we compiled an overview of all bird, mammal, reptile, and fish species that use *M. flexuosa* as a food, nesting, or habitat resource, from a defined set of literature (see “Methods”). Although many amphibians are also likely to be associated with *M. flexuosa*, we excluded this group of vertebrates from further analyses and discussion as amphibians are especially lacking adequate research in the Neotropics, and a systematic review would thus return underestimations of this taxon’s interactions with *M. flexuosa* (Fouquet et al. 2007).

With this initial step we aimed to give an example of the sheer richness of vertebrate species that interacts with *M. flexuosa*. But, we also used it answer how many vertebrates highly depend on this palm—species that will be severely affected if this species were to decline in abundance or distribution. Similarly, we asked how many of the vertebrate species that utilize *M. flexuosa* as a resource for food and nesting can themselves be considered keystone species. If many species depend strongly on *M. flexuosa* for multiple types of resources, and if *M. flexuosa* affects the survival of other keystone species, then we may tentatively conclude that *M. flexuosa* is a species akin to a higher-order keystone species that affects complex interaction chains—not unlike a hyperkeystone species.

Although out of the scope of this systematic review, a case for the importance of *M. flexuosa* would be even stronger if one was to consider the role this palm plays in providing resources to other organisms (invertebrates, plants, etc.), in sustaining and creating habitat as an ecosystem engineer or foundation species, and in altering ecological processes such as carbon fixation. Thus, we also searched for evidence for these roles, without aiming to provide a complete systematic overview, to illustrate some of the complexity and variety of ecological processes in which *M. flexuosa* is involved. We conclude that the impact of this palm is far beyond that of most other plants species in the Neotropics, that potential negative effects of reductions in *M. flexuosa* are many and complex, and thus label it as a species of utmost priority for conservation.

Methods

Between March of 2017 and February of 2018, we conducted a systematic search for literature on interactions between *M. flexuosa* and vertebrates. We searched primary literature in Google Scholar for evidence of interactions, using the keywords ‘vertebrates’, ‘avian’, ‘mammal’, ‘primate’, ‘rodent’, ‘fish’, and ‘reptile’, in combination with the term ‘*Mauritia flexuosa*’. For a more complete coverage of existing literature, we repeated this search using commonly used regional synonyms for *M. flexuosa* (*aguaje*, Peru; *buriti*; Brazil; *moriche*, Venezuela; *canangucha*, Colombia; *morete*, Ecuador; *palma real*, Bolivia) or the swamps in which the palms are usually found (*aguajal*, Perú; *veredas*, *buritizal*, Brazil; *cananguchal*, Colombia, *moretal*, Ecuador; *morichal*, Venezuela; *palm swamp*, general).

We scrutinized entries on the first 15 pages of returned search results per keyword combination and repeated each query in Spanish and Portuguese.

We found useful information in the articles cited throughout this paper as well as in literature cited in Tables S1 and S2. We completed our search by thoroughly scanning the Handbook of the Birds of the World Alive (del Hoyo et al. 2017), Handbook of the Mammals of the World, volume 3: Primates (Mittermeier et al. 2013), and multiple chapters of the book *Morichales, cananguchales y otros palmares inundables de Suramérica*, edited by Lasso et al. (2016), which provides an exhaustive summary of the ecology of palm swamps in South America. We listed references to species-specific interactions highlighted in the text in Tables S2 and S3—in a column behind the species of interest—and ask the reader to consult these lists for further reference.

Next, we categorized the type of resource *M. flexuosa* provided to each species. We considered *M. flexuosa* to be a food resource when vertebrates fed on its fruits, seeds, flowers or insects closely associated with it. We deemed *M. flexuosa* to be a resource for nesting if a species was known to nest directly in the palm or uses its leaves for nesting material. Finally, we categorized *M. flexuosa* as a provider of habitat if a vertebrate species was associated with the habitat (e.g., palm swamps) created, maintained, or defined by *M. flexuosa*. Species that were merely recorded in palm swamps dominated by *M. flexuosa* were included in this latter category.

Per definition, all species that feed on *M. flexuosa*, or use it for nest sites or materials, are also associated with *M. flexuosa* habitat. We ranked the strength a species' interaction with *M. flexuosa* as: (a) low when a species is occasionally found in or near *M. flexuosa* trees or swamps, but also is known to occur in other habitat types; as (b) intermediate when known to directly interact with *M. flexuosa* through feeding or nesting; or (c) as high when a species exclusively feeds on, or nests in, *M. flexuosa*.

We adopted the conservation status of each species from IUCN assessments (in order of increased threat: Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered; status as found on <http://www.iucnredlist.org/>, accessed January and February 2018). We used IUCN nomenclature for reptiles and fish but followed del Hoyo et al. (2017) for birds and Mittermeier et al. (2013) for primates, as these resources provide more recent taxonomic updates for these taxa.

For those species that use *M. flexuosa* as a food or nesting resource we also listed whether these species could be themselves be considered keystone species. The identification of keystone species can be difficult (see e.g., Power et al. 1996), and depends largely on the definition of the concept and the spatial scale at which one analyzes a species impact on its environment. Moreover, there is a paucity of natural history data, or at least publications on the matter, for many species in the Neotropics. Given these complications we adopted a fairly straightforward criterion to determine whether a species holds a keystone role, a criterion that can be applied to all species. For this, we considered that relatively large-bodied (for their respective taxon) vertebrates, that are usually found (in a natural setting) in relatively low abundances across relatively large ranges, and that play a defined ecological role (e.g., seed dispersal), are likely to be keystone species that have a larger impact on ecosystem dynamics, and on ecological network stability, than can be expected from their abundance (following e.g., considerations by Sinclair (2003) and Woodward et al. (2005)). We did not consider smaller species (e.g., small rodents (Brewer and Rejmánek 1999)), although these can also play significant roles in ecological processes, to be keystone species. Smaller-bodied species are often relatively abundant compared to large bodied species, this applies at least to mammals and likely birds in Neotropical terrestrial systems (Robinson and Redford 1986), but are often more specialized in both food

and habitat requirements, which usually leads to a large species spatial turn-over in heterogeneous environments (Bakker and Kelt 2000). As a result, the removal of a single small vertebrate is unlikely to lead to ecosystem or food-web destabilizing or cascading effects are across multiple habitats (Woodward et al. 2005; Worm and Paine 2016).

Results

At least 74 species use *M. flexuosa* as a food or nest resource (Figs. 1 and 2, Tables 1, S1). This includes at least 38 birds, 30 mammals, five reptiles, and a fish. If we also consider those vertebrates that are associated with *M. flexuosa*-related habitat, the total number increases considerably, to a total of 940 species (Table S2). Of the species that interact directly with *M. flexuosa*, nine are listed as Vulnerable and four as Endangered. The dependency of species on *M. flexuosa* is rather difficult to quantify, but we estimate that at least eight species are highly dependent on this palm for the provision of food or nest sites.

Mauritia flexuosa as a food resource for vertebrates

At least 53 vertebrate species feed on the fruits, flowers, or seeds of *M. flexuosa*, often dispersing seeds as a result. As such, we also note the existence of two-way interactions between keystone species, as large seed dispersers such as the maned wolf (*Chrysocyon brachyurus*) and blue-and-yellow macaw (*Ara ararauna*) are considered keystone species themselves (Trolle et al. 2006; Baños-Villalba et al. 2017). The red-bellied macaw (*Orthopsittaca manilata*) is a species especially worth highlighting, as it feeds nearly exclusively

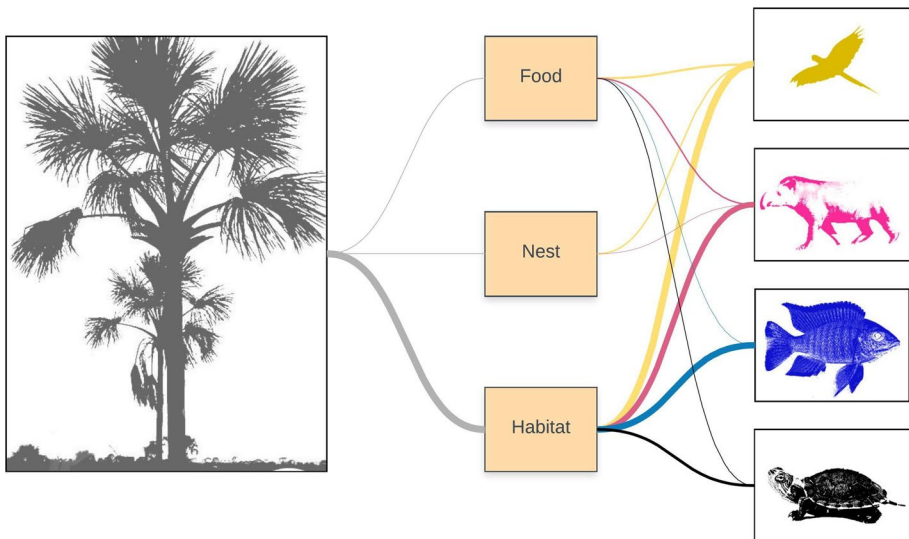


Fig. 1 Interactions of birds, mammals, fish and reptiles with *Mauritia flexuosa* as a provider of nest resources, food resources, or habitat. The size of the connecting lines is representative of the number of species that interact with *M. flexuosa* via a particular resource

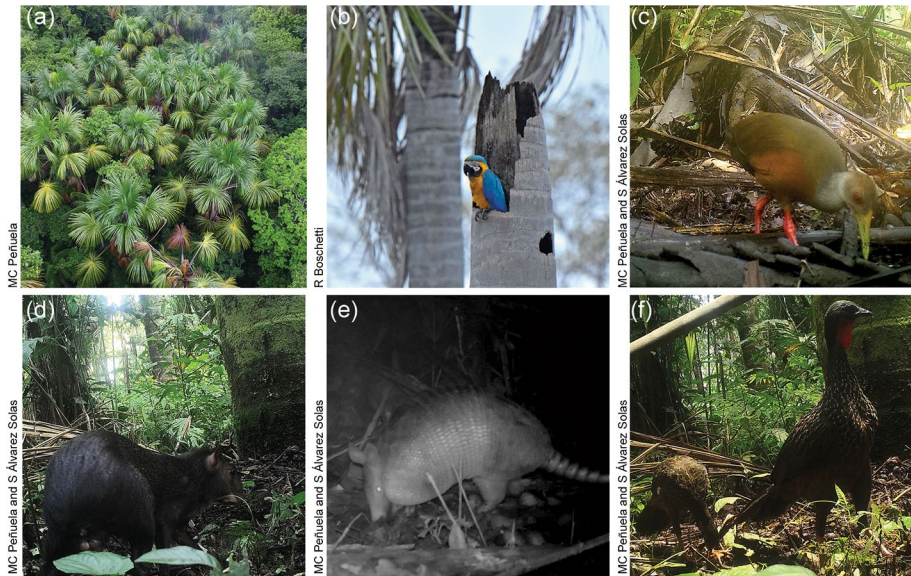


Fig. 2 Five of the nearly thousand vertebrate species that interact with *Mauritia flexuosa* by using the nest sites, food resources, and habitat it provides. **a** A *Mauritia flexuosa* dominated palm swamp. **b** Blue-and-yellow macaw (*Ara ararauna*) nesting in a dead trunk. **c** A gray-necked wood-rail (*Aramides cajaneus*) passing through a palm swamp foraging on *M. flexuosa* fruits. **d** Black agoutis (*Dasyprocta fuliginosa*) are some of the most important dispersers of *M. flexuosa* seeds. **e** Nine-banded armadillos (*Dasybus novemcinctus*) live and forage under the canopy of *M. flexuosa*. **f** A small flock of Spix's guan (*Penelope jacquacu*) pass underneath a large *M. flexuosa* while feeding on fallen *M. flexuosa* fruits and other food

on fruits of *M. flexuosa*. This bird is highly dependent upon *M. flexuosa*, but also serves as one of its main seed dispersers.

Some of the most important seed dispersers of *M. flexuosa* are rodents. For example, the black agouti (*Dasyprocta fuliginosa*) and paca (*Cuniculus paca*) can disperse up to 64% and 23% of seeds of *M. flexuosa* respectively (Acevedo-Quintero and Zamora-Abrego 2016). Additionally, it is important to recognize the role of large primates such as spider monkeys (e.g. *Ateles belzebuth*) in dispersing vast numbers of *M. flexuosa* seeds.

The yellow-footed tortoise (*Chelonoidis denticulate*) and red-footed tortoise (*Chelonoidis carbonaria*) feed on the flowers of *M. flexuosa*. In addition, birds such as crimson-crested woodpecker (*Campephilus melanoleucos*), green ibis (*Mesembrinibis cayennensis*) and moriche oriole (*Icterus chryscephalus*), as well as primates such as tamarin (*Saguinus* sp.), capuchin (*Sapajus* and *Cebus* sp.) and squirrel monkeys (*Saimiri* sp.), feed on insects associated with *M. flexuosa* fruits or stems.

***Mauritia flexuosa* as a resource for nest sites or nest materials for vertebrates**

Both birds and mammals use *M. flexuosa* as a nest site or for nesting materials. At least 23 bird species use *M. flexuosa* for this purpose, including many parrots (Psittacidae) that nest inside hollows and cavities in the trunk of *M. flexuosa*. Mammals such as Spix's night monkey (*Aotus vociferans*) and kinkajou (*Potos flavus*) sleep in the crowns

Table 1 Summary of the number of vertebrate species that interact with *Mauritia flexuosa*

Taxon	Food resource	Nest resource	Habitat resource	Threatened	Species highly dependent on <i>M. flexuosa</i>	Number of keystone species ^a	Total
Birds (Aves)	22	25	404	14	7	10	451
Mammals (Mammalia)	28	4	143	13	0	9	175
Fish (Peces)	1	0	262	0	1	0	263
Reptiles (Reptilia)	5	0	46	1	0	0	50
Total	56	29	853	28	8	19	940^b

^aThe number of species per taxon that are themselves considered a keystone species

^bThe total number of species does not equal the sum of species that use *Mauritia flexuosa* for food, nesting, or habitat, as some species interact with *M. flexuosa* in multiple ways

of the palms, whereas Ferreira's spiny tree-rat (*Mesomys hispidus*) and the black-tailed hairy dwarf porcupine (*Coendou melanurus*) use palm leaves to construct shelters.

Species that use *M. flexuosa* as a resource for nest sites or nest materials include keystone species such as the top predator harpy eagle (*Harpia harpyja*), which occasionally nest on top of the crown of *M. flexuosa*. However, it is the Neotropical palm-swift (*Tachornis squamata*) that is an especially illustrative *M. flexuosa*-dependent species, as it only builds its nest inside dead leaves of *M. flexuosa*, and nowhere else.

***Mauritia flexuosa* as a habitat resource, ecosystem engineer, or foundational species**

At least 451 birds, 175 mammals, 263 fish, and 50 reptiles associate to some extent with *M. flexuosa* through their habitat preferences (Table S2). *M. flexuosa*-associated habitats are diverse and range from single palms in savanna-type habitat to swamps with dense stands of palms and closed canopies. Vertebrates associate with these different habitats to varying extents. For example, species such as the Llanos long-nosed armadillo (*Dasypus sabanicola*), dwarf dog-faced bat (*Molossops temminckii*), and tiny yellow bat (*Rhogeessa minutilla*) associate exclusively with closed canopy *M. flexuosa* dominated swamps, whereas species such as the grassland-associated Southern lapwing (*Vanellus chilensis*) are likely to only briefly pass through swamps where *M. flexuosa* are prevalent.

With this consideration of the role of *M. flexuosa* in the provision it is also important to reiterate the numerous interactions that are likely to exist between *Mauritia flexuosa* and invertebrates, plants, and other organisms. For many of these organisms, for example insects or fungi that live inside *M. flexuosa* structures such as flowers or rotten trunks, *M. flexuosa* is likely to provide habitat and food simultaneously (Lasso et al. 2016). In turn, these species interact again with other vertebrate biota or ecological processes. For example, certain species of Hemiptera—many of which are considered potential agricultural pests or disease vectors—are commonly associated with *M. flexuosa* (Gurgel-Gonçalves et al. 2012). So are the larva of the beetle *Rhynchophorus palmarum* (Cerda et al. 2001), which are commonly consumed by people across the Neotropics, certain species of Lepidoptera (Frajia and Fajardo 2006), and many other insects that are important sources of food for a variety of vertebrates (Aquino 2005).

For many organisms, the habitat association with *M. flexuosa* could be the result of shared preferences for a specific set of abiotic and biotic conditions. For example, both *M. flexuosa* and associated species might thrive in a habitat that is flooded or has water-logged soils with a particular pH, micro-topography, and drainage condition (Galeano et al. 2015). For example, up to 40% of plants species found in palm swamps in Venezuela are near exclusive to such habitat (Ramirez and Brito 1990). The very presence of *M. flexuosa* likely perpetuates the existence of these habitats, and *M. flexuosa* is directly involved in the maintenance of favorable conditions (e.g. providing shade in otherwise sun-drenched savannas and grasslands). For example, without the dominant canopy cover of *M. flexuosa*, many swamps would experience changes in abiotic conditions and an increase in densities of woody species (Endress et al. 2013). Finally, we note that palm swamps, including those dominated by *M. flexuosa*, are also known for their relatively high capacity for carbon storage (Goodman et al. 2013), though the role of *M. flexuosa* in this process is still a topic of investigation (see “Discussion”).

Keystone species that use *Mauritia flexuosa* as a resource

At least ten bird species and nine mammals, of which respectively one and six species are listed as Vulnerable or Endangered, that depend to some extent on *M. flexuosa* as a food or nesting resource can be considered keystone species themselves. These species include seed dispersers such as macaws, primates and tapirs, but also top predators and scavengers. It is worth mentioning that we included macaws in our list of likely keystone species (following e.g., Baños-Villalba et al. 2017) but no other parrot species (Psittacidae). However, evidence that other parrots could also be key seed dispersers is starting to increase (Tella et al. 2015), and we thus deem our estimate that ‘at least ten keystone bird species’ interact with *M. flexuosa* a very conservative estimate, acknowledging that this number could well be higher.

Discussion

Mauritia flexuosa provides a diversity of resources to a vast number of vertebrate species, some of which are keystone species themselves, is important to a host of other organisms (invertebrates, plants, etc.), and plays a role in a variety of other, often complex, ecological processes such as habitat formation and carbon sequestration. Other palm species have been considered to provide keystone resources or structures, for example *Euterpe edulis* (de Barros Leite et al. 2012), but *M. flexuosa* provides these keystone resources across a large range and a variety of habitats and to an especially large number of species. Moreover, some of species are partially or fully dependent on *M. flexuosa*’s fruits, leaves, flowers, or habitat-creating characteristics for survival, and potential removal of *M. flexuosa* of ecosystems would have multiple cascading effects, for example mediated through population declines among associated keystone species. Therefore, conservation of large densities of *M. flexuosa*, and maintenance of existing distribution patterns of *M. flexuosa* dominated palm swamps, is key for both ecosystem stability and the survival of a substantial portion of Neotropical biodiversity, especially those species currently considered threatened by anthropogenic disturbances such as deforestation or climate change.

In fact, removal of *M. flexuosa* from any ecosystem would imply the removal of a node in a network of ecological interactions more complex and substantial than we present in this article. For one, potential declines or removal of any of the keystone species that interact with *M. flexuosa* as a result of decline of this palm’s abundance or distribution could induce a range of cascading effects, for example on forest regeneration (see e.g., the effects of macaws on shaping Amazonian ecosystems (Baños-Villalba et al. 2017) or on rates of herbivory and associated effects on plants (e.g., top-down control of herbivore populations by avian predators, like the harpy eagle (*Harpia harpyja*); Mäntylä et al. 2011). Red-bellied Macaw (*Orthopsittaca manilatus*), a species that near exclusively nests in dead palm trunks, is at least one keystone species that will likely be severely affected by declines in abundance or distribution of *M. flexuosa* (Brightsmith 2005). Other keystone species might be able to find alternative resources if *M. flexuosa* is not readily available, though it might be worthwhile mentioning that some species that only sparsely use resources provided *M. flexuosa* could very well depend on it during periods of scarcity of alternative resources (e.g., king vultures (*Sarcoramphus papa*) only rarely forage on *M. flexuosa* fruits, but may depend on it for survival when carrion is not readily available; Schlee 2005).

Second, although we acknowledge that some species listed in our list of habitat-associated species (Table S2), for example grassland-associated species such as the southern lapwing (*Vanellus chilensis*), might have very weak and infrequent interactions with *M. flexuosa*, we also lack detailed dietary data of many species known to inhabit *M. flexuosa*-associated habitat, and thus likely underestimated the number of species feeding on *M. flexuosa*. The diet and ecology of fish is particularly understudied, and it is very likely that a number of fish species also feed on fruits of *M. flexuosa*. This hypothesis is supported by observations made by local fishermen (Braga and Rebêlo 2014).

Third, as ecological data are missing for many taxa not reviewed in this article, we opted to exclude them from our summaries. This does not imply that only birds, mammals, reptiles, and fish interact with *M. flexuosa*. We briefly mention the importance of this palm for insects, but also acknowledge that species such as frugivorous bats are likely to feed on the fruits of *M. flexuosa* (as suggested by e.g., Lasso et al. (2016)), and that certain amphibians use *M. flexuosa* as a nesting resource (e.g., the Amazonian canopy frog (*Phrynohyas resinifictrix*; Schiesari et al. 2003)). In short, our estimate of the number of species that interact or depend on *M. flexuosa* is a conservative one, and the importance of *M. flexuosa* for the biota of the Neotropics might be even larger than we estimate here.

In addition, although we briefly address the role of *M. flexuosa* in habitat formation and associated abiotic processes (e.g., carbon sequestration, but also alterations of abiotic conditions of soil and water), very few empirical studies address this topic directly. For example, it is not yet clearly understood whether peat formation follows *M. flexuosa* colonization of an ecosystem or provides the conditions for it (though Roucoux et al. (2013) indicate that peat formation can both precede the establishment of *M. flexuosa* and continue during periods of *M. flexuosa* dominance). Similarly, it is worth noting that *M. flexuosa* is not found in all Amazonian peatlands, nor do all *M. flexuosa*-palm swamps contain peat (Lähteenoja et al. 2009). And finally, we are only slowly starting to understand the nature of abiotic cycles in palm swamps (see e.g., Chacón et al. 2018). That said, although it is clear that additional studies will be required, it also likely that removal of *M. flexuosa* will have pronounced effects on processes such as carbon sequestration, if only for reductions in this palm's substantial contribution to the above-ground storage of carbon in the Amazon (Draper et al. 2014). This enhances the suggestion that *M. flexuosa* plays key roles across multiple ecological dynamics, including those that involve abiotic processes.

Finally, we need to emphasize again the key role *M. flexuosa* plays in the provision of resources, beyond aforementioned ecosystem services like carbon fixation, to people. Use of *M. flexuosa*-derived products by local communities has a long history (Virapongse et al. 2017), but recent years have also seen much commercial interest in the nutritional and medical benefits of *M. flexuosa* (Koolen et al. 2013). Unfortunately, and despite its relatively high abundance and wide-spread distribution, these interests have made *M. flexuosa* locally threatened by unsustainable harvest and habitat conversion (Endress et al. 2013). Although there are economic incentives for sustainable management (Manzi and Coomes 2009; Martins et al. 2012), effective scaling-up of sustainable harvest has proven difficult. To counter further loss of *M. flexuosa*, we will need to invest in research on population dynamics and cultivation techniques, and need to address declines in the abundance of seed dispersers and pollinators (Endress et al. 2013; Gilmore et al. 2013).

We urge that incentives for sustainable use need to be intensified across the Neotropical region. Use of *M. flexuosa* should be aligned with efforts to promote sustainable trade in palm products (Brokamp et al. 2011) and with the establishment of adequate agroforestry strategies (Porro et al. 2012). Across the Neotropics, we need to prioritize the future of this important species in conservation and management (Goulding and Smith 2007; Virapongse

et al. 2017). Protection of this ‘tree of life’ (Von Humboldt and Bonpland 1853) is not only key to the future of many Neotropical ecosystems and their inhabitants, but also to people and ecosystems globally.

References

- Acevedo-Quintero JF, Zamora-Abrego JG (2016) Papel de los mamíferos en los procesos de dispersión y depredación de semillas de *Mauritia flexuosa* (Arecaceae) en la Amazonía colombiana. *Rev Biol Trop* 64:5–15
- Aquino R (2005) Alimentación de mamíferos de caza en los «aguajales» de la Reserva Nacional de Pacaya-Samiria (Iquitos, Perú). *Rev Peruana Biol* 12:417–425
- Bakker VJ, Kelt DA (2000) Scale-dependent patterns in body size distributions of neotropical mammals. *Ecology* 81(12):3530–3547
- Baños-Villalba A, Blanco G, Díaz-Luque JA et al (2017) Seed dispersal by macaws shapes the landscape of an Amazonian ecosystem. *Sci Rep* 7(1):7373
- Bednarz JC, Ripper D, Radley PM (2004) Emerging concepts and research directions in the study of cavity-nesting birds: keystone ecological processes. *Condor* 106:1–4
- Bonnet X, Brischoux F, Pearson D et al (2009) Beach rock as a keystone habitat for amphibious sea snakes. *Environ Conserv* 36:62–70
- Braga TMP, Rebêlo GH (2014) Traditional knowledge of the fishermen of the lower Juruá river: aspects related to the feeding habits of fish in the region [conhecimento tradicional dos pescadores do baixo rio Juruá: Aspectos relacionados aos hábitos alimentares dos peixes da região]. *Interciencia* 39:659–665
- Brewer SW, Rejmánek M (1999) Small rodents as significant dispersers of tree seeds in a Neotropical forest. *J Veg Sci* 10(2):165–174
- Brightsmith DJ (2005) Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. *Wilson Bull* 117:296–305
- Brokamp G, Valderrama N, Mittelbach M et al (2011) Trade in palm products in north-western South America. *Bot Rev* 77:571–606
- Cerda H, Martínez R, Briceno N et al (2001) Palm worm: (*Rhynchophorus palmarum*) traditional food in Amazonas, Venezuela—nutritional composition, small scale production and tourist palatability. *Ecol Food Nutr* 40:13–32
- Chacón N, Herrera R, Méndez C et al (2018) Mechanisms involved in soil ammonium production in a *Mauritia flexuosa* palm swamp community. *Wetlands* 38(3):641–646
- Davic RD (2003) Linking keystone species and functional groups: a new operational definition of the keystone species concept. *Conserv Ecol* 7(1):r11. <http://www.consecol.org/vol7/iss1/resp11>
- de Barros Leite A, Brancalion PH, Guevara R et al (2012) Differential seed germination of a keystone palm (*Euterpe edulis*) dispersed by avian frugivores. *J Trop Ecol* 28(6):615–618
- De Grenade R (2013) Date palm as a keystone species in Baja California peninsula, Mexico oases. *J Arid Environ* 94:59–67
- De Visser S, Thebault E, De Ruiter PC (2013) Ecosystem engineers, keystone species. Springer, Dordrecht
- del Hoyo J, Collar NJ, Christie DA et al (2017) Handbook of the birds of the world. Lynx Editions, Barcelona
- Díaz-Martin Z, Swamy V, Terborgh J et al (2014) Identifying keystone plant resources in an Amazonian forest using a long-term fruit-fall record. *J Trop Ecol* 30:291–301
- Draper FC, Roucoux KH, Lawson IT et al (2014) The distribution and amount of carbon in the largest peatland complex in Amazonia. *Environ Res Lett* 9(12):124017
- Ellison AM, Bank MS, Clinton BD et al (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* 3:479–486
- Endress BA, Horn CM, Gilmore MP (2013) *Mauritia flexuosa* palm swamps: composition, structure and implications for conservation and management. *For Ecol Manage* 302:346–353
- Fouquet A, Gilles A, Vences M et al (2007) Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. *PLoS ONE* 2:e1109
- Fraija N, Fajardo GE (2006) Caracterización de la fauna del orden Lepidoptera (rhopalocera) en cinco diferentes localidades de los llanos orientales colombianos. *Acta Biol Colomb* 11:55–68
- Galeano A, Urrego LE, Sánchez M et al (2015) Environmental drivers for regeneration of *Mauritia flexuosa* Lf in Colombian Amazonian swamp forest. *Aquat Bot* 123:47–53

- Gibbons P, Lindenmayer D, Fischer J et al (2008) The future of scattered trees in agricultural landscapes. *Conserv Biol* 22:1309–1319
- Gilmore MP, Endress BA, Horn CM (2013) The socio-cultural importance of *Mauritia flexuosa* palm swamps (aguajales) and implications for multi-use management in two Majjuna communities of the Peruvian Amazon. *J Ethnobiol Ethnomed* 9:29
- Goodman RC, Phillips OL, del Castillo Torres D et al (2013) Amazon palm biomass and allometry. *For Ecol Manage* 310:994–1004
- Goulding M, Smith N (2007) Palms: sentinels for Amazon conservation. Missouri Botanical Garden Press, St. Louis
- Gurgel-Gonçalves R, Cura C, Schijman AG et al (2012) Infestation of *Mauritia flexuosa* palms by triatomines (Hemiptera: Reduviidae), vectors of *Trypanosoma cruzi* and *Trypanosoma rangeli* in the Brazilian savanna. *Acta Trop* 121:105–111
- Heithaus MR, Frid A, Wirsing AJ et al (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 23:202–210
- Horn CM, Gilmore MP, Endress BA (2012) Ecological and socio-economic factors influencing aguaje (*Mauritia flexuosa*) resource management in two indigenous communities in the Peruvian Amazon. *For Ecol Manage* 267:93–103
- Khorsand Rosa R, Koptur S (2013) New findings on the pollination biology of *Mauritia flexuosa* (Arecaceae) in Roraima, Brazil: linking dioecy, wind, and habitat. *Am J Bot* 100(3):613–621
- Koolen HH, da Silva FM, Gozzo FC et al (2013) Antioxidant, antimicrobial activities and characterization of phenolic compounds from buriti (*Mauritia flexuosa* L. f.) by UPLC–ESI-MS/MS. *Food Res Int* 51:467–473
- Lähteenoja O, Ruokolainen K, Schulman L et al (2009) Amazonian peatlands: an ignored C sink and potential source. *Glob Chang Biol* 15(9):2311–2320
- Lasso CA, Colonnello G, Moraes M (2016) XIV. Morichales, cananguchales y otros palmares inundables de Suramérica. Parte II: Colombia, Venezuela, Brasil, Perú, Bolivia, Paraguay, Uruguay y Argentina. Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá
- Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures—implications for conservation. *Biol Conserv* 132:311–321
- Mäntylä E, Klemola T, Laaksonen T (2011) Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia* 165(1):143–151
- Manzi M, Coomes OT (2009) Managing Amazonian palms for community use: a case of aguaje palm (*Mauritia flexuosa*) in Peru. *For Ecol Manage* 257:510–517
- Martins RC, Filgueiras TS, Ulysses P (2012) Ethnobotany of *Mauritia flexuosa* (Arecaceae) in a maroon community in central Brazil. *Econ Bot* 66:91–98
- Mills LS, Soulé ME, Doak DF (1993) The keystone-species concept in ecology and conservation. *BioScience* 43:219–224
- Mittermeier RA, Rylands AB, Wilson DE (2013) Handbook of the Mammals of the World. Primates, vol 3. Lynx Edicions, Barcelona
- Mouquet N, Gravel D, Massol F et al (2013) Extending the concept of keystone species to communities and ecosystems. *Ecol Lett* 16:1–8
- Nason JD, Herre EA, Hamrick J (1998) The breeding structure of a tropical keystone plant resource. *Nature* 391:685–687
- Paine RT (1995) A conversation on refining the concept of keystone species. *Conserv Biol* 9(4):962–964
- Paine RT (1969) A note on trophic complexity and community stability. *Am Nat* 103:91–93
- Peres CA (2000) Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *J Trop Ecol* 16:287–317
- Porro R, Miller RP, Tito MR et al (2012) Agroforestry in the Amazon region: a pathway for balancing conservation and development. In: Nair PKR (ed) *Agroforestry—the future of global land use*. Springer, Dordrecht
- Power ME, Tilman D, Estes JA et al (1996) Challenges in the quest for keystones: identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *Bioscience* 46(8):609–620
- Ramírez N, Brito Y (1990) Reproductive biology of a tropical palm swamp community in the Venezuelan llanos. *Am J Bot* 77:1260–1271
- Robinson JG, Redford KH (1986) Body size, diet, and population density of Neotropical forest mammals. *Am Nat* 128(5):665–680
- Roucoux KH, Lawson IT, Jones TD et al (2013) Vegetation development in an Amazonian peatland. *Palaeogeogr Palaeoclimatol Palaeoecol* 374:242–255

- Schiesari L, Gordo M, Hödl W (2003) Treeholes as calling, breeding, and developmental sites for the Amazonian canopy frog, *Phrynohyas resinificatrix* (Hylidae). *Copeia* 2:263–272
- Schlee M (2005) King vultures (*Sarcoramphus papa*) forage in moriche and curucit palm stands. *J Raptor Res* 39(4):458–461
- Stevenson P (2005) Potential keystone plant species for the frugivore community at Tinigua Park, Colombia. In: Dew JL, Boubli JP (eds) *Tropical fruits and frugivores: the search for strong interactors*. Springer, Dordrecht
- Sinclair ARE (2003) Mammal population regulation, keystone processes and ecosystem dynamics. *Phil Trans R Soc B* 358(1438):1729–1740
- Stagoll K, Lindenmayer DB, Knight E et al (2012) Large trees are keystone structures in urban parks. *Conserv Lett* 5:115–122
- Tella JL, Baños-Villalba A, Hernández-Brito D et al (2015) Parrots as overlooked seed dispersers. *Front Ecol Environ* 13(6):338–339
- Ter Steege H, Pitman NC, Sabatier D et al (2013) Hyperdominance in the Amazonian tree flora. *Science* 342:1243092
- Terborgh JW (1986) Keystone plant resources in the tropical forest. In: Soule I, Michael E (eds) *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland
- Trolle M, Noss AJ, De Lima ES et al (2006) Camera-trap studies of maned wolf density in the Cerrado and the Pantanal of Brazil. *Biodivers Conserv* 16:1197–1204
- Tubelis DP (2009) Veredas and their use by birds in the Cerrado, South America: a review. *Biota Neotrop* 9:363–374
- Vegas-Vilarrubia T, Baritto F, López P et al (2010) Tropical histosols of the lower Orinoco Delta, features and preliminary quantification of their carbon storage. *Geoderma* 155:280–288
- Virapongse A, Endress BA, Gilmore MP et al (2017) Ecology, livelihoods, and management of the *Mauritia flexuosa* palm in South America. *Glob Ecol Conserv* 10:70–92
- Von Humboldt A, Bonpland A (1853) Personal narrative of travels to the equinoctial regions of America: during the years 1799–1804. Henry G, Bohn
- Waller DM, Alverson WS (1997) The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* (1973–2006). 25:217–226
- Woodward G, Ebenman B, Emmerson M et al (2005) Body size in ecological networks. *Trends Ecol Evol* 20:402–409
- Worm B, Paine RT (2016) Humans as a hyperkeystone species. *Trends Ecol Evol* 31:600–607