

## Research Article

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# The palm *Syagrus coronata* proliferates and structures vascular epiphyte assemblages in a human-modified landscape of the Caatinga dry forest

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## Abstract

The proliferation of disturbance-adapted species in human-modified landscapes may change the structure of plant communities, but the response of biodiversity to human disturbances remains poorly understood. We examine the proliferation of the palm, *Syagrus coronata*, in disturbed forest stands and its impacts on the structure of vascular epiphyte assemblages in a human-modified landscape of Brazilian Caatinga dry forest. First, we compared *S. coronata* density between old-growth and regenerating forest stands. We then surveyed vascular epiphytes on 680 phorophytes (*S. coronata* and non-palm/control species) across five habitat types with different disturbance levels. There was an eight-fold increase in *S. coronata* density in regenerating areas compared with in old-growth forest. *Syagrus coronata* supported richer epiphyte assemblages at local (i.e. per palm) and landscape (i.e. pooling all palms) scale than control phorophytes, supporting more than 11 times the number of species of control phorophytes at both scales. Epiphyte assemblages were more abundant, species-rich and dominated by abiotically dispersed species in forest sites with intermediate disturbance levels (regenerating forest stands). More than simply operating as an exclusive phorophyte for more than 90% of the epiphyte species we recorded here, *S. coronata* favours epiphyte persistence and structures their assemblages across human-modified landscapes of the Caatinga forest.

## Introduction

Human-driven disturbances of tropical forests are reorganizing their biodiversity from population to ecosystem level by converting them into human-modified landscapes, particularly through habitat loss, the creation of forest edges and the exploitation of forest resources (Laurance *et al.* 2002, Malhi *et al.* 2014). In this emerging scenario, a winner-loser replacement of native species occurs, leading to local/regional extirpation of several species and the proliferation of others (McKinney & Lockwood 1999, Tabarelli *et al.* 2012). Such population-level changes in plant species have been documented to alter the structure of whole plant communities relative to taxonomic, functional and phylogenetic attributes (Ribeiro *et al.* 2015, 2016; Rito *et al.* 2017b, Santos *et al.* 2014, Santo-Silva *et al.* 2013), with potential impacts on biodiversity persistence, patterns of ecosystem functioning and the provision of ecosystem services, such as carbon sequestration and storage (Magnago *et al.* 2015, Oliveira *et al.* 2008).

The proliferation of disturbance-adapted species as a response of tropical biodiversity to human-driven disturbances and their potential multiple cascades has only recently received attention (see Lopes *et al.* 2009, Tabarelli *et al.* 2012). One potential cascade of effects may involve some palm species and their associated communities of epiphytes. Tropical epiphytes represent a highly diverse plant group, with several species, or ecological groups, that are considered sensitive to human disturbances because they depend on particular microclimatic conditions (e.g. light and humidity) (Zotz & Bader 2009) and specific phorophytes or host plants (Aguirre *et al.* 2010, Benzing 1990, Mendieta-Leiva & Zotz 2015, Sanger & Kirkpatrick 2017), such as the disturbance-sensitive large trees in the Atlantic forest (Siqueira-Filho & Tabarelli 2006). On the other hand, many epiphytes may proliferate if the phorophytes with physical characteristics they depend on are disturbance-adapted species, which might explain in part the reports in the literature of contrasting responses by epiphyte communities across

human-disturbed tropical forests (Hietz *et al.* 2006, Nkongmeneck *et al.* 2002, Nöske *et al.* 2008, Werner & Gradstein 2009).

Several arborescent palm species, such as *Astrocaryum acaule*, *A. mexicanum*, *Attalea humilis*, *A. oleifera*, *A. speciosa*, *Bactris maraja* and *Lepidocaryum tenue*, are known to increase their densities in disturbed habitats (Aguiar & Tabarelli 2010, Campos *et al.* 2017, Martínez-Ramos *et al.* 2016, May *et al.* 1985, Pimentel & Tabarelli 2004, Scariot 1999, Souza & Martins 2003). Following human-driven disturbances, the increased recruitment rates in response to increased light availability (Souza & Martins 2003) and changes in dispersal–predation dynamics caused by poaching are two of the mechanisms that lead these palm species to proliferate (Pimentel & Tabarelli 2004, Wright *et al.* 2000). Some palm species may play an important role in epiphyte community assembly because they keep senescent leaf sheaths covering the stem, which favour the accumulation of nutrient-rich sediments that allow plant development and may contain a particular seed bank (Bernal & Balslev 1996, Corrêa *et al.* 2012, Nadkarni & Haber 2009), including not only true epiphytes and hemiepiphytes, but also accidental and facultative epiphytes (Castro *et al.* 2016, Oliveira *et al.* 2015). In addition, palm stems can represent a safe site for epiphytic species with decreased mortality risk and an increased probability of plant establishment (Benzing 1990, Corrêa *et al.* 2012). Therefore, palm species may represent an important phorophyte for epiphyte communities in human-disturbed tropical forests. Despite this, the potential role played by palms as phorophytes has received very little attention, particularly in tropical dry forests, one of the most threatened forest types in the world (Miles *et al.* 2006).

The Brazilian Caatinga is the largest and one of the most species-rich seasonally dry tropical forests globally, covering an area of 912 529 km<sup>2</sup> of north-eastern Brazil (Silva *et al.* 2017). The Caatinga has been experiencing conversion of its natural vegetation into human-modified landscapes since the arrival of the Europeans in the 16th century. Nowadays, the extant vegetation consists of mosaics of croplands, pastures, fallows, and old-growth and regenerating forest stands of varying ages (Silva *et al.* 2017). In this human-dominated scenario, some plant species benefit by increasing their relative abundance, not only due to the altered physical environment (Ribeiro *et al.* 2015, 2016; Ribeiro-Neto *et al.* 2016, Rito *et al.* 2017b), but also due to human use and protection (Noblick 2017). This may well be the case for *Syagrus coronata* (Mart.) Becc. (Arecaceae), a palm tree endemic to the Caatinga that is exploited by local human populations for multiple purposes, such as food, construction and craftwork (Noblick 2017, Rufino *et al.* 2008). Although *S. coronata* supports species-rich epiphyte assemblages in the Caatinga (Oliveira *et al.* 2015), it is unclear whether it plays an important role in species persistence and, therefore, acts as a community-structuring force across Caatinga human-modified landscapes; i.e. a pervasive cascade associated with the proliferation of disturbance-adapted species.

Here, we investigated whether the palm, *S. coronata*, proliferated in a human-modified landscape of Caatinga dry forest and how this species affected the structure of epiphyte assemblages. First, we documented *S. coronata* density in old-growth and regenerating stands of Caatinga to evaluate if the palm proliferates in disturbed habitats. Second, we recorded the vascular epiphyte flora supported by *S. coronata* and by non-palm/control phorophytes across five habitats ranging from crop/pasture to old-growth forest stands. We expected (1) *S. coronata* to provide microhabitats for several epiphyte species, including not only true epiphytes but also plants from other life forms, as palm leaf sheaths and stipe scars

represent a microhabitat with unique characteristics in our landscape; and (2) *S. coronata* to exhibit distinct cross-habitat epiphyte assemblages, with more disturbed habitats exhibiting epiphyte assemblages with relatively low species richness and reduced numbers of individuals, as well as few biotically dispersed species and individuals, which are at a disadvantage in disturbed sites. Beyond simply documenting the role played by a specific phorophyte in the persistence of epiphyte species, we highlight the cascade of effects connecting human disturbance, proliferation of disturbance-adapted species and community organization at the landscape level.

## Methods

### Study area

This study was carried out in the Catimbau National Park (8°24'00''–8°36'35''S, 37°0'30''–37°1'40''W), a 607-km<sup>2</sup> protected area in north-east Brazil. The regional climate is semiarid, with an average annual temperature of 23°C and precipitation ranging from 550–1100 mm (Rito *et al.* 2017a). Quartzite sandy soils predominate and support low-stature dry forests, with some enclaves of shrubby vegetation over rocky terrain. Fabaceae, Euphorbiaceae, Boraginaceae and Burseraceae are the dominant and most species-rich families (Rito *et al.* 2017a). Since the arrival of European populations in the 16th century, the Caatinga dry forest has been converted into human-modified landscapes via slash-and-burn agriculture and livestock production (Silva *et al.* 2017). Such landscapes, including an expressive portion of the Catimbau National Park, can be referred to as vegetation mosaics consisting of old-growth and regeneration forest stands of varying age plus active and abandoned crop/pasture fields (Souza *et al.* 2019).

### *Syagrus coronata*

*Syagrus coronata* is a palm tree, with a single stem that grows to 3–12 m in height and is endemic to the Caatinga region (Noblick 2017) (Figure 1). The leaves, of about 2–3 m in length, grow at regular intervals forming a spiral along the stipe (Drummond 2007, Noblick 2017). When a leaf is shed, a scar remains in the stipe, as well as on a portion of the sheath (up to 30 cm long), which allows the accumulation of nutrients and water in the rainy seasons (Drummond 2007). Flowers are unisexual, with male and female flowers in the same inflorescence, and the fruits are ellipsoid drupes arranged in clusters (Noblick 2017). The peak of flowering and fruiting of *S. coronata* is from December to March, but this palm flourishes and fruits all year round (Noblick 2017).

Because it flourishes and fruits year-round and remains green in the dry season, *S. coronata* is commonly used by human populations for many purposes (Noblick 2017, Rufino *et al.* 2008). Almost all parts of the palm are used: fruits as food for humans and domestic animals, the trunk and leaves for construction and craftwork, the trunk as fuelwood and the watery endosperm for medicinal purposes (Rufino *et al.* 2008). Thus, palms are often maintained close to human dwellings and persist even in very disturbed areas. In fact, the formation of dense populations of *S. coronata* in disturbed areas is very common in the Catimbau National Park, particularly in abandoned croplands and cattle pastures (personal observation), suggesting that this species may benefit from disturbances, as do other tropical palm species (Aguiar & Tabarelli 2010, Pimentel & Tabarelli 2004, Scariot 1999, Souza & Martins 2003). Previous studies (e.g. Castro *et al.* 2016, Oliveira *et al.* 2015) have



**Figure 1.** *Syagrus coronata* in the Catimbau National Park, north-east Brazil. Burned area where *S. coronata* palms proliferate (a), *Serpocaulon* sp. (b), *Anthurium affine* (Araceae) (c), *Catasetum purum* (Orchidaceae) (d), *Aechmea leptantha* (e), *Neoglaziovia variegata* (Bromeliaceae) (f), fruiting individuals of *Pilosocereus pachycladus* (g), *Tacinga inamoena* (Cactaceae) (h) and mosses covering the palm trunk and leaf sheaths (i).

also documented many epiphytes inhabiting *S. coronata*, including true epiphytes and those taking other life-forms.

### *Syagrus coronata* density

To investigate the response of *S. coronata* to human disturbance, particularly shifting cultivation, all palms (DSH  $\geq 3$  cm and  $\geq 1$  m tall) were sampled across 35 0.1-ha plots (20  $\times$  50 m), distributed in two habitat types: (1) old-growth forest – 20 plots across sites with no signs of agricultural land use, thereby exhibiting aboveground biomass higher than regenerating forest stands in our focal landscape (Souza *et al.* 2019); and (2) stands of regenerating forest – 15 plots in areas previously used for small crops (i.e. shifting cultivation), particularly beans, cassava and corn, which were abandoned

from four to 70 years ago (Table S1, Supplementary material). Plots were at least 2 km apart and their spatial location intended to cover most of the precipitation and regeneration gradients (see Rito *et al.* 2017a, Souza *et al.* 2019). The age of regenerating forest stands or time since land abandonment was established through interviews with local residents as already published (Souza *et al.* 2019).

### Epiphyte sampling

For the inventory of epiphytes, we selected 680 phorophytes, 340 *S. coronata* palms and 340 non-palms (hereafter control phorophytes) in a paired sampling design, across 17 sites covering a wide range in terms of land use and vegetation structure. These 17 sites were at least 1 km apart and assigned to five classes of disturbance

intensity (from the most to the least disturbed): (1) cropland (one plot) – an agriculturally used field still supporting some individuals of *S. coronata*; (2) active cattle pastures (two sites) – fenced areas for cattle grazing, dominated by grasses and with low densities of cacti and *S. coronata*; (3) stands of regenerating forest (eight sites) – second-growth forest stands of 4–20 years after land abandonment; (4) shrubby Caatinga (three sites) – patches of old-growth Caatinga vegetation dominated by shrubs up to 3 m tall; and (5) old-growth forest (three sites) – patches of Caatinga dominated by trees > 6 m tall without evidence of shifting cultivation. In each site, we selected haphazardly 20 *S. coronata* palms 1.5–6 m tall ( $4.2 \text{ m} \pm 1.3$ ), at least 10 m apart and counted and registered all epiphyte individuals presented in leaf sheaths and scars. We selected the nearest ( $\geq 10 \text{ m}$  distant) tree to each *S. coronata* palm as control phorophytes. All control phorophytes present characteristics of adult/old trees in Caatinga, with  $4.4 \text{ m} \pm 2.1$  tall, similar to the palms sampled in this study (see above). We understand that the best option would be to use another palm species as a control phorophyte, but *S. coronata* is the only native palm in our landscape. Epiphytes were sampled from August 2014 to May 2015, during the dry and wet seasons. The number of sites and palms sampled reflects their availability in our focal landscape, resulting in an unequal sampling effort. In order to estimate how much habitat *S. coronata* provides for epiphytes, both scars and leaf sheaths were counted in each sampled palm.

### Functional groups of epiphytes

All epiphytes were identified at least to family level and assigned into functional groups based on their relationship with the host (i.e. life form) and according to their dispersal mode. Four life forms were considered: (1) accidental – plants without specific adaptations for canopy life that were growing accidentally on the phorophyte and whose roots did not make contact with the ground (this category included shrubs and cacti); (2) facultative – those that can inhabit both the canopy and the ground; (3) hemiepiphytes – plants which start their life cycle as epiphytes but reach the ground later; (4) true epiphytes or holoeipiphytes (hereafter *true epiphytes*) – epiphytes that spend their entire life without coming into contact with the ground (Benzing 1990). Dispersal modes were defined as: (1) biotically dispersed – those species that produce fresh pulp, aril or other features that attract animals; and (2) abiotically dispersed – including species with structures that promote wind-dispersal such as plumes or winged seeds (anemochoric), weight-dispersed species (barochoric), and those with ballistic discharge of seeds due to explosive dehiscent fruits (van der Pijl 1982). Ballistic dispersal is commonly observed in Euphorbiaceae (Griz & Machado 2001, Webster 1994), while ballistic and barochoric dispersal are frequent in Fabaceae species (Griz & Machado 2001), the two most speciose families in the Caatinga (Ribeiro *et al.* 2015, Rito *et al.* 2017a).

### Data analysis

First, to examine the proliferation of *S. coronata* in disturbed habitats, we compared the population densities of old-growth ( $n = 20$ ) and regenerating forest ( $n = 15$ ) stands using a Wilcoxon test. Due to an extensive range in time since abandonment across regenerating forest stands (i.e. the age of forest stands), we also performed a linear regression to test the relationship between this variable and *S. coronata* density. Differences in epiphyte richness between *S. coronata* and control phorophytes were analysed using two methods. At local scale, we compared the epiphyte species richness

per phorophyte using Wilcoxon tests. At landscape scale, differences in terms of species richness supported by phorophytes were analysed using species accumulation curves constructed using the Vegan package in R. In both methods, we performed the analysis twice – once considering all epiphyte life forms, and once considering only true epiphytes.

To evaluate the effect of habitat type on the epiphyte assemblages supported by *S. coronata*, we first examined between-habitat differences in epiphyte species richness and abundance per palm by performing GLMs followed by Tukey's post hoc comparisons, considering each individual of *S. coronata* as one sample. As the number of leaf sheaths differed greatly in individuals of *S. coronata* (11–900 sheaths), we also adopted the number of sheaths as a factor in the GLMs. Second, we evaluated total species richness via individual-based rarefaction curves (Chao *et al.* 2014). We extrapolated rarefaction estimates of species richness and calculated their 95% of confidence intervals using the iNEXT function of the iNEXT package in R. Third, we performed G tests to evaluate between-habitat differences in the proportion of biotically and abiotically dispersed species. Fourth, we documented levels of taxonomic similarity between habitats via non-metric multidimensional scaling (NMDS) based on a Bray–Curtis dissimilarity matrix using the Vegan package in R. Species abundances were sqrt-transformed to avoid any bias resulting from highly abundant species. Given that some palms presented a relatively low number of epiphytes, we performed NMDS treating each site as a sample to avoid any bias from low abundance communities. To infer the contribution of biotically dispersed species to patterns of taxonomic similarity, we performed a GLM using this variable as an exploratory variable for NMDS scores. Finally, an indicator species analysis (Dufrene & Legendre 1997) was carried out for the assemblages across the five habitats. All analyses were performed in R (version 3.5.3).

### Results

A total of 106 *S. coronata* individuals were sampled across the 35 0.1-ha plots, with an average of  $3.02 \pm 5.2$  individuals (mean  $\pm$  SD) per plot (0.1 ha). Palm density was eight times higher in regenerating ( $6.07 \pm 6.7$  palms/0.1 ha) compared with old-growth forest stands ( $0.75 \pm 1.5$  palms/0.1 ha) ( $W = 72.5$ ;  $P < 0.05$ ; Figure 2). No relationship was found between the age of secondary forest stands and *S. coronata* density ( $R^2 = 0.06$ ,  $P < 0.376$ ).

Across the 680 phorophytes sampled in the five habitat types, a total of 59 species from 31 genera and 26 families were recorded. Bromeliaceae and Cactaceae (12.1% of recorded species, in each family), Euphorbiaceae (8.6%), Orchidaceae and Fabaceae (6.9% each) were the most species-rich families, while *Cataseum purum* (28.7% of all individuals), *Vanilla palmarum* (16.8%) and *Pilosocereus pachycladus* (7%) were the most abundant species. However, only 25% were true epiphytes, 26% were facultative, 24.4% were accidental epiphytes and 4.1% were hemiepiphytes (Table S2, Supplementary material). On average, palms exhibited  $101.6 \pm 77.2$  sheaths and up to 2000 scars on a single individual ( $207.7 \pm 110.7$ ).

*Syagrus coronata* supported all the epiphyte species recorded at the landscape scale (i.e. 59 species), including true epiphytes and species from other life forms. On the other hand, only four species were recorded on control phorophytes, all true epiphytes from the Bromeliaceae family, with most individuals belonging to the *Tillandsia* genus. A total of 93.1% of species from all life forms were exclusively recorded on *S. coronata*, particularly in the palm leaf



**Figure 2.** Density of the palm *Syagrus coronata* (individuals/0.1 ha) found in old-growth and regenerating forest stands of Caatinga in the Catimbeau National Park, north-east Brazil. Boxes indicate 25th and 75th percentiles, while error bars indicate 10th and 90th percentiles. Solid and dashed lines show median and mean, respectively, while black points indicate the outliers.

sheath. In terms of true epiphytes, 69.2% of species were recorded exclusively in *S. coronata*. At local scale, *S. coronata* supported, on average, much more epiphyte species than control phorophytes when considering either all life forms (species richness more than 11 times higher;  $V = 38.338$ ,  $P < 0.001$ ; Figure 3A) or true epiphytes exclusively (more than 5 times higher;  $V = 18.884$ ,  $P < 0.001$ ; Figure 3B). At landscape scale (i.e. collapsing all sampled phorophytes via rarefaction curves), *S. coronata* exhibited a total number of species almost 15 times greater than control phorophytes. In addition, the species rarefaction curve suggested we did not capture all epiphyte species which inhabit *S. coronata*, while the rarefaction curves for our control phorophytes appeared to have reached an asymptote (Figure 3C). When considering only true epiphytes, *S. coronata* hosted four times more species than control phorophytes (Figure 3D).

The role played by *S. coronata* palms supporting epiphytes was dependent on habitat type – epiphyte richness and abundance per palm were higher in habitats that experienced intermediate regimes of disturbance. For example, cattle pastures, regenerating stands and shrubby Caatinga exhibited values higher than croplands and old-growth Caatinga in terms of epiphyte abundance (Figure 4A;  $F = 7.65$ ,  $P < 0.0001$ ) and species richness (Figure 4B;  $F = 9.08$ ,  $P < 0.0001$ ). However, individual-based rarefaction curves for all habitat types suggested epiphyte richness on *S. coronata* is probably higher than sampled here (Figure 5). Epiphyte assemblages recorded on *S. coronata* also differed in terms of prevailing dispersal mode, since those in cattle pastures, regenerating stands and shrubby Caatinga exhibited the lowest relative abundance of biotically dispersed epiphytes ( $G = 76.77$ ,  $g.l. = 4$ ,  $P < 0.0001$ ; Figure 6A). However, epiphyte assemblages supported by *S. coronata* were similar across habitats in terms of relative richness of biotically dispersed species ( $G = 6.03$ ,  $g.l. = 4$ ,  $P = 0.197$ ; Figure 6B).

Epiphyte assemblages in *S. coronata* were taxonomically distinct across the focal habitats. The NMDS ordination indicated relatively similar assemblages across sites experiencing the same disturbance level (stress = 0.21; Figure 7), but this pattern was not explained by the percentage of biotically dispersed species ( $R^2 = 0.10$ ,  $P = 0.206$ ). Finally, the indicator species analysis suggested the existence of cross-habitat differences in assemblages by

identifying *Talinum paniculatum* as an indicator of pastures (indicator value = 0.84,  $P = 0.031$ ) and a Poaceae species as an indicator of cropland assemblages (indicator value = 0.62,  $P = 0.007$ ).

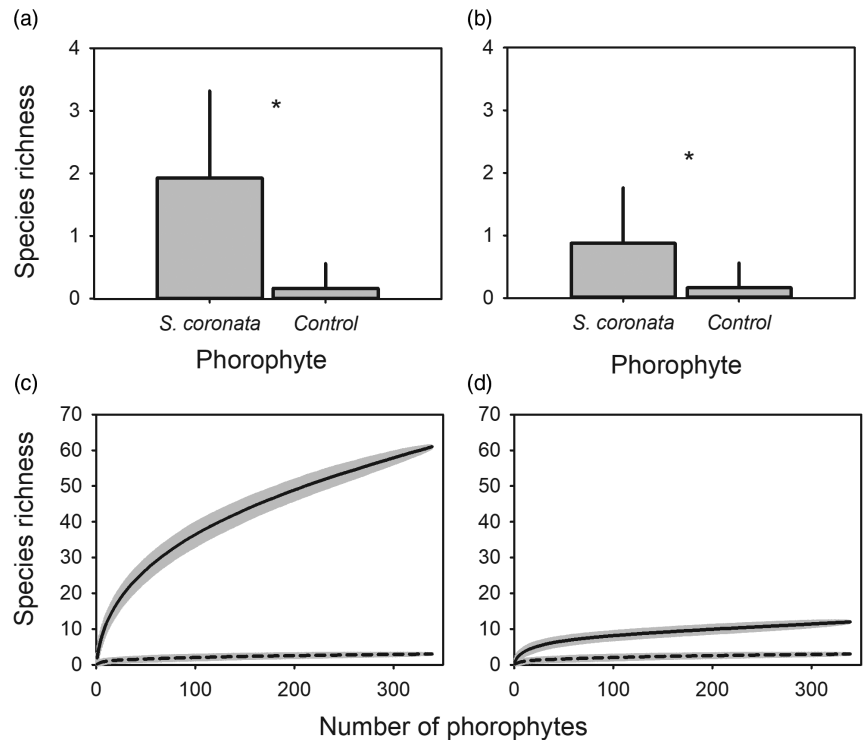
## Discussion

Our study suggests that the palm *S. coronata* benefits from human disturbances and becomes particularly abundant across regenerating forest stands, while also inhabiting pastures and old fields in human-modified landscapes of the Caatinga dry forest. *Syagrus coronata* populations support abundant and diverse vascular plant assemblages, consisting not only of true epiphytes but also facultative, hemiepiphytes, shrubs and small tree species (here classified as accidental epiphytes). Interestingly, many shrub, tree and cactus species recruit on *S. coronata* individuals, including some species that manage to conclude the reproductive phase of their life cycles on the palms.

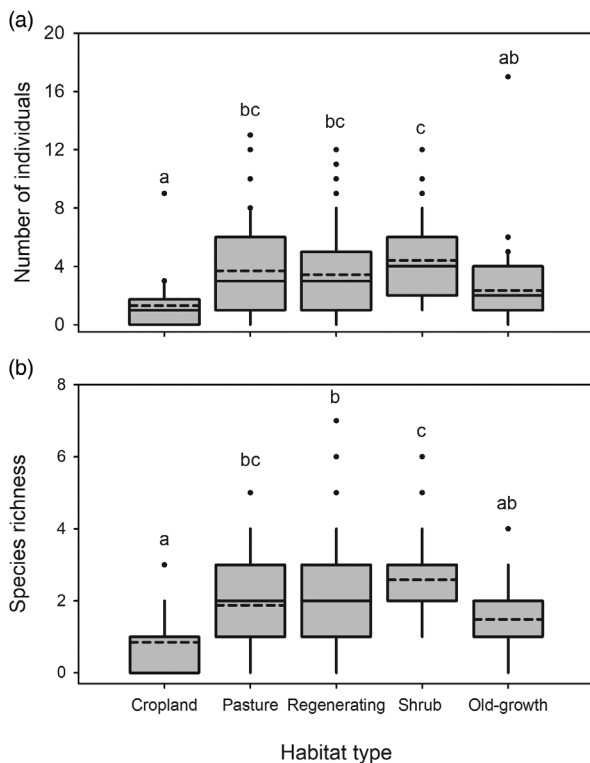
In fact, *S. coronata* appears to be an exclusive phorophyte plant species in human-modified landscapes of Caatinga dry forest, including true and non-true epiphytes. Differently from control phorophytes, *S. coronata* can accumulate in the palm sheaths and scars a substrate similar to those found on the ground, which favour the establishment of epiphytes from all life forms across a wide range of habitats from pasture to old-growth forest. Moreover, *S. coronata* is able to support relatively distinct assemblages, including in pastures, as suggested by the selection of *Talinum paniculatum* as an indicator species. Finally, *S. coronata* provides an irreplaceable ecological role across a wide range of habitats from pasture to old-growth forest, as ~70% of true epiphyte species rely exclusively on these palms, including six orchids and bromeliad species.

The higher density of *S. coronata* in regenerating stands contradicts the idea that this palm is threatened by human exploitation in the Caatinga (Johnson 1996, Rufino *et al.* 2008) and suggests that this species is in fact a *winner* (*sensu* Tabarelli *et al.* 2012) because it proliferates across second-growth stands of the Caatinga dry forest (also see Souza *et al.* 2019). The eight-fold increment in *S. coronata* population density we documented is much higher than those reported for other palm species in disturbed habitats (e.g. Campos *et al.* 2017, Martínez-Ramos *et al.* 2016). Increments in arboreal palm density across disturbed forest habitats are commonly associated with an increase in light incidence (Souza & Martins 2003) and changes in the rates of seed predation and dispersal (Pimentel & Tabarelli 2004, Wright *et al.* 2000). In our focal landscape, exotic goats eat the fruits of *S. coronata* and regurgitate a substantial number of their seeds throughout the entire landscape (M. Tabarelli, personal observation), which might help this palm species to persist across a variety of habitats due to long-distance seed dispersal events. Local people also collect and eat fruit pulps, discarding the seeds along paths.

In addition to effective seed dispersal by exotic species (e.g. goats and humans), the distribution of *S. coronata* in ecologically distinct habitats in our focal landscape suggests that it is able to tolerate (1) environmental stress associated with open habitats, such as extreme temperatures, intense luminosity and soil desiccation, and (2) human-imposed defoliation, fire and browsing by livestock such as goats. In fact, *S. coronata* appears to be a stress-tolerant and aggressive colonizer, as are other light-demanding palm species, e.g. *Attalea humilis*, *A. oleifera*, *A. speciosa* (Aguilar & Tabarelli 2010, Campos *et al.* 2017, Henderson *et al.* 1995, Lorenzi *et al.* 2004, May *et al.* 1985). Moreover, farmers frequently leave some palms when clearing forest for pasture or



**Figure 3.** Average species richness (a and b) and species rarefaction curves of epiphytes (c and d) found on the palm *Syagrus coronata* (solid lines) and other phorophytes (dashed lines) in areas of Caatinga in the Catimbau National Park, north-east Brazil. In A and C we take into account all types of epiphytes, while in B and D we analysed only true epiphytes. Error bars indicate standard deviation. \*  $P < 0.05$ .

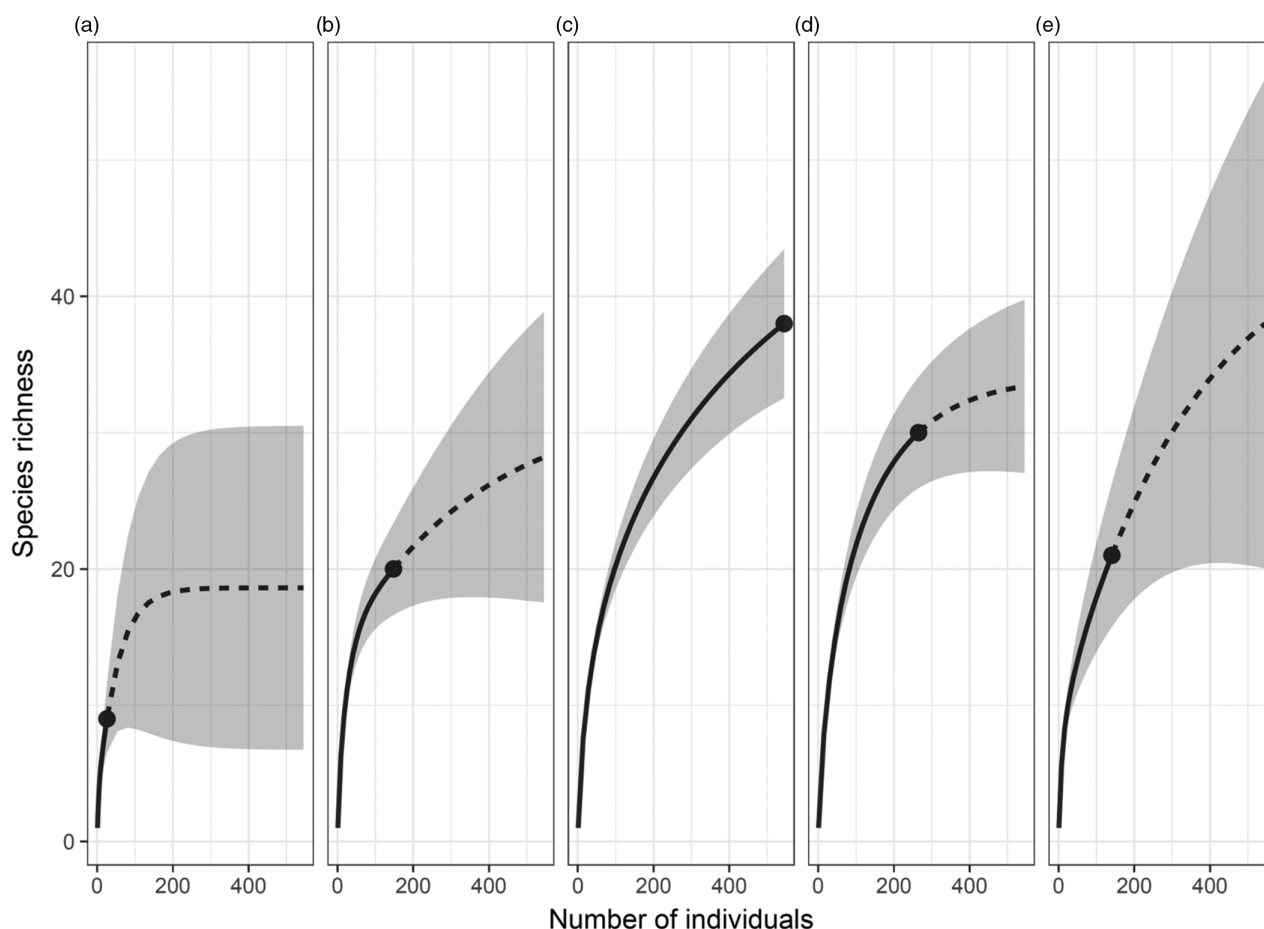


**Figure 4.** Number of individuals (a) and species richness (b) of vascular epiphytes on the palm *Syagrus coronata* in areas of Caatinga with different levels of disturbance in the Catimbau National Park, north-east Brazil. Boxes indicate 25th and 75th percentiles, while error bars indicate 10th and 90th percentiles. Solid and dashed lines show median and mean, respectively, while black points indicate the outliers. In B, median is equal to 75th percentile for croplands, equal to mean for regenerating forest stands, and equal to the 25th percentile for shrubby and old-growth Caatinga.

crops as they are useful. *Syagrus coronata* has a long list of uses by rural populations, such as providing forage for cattle during the dry season, providing raw materials for construction and craftwork, as well as being used as a food source and for medicinal purposes (Noblick 2017, Rufino *et al.* 2008).

Our findings also highlight the value of palms for biodiversity persistence, as *S. coronata* supports rich epiphyte communities in both natural and human-modified landscapes (Castro *et al.* 2016, Corrêa *et al.* 2012, Oliveira *et al.* 2015). These findings contrast to those documented across oil palm plantations, which exhibit reduced biodiversity value by supporting not only impoverished epiphyte communities (Böhnert *et al.* 2016, Einzmann & Zotz 2016) but also of arthropods associated with these plants (Fayle *et al.* 2010, Turner & Foster 2009). Other studies also have documented a diverse flora supported by some palm species, such as *S. coronata* in the Caatinga dry forest; e.g. 16 epiphyte species supported by *S. coronata* in the Catimbau National Park (Castro *et al.* 2016, Oliveira *et al.* 2015), 17 epiphyte/hemiepiphyte species on *Sabal mexicana* across disturbed habitats in México (Aguirre *et al.* 2010), and seeds from 75 species in the palm sheaths of *Attalea phalerata* in the Pantanal (Corrêa *et al.* 2012). As the only palm species exhibiting long-standing sheaths in our focal landscape (see Rito *et al.* 2017a), *S. coronata* represents an irreplaceable habitat for many true epiphytes such as Orchidaceae species, which are recognized as vulnerable and under threat of extinction (CITES 2019). Beyond true epiphytes, shrub and tree species (e.g. *Caesalpinia microphylla*, *Mimosa ophthalmocentra* and *Croton* species) also recruit on *S. coronata* palms, but most of these species (except cactus species) are not expected to reproduce successfully (e.g. *Croton* shrubs); i.e. palms can operate as seed traps rather than a safe recruitment site.

Furthermore, our findings suggest that this palm-mediated ecological service is available across all habitats (from pastures to

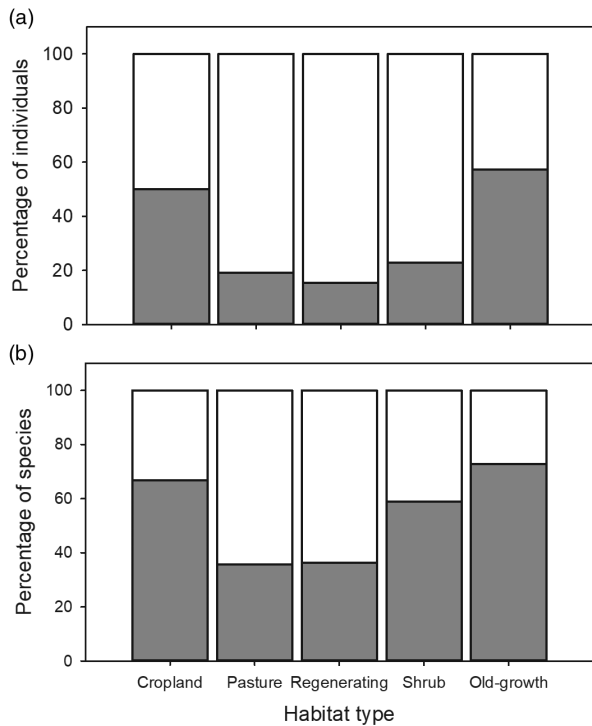


**Figure 5.** Individual-based species accumulation curves for vascular epiphyte species on the palm *Syagrus coronata* in croplands (a), cattle pastures (b), regenerating stands of Caatinga (c), shrub Caatinga (d) and old-growth forest (e) in the Catimbau National Park, north-east Brazil. Solid lines represent interpolated data, while dashed lines represent extrapolated data.

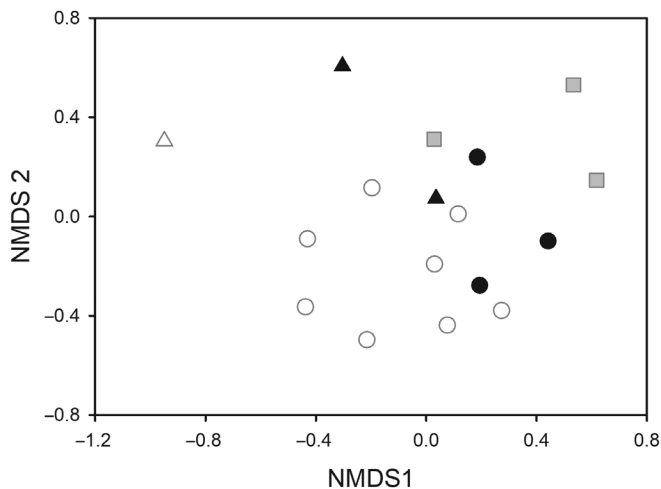
old-growth forest), with the structure of epiphyte assemblages responding accordingly, in terms of abundance, species richness and functional and taxonomic composition, resulting in more abundant and species-rich assemblages (~33% increment) in regenerating forest stands and areas of shrubby Caatinga. It has previously been proposed that the abundance of epiphyte species is strongly influenced by some of the physical characteristics of their hosts, such as bark peeling (Talley *et al.* 1996, Zimmerman & Olmsted 1992) or the persistence of leaf sheaths, which may facilitate the accumulation of water and nutrients as well as capture seeds and reduce seed mortality (Aguirre *et al.* 2010, Bernal & Balslev 1996, Corrêa *et al.* 2012). In the case of *S. coronata*, its structure consists of an immense set of leaf sheaths that remain attached to the trunk even after leaf fall (Noblick 2017), which contributes to the accumulation of substrate and water, resulting in a humid substrate near the palm trunk. As we have documented here for six species, stipe scars may also capture seeds and offer support for epiphytes, even though this structure is not expected to retain sediments. Moreover, *S. coronata* is evergreen (in contrast to the predominance of deciduous plant species in the Caatinga flora) and its dense foliage, organized symmetrically around the stipe, probably provides mesic/relatively shaded microhabitats year-round, as suggested by the abundant moss cover we anecdotally documented in the Catimbau landscape (see Figure 1i). Thus,

the refuge provided by *S. coronata*, in the context of the seasonal water scarcity, frequently prolonged droughts and hot summers of the Caatinga (Sampaio 1995), probably facilitates the persistence of diverse epiphyte species.

From this perspective, differences in microclimatic conditions, seed rain arriving on palms and palm abundance probably represent the main drivers for cross-habitat differences exhibited by epiphyte assemblages documented here. *Syagrus* species have been reported to serve as a food source for a myriad of vertebrates, including species from the Psittacidae (Andrade *et al.* 2015), Ramphastidae, Thraupidae and Procyonidae families (Silva *et al.* 2011). In the case of *A. phalerata*, most seeds recorded on sheaths were believed to reach palms via dispersal by bats as they use palms as feeding roosts (Corrêa *et al.* 2012). In fact, *A. phalerata* is able to support a dense seed bank (~50 seeds per palm stem) as high as 10% of the local vascular flora in the Pantanal, with a substantial proportion of seeds being defecated by bats (Corrêa *et al.* 2012). In the Catimbau landscape, crop and pasture fields are likely to be more desiccated habitats, but remaining palms may operate as exclusive perches for birds and roost for bats, both vertebrate groups operating as seed dispersers (see Evelyn & Stiles 2003, Morante-Filho *et al.* 2018). On the other hand, secondary-growth and shrubby Caatinga are more suitable habitats for epiphyte development, with dense palm clusters attracting much more seed dispersers as compared with the other



**Figure 6.** Percentage of vascular epiphyte individuals (a) and species (b) dispersed abiotically (white) and biotically (grey) found on the palm *Syagrus coronata* in areas of Caatinga with different levels of disturbance in the Catimbau National Park, north-east Brazil.



**Figure 7.** Non-metric multidimensional scaling (NMDS) of vascular epiphyte assemblages found on the palm *Syagrus coronata* on the basis of taxonomic similarity in areas of Caatinga with different levels of disturbance in the Catimbau National Park, north-east Brazil. Open triangle, closed triangles, open circles, closed circles and squares indicate croplands, pastures, regenerating patches, shrubby Caatinga and old-growth forest, respectively.

habitats. In synthesis, we propose that dense clusters of *S. coronata* inhabiting second-growth forest stands represent environmentally suitable habitats for epiphytes, capturing much more seeds per palm.

The conversion of old-growth forest into human-modified landscapes has been proposed to reorganize biodiversity, from population to ecosystem level (Gardner *et al.* 2009, Newbold

*et al.* 2015). This reorganization imposes a myriad of negative effects, including species extirpation, the collapse of species interactions and the impoverishment of native assemblages, as previously proposed for epiphytes (Nöske *et al.* 2008, Werner & Gradstein 2009). In the Caatinga dry forest, shifting cultivation and pastures followed by land abandonment creates suitable habitats, particularly second-growth forest stands, for the proliferation and persistence of *S. coronata*. By being an exclusive phorophyte, the response of *S. coronata* to disturbance favours the persistence of true epiphytes, while reorganizing epiphyte assemblages at landscape scale. This cascade to community-level from a population-level response to disturbance highlights one of the consequences the proliferation of disturbance-adapted species can pose across human-modified landscapes.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0266467420000073>

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