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3 **Title: Acaulescent palms are resilient to disturbances: experimental and global evidence**

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15

16 **Abstract**

17

18 **Background and aims:** Natural or anthropogenic disturbances influence aerial biomass and drive  
19 distinct resilience strategies in plants. Resprouting ability is considered one of the primary  
20 response traits in post-disturbance recovery. The afforestation of many Cerrado ecosystems (the  
21 world’s most species-rich tropical savanna) generates a change in the environment of native plants.  
22 In this study, we investigated the responses of acaulescent palm species to different disturbances

1 in the Brazilian Cerrado and globally. We hypothesised that acaulescent palms share functional  
2 traits that support persistence across disturbance regimes, regardless of geographic origin.

3 **Methods:** We first investigated the effects of disturbance (biomass removal) on two acaulescent  
4 palms from the Cerrado, *Allagoptera campestris* and *Syagrus loefgrenii*, subjected to different  
5 historical contexts (unaffected, under a pine afforestation, and under a Cerrado regeneration). We  
6 assessed and compared above- and belowground traits of plants from areas with different histories.  
7 We then assessed the resprouting ability after the removal of the aboveground biomass and  
8 compared the number of leaves, plant height and number of ramets to the pre-removal state over  
9 one year. To place our findings in a broader context, we compiled a global database of acaulescent  
10 palms (APALM) and conducted a meta-analysis of disturbance responses.

11 **Key results:** The two target species altered their morphological traits in response to environmental  
12 changes caused by long-term pine cultivation. Yet, the target species were able to resprout after  
13 the removal of aboveground biomass. Almost 10% of all palm species are acaulescent (geophytes).  
14 The meta-analysis showed that disturbances had either positive or non-significant effects on  
15 belowground traits across species.

16 **Conclusions:** Acaulescent palms are resilient to disturbances. Even when exposed to repeated  
17 disturbances, they manage to resprout and recover due to their multiple morphological adaptations.  
18 The diversity observed in belowground system architecture, ranging from differences in  
19 ramification to shifts in growth habit under varying conditions, illustrates adaptive capacity in  
20 disturbance-prone ecosystems.

21  
22 **Key-words:** Ramified rhizome; Arecaceae; Resprouting; Vegetative propagation; Meta-analysis;  
23 Geophyte palms; Bud bank.

## 24 25 **Introduction**

26 Disturbance, defined as ‘relatively discrete events that disrupt ecosystem, community, or  
27 population structure and alter the physical environment’ (Pickett and White, 1985), is a  
28 widespread phenomenon in ecosystems worldwide, and plays a central role in shaping vegetation  
29 dynamics. Resprouting ability is one of the primary response traits for rapid post-disturbance

1 recovery, as it enables plant survival and the formation of new shoots after the loss of  
2 aboveground biomass (Clarke *et al.*, 2013, Pausas *et al.*, 2016). Resprouting depends on the  
3 presence of a viable bud bank and the availability of energy resources stored in surviving tissues  
4 (Clarke *et al.*, 2013; Vesk and Westoby, 2004). The bud bank can be located in aerial stems  
5 (Charles-Dominique *et al.* 2015; Chiminazzo *et al.*, 2021; De Antonio *et al.*, 2020), basal regions  
6 (i.e. the root crown), and in a variety of belowground systems (e.g. rhizomes, xylopodia and  
7 gemiferous roots; Pausas *et al.*, 2018) where buds are well protected by the soil, or in a  
8 combination of both above- and belowground organs.

9 One particular growth form that exemplifies the importance of protected belowground  
10 bud banks is acaulescence (Pausas *et al.*, 2018). Acaulescence, that is, the absence of an  
11 aboveground stem or trunk, is an ecologically and evolutionarily important growth form in plants  
12 (Tribble *et al.*, 2021). Plants exhibiting this growth form enhance their survival after  
13 disturbances, such as frequent fires, by protecting their apical meristem belowground. Using  
14 their energy reserves stored in belowground organs, they can quickly regenerate the aerial  
15 biomass during favourable conditions (Alonso and Machado, 2007; Appezzato-da-Glória, 2015).

16 Palms (Arecaceae) are an ecologically diverse angiosperm family that dominates many  
17 tropical and subtropical ecosystems and holds major economic, cultural, and ecological  
18 significance worldwide (Tomlinson, 1979). Current taxonomic syntheses indicate that roughly  
19 250 of the 2585 described palm species (Palmweb, 2022) are acaulescent (Quattrocchi, 2018)  
20 with belowground stems (i.e. rhizomes), making them geophytes. Acaulescent palms are  
21 scattered across the palm phylogeny (Kissling *et al.*, 2019) and exhibit higher speciation rates  
22 than non-aculescent lineages due to their evolutionary transition from wet to seasonally dry  
23 habitats (Cássia-Silva *et al.*, 2022). Among the suite of response traits displayed by palms, the  
24 ability to branch rhizomes after disturbances is considered a key adaptive feature because it  
25 enables spatial spread. For instance, *Allagoptera arenaria* (Gomes) Kuntze ramifies its main  
26 belowground axis and forms dense clusters of rhizomes following recurrent fires (Menezes and  
27 Araujo, 2004). This belowground branching pattern not only plays a role in resprouting after  
28 disturbance, but it is also important for plant competition, nutrient acquisition, and reproduction  
29 (Klimešová *et al.*, 2018).

1 Cerrado, the world's most species-rich tropical savanna and a recognised biodiversity  
2 hotspot (Klink and Machado, 2005; Strassburg *et al.*, 2017), has been shaped by a long  
3 evolutionary history of recurrent fires (Pilon *et al.*, 2021; Zupo *et al.*, 2021). These selective  
4 pressures have also played a fundamental role in filtering plant functional traits, resulting in a  
5 vegetation mosaic with patches dominated by species with a broad array of fire adaptive  
6 strategies, including thick corky bark on aerial stems (Simon and Machado, 2012; Dantas *et al.*,  
7 2016) and robust belowground storage organs (Appezato-da-Glória, 2015, Pausas *et al.*, 2018).  
8 Such traits enhance resilience by enabling rapid recovery and persistence under frequent and  
9 intense disturbance regimes. Although the Cerrado is recognised for its remarkable biodiversity  
10 and ecological importance, it is experiencing a considerable loss of its extension driven by land-  
11 use change (Strassburg *et al.*, 2017), including afforestation with non-native (e.g. *Pinus spp.*)  
12 species. Such activities facilitate biological invasions and reduce native species richness (de  
13 Abreu and Durigan, 2011; de Abreu *et al.*, 2011; Durigan *et al.*, 2013). However, some native  
14 plants, including some palms, survive under these afforestation projects where their environment  
15 is strongly modified. Although the diversity and regenerative role of belowground structures in  
16 native Cerrado plants have been well documented (Silva *et al.*, 2020; 2021; Ferraro *et al.*, 2021),  
17 no such information exists for acaulescent palms. This gap is particularly striking given the wide  
18 distribution and ecological relevance of these species, which remain largely unstudied in terms of  
19 their morphological adaptations and persistence strategies in disturbance-prone environments.  
20 Here we ask the following questions: 1) How do acaulescent palm species from the Cerrado  
21 respond to disturbance (aboveground biomass removal) under different historical contexts  
22 (unaffected Cerrado, Cerrado under pine afforestation, and Cerrado under regeneration); (2)  
23 What is the diversity of belowground systems among acaulescent palms globally; (3) How do  
24 acaulescent palms respond to disturbances according to a quantitative synthesis of the literature.  
25 To answer the first question, we performed an experimental study on two acaulescent plants from  
26 the Brazilian Cerrado (a savanna-type ecosystem) with different habits: *Allagoptera campestris*  
27 (solitary, with a short non-ramified rhizome) and *Syagrus loefgrenii* (in clumps emerging from a  
28 ramified rhizome). These species experienced different disturbance histories, including growing  
29 in the understory of areas afforested with pine, and the subsequent removal of the pines (Cerrado  
30 restoration). We removed the aboveground biomass of the palms that had undergone these  
31 different histories and monitored their response (e.g., resprouting). Thus, we predicted that plants

1 from the control area (natural Cerrado) would recover more effectively after the aboveground  
2 biomass removal compared to those inhabiting the pine afforestation or the areas undergoing  
3 Cerrado restoration.

4 To answer the second and third questions (above), we compiled a global database on  
5 acaulescent palms from published literature, classified the belowground systems of all known  
6 acaulescent palms, and performed a meta-analysis with all studies in which disturbances were  
7 applied to acaulescent palms.

8

## 9 **Material and Methods**

### 10 ***Target species and study areas***

11 We selected two native acaulescent palm species with different belowground structures  
12 that are common in Cerrado areas: *Allagoptera campestris* (Mart.) Kuntze, a small palm, solitary  
13 (rarely caespitose), with a single-axis rhizome (Moraes, 1996); and *Syagrus loefgrenii* Glassman,  
14 endemic to Brazil, usually caespitose, that forms clumps from a ramified rhizome (Noblick,  
15 2017).

16 The studies were conducted at the Santa Bárbara Ecological Station (SBES; 2712 ha),  
17 located in São Paulo state, Southeast Region of Brazil (22°48'59" S; 49°14'12" W). It is located  
18 at 600–680 m asl, the climate is Köppen Cwa type, and presents well-defined rainy and dry  
19 seasons, with annual precipitation ranging from 1000–1300 mm and average temperature ranging  
20 from 18 °C in winter to 23 °C in summer. The SBES comprises a mosaic of Cerrado vegetation  
21 types with different physiognomies, ranging from grasslands to semideciduous forest, in addition  
22 to plantations of commercial pine trees (with Cerrado species remaining underneath), natural  
23 areas invaded by *Pinus elliotti* Engelm., and areas under regeneration after the removal of pine  
24 followed by fire treatments (Melo and Durigan, 2011). We selected palms of the two species in  
25 three different study sites in the SBES with different disturbance history: a) a Cerrado area  
26 (NCE), that is, an open savanna, excluded from fire for at least 15 years (Fig. 1A, control area);  
27 b) the understory of a pine plantation (from the 1970s) in a former Cerrado area (UPI; Fig. 1B,  
28 disturbed area); and c) an area where Cerrado is regenerating (CER) after 40 years of pine

1 cultivation that underwent the clear-cutting of the pine trees in 2012, followed by a fire treatment  
2 in 2014, for the removal of the remaining material (Fig. 1C). These disturbance histories  
3 represent relatively new scenarios for native vegetation. Afforestation reduces light availability  
4 from canopy closure and generates thick leaf litter on the soil surface (de Abreu and Durigan,  
5 2011); whereas areas where pine was removed and the remaining biomass burned, understory  
6 plants are suddenly exposed to direct sunlight (da Silva *et al.*, 2022) and regenerate through the  
7 belowground systems (Silva *et al.*, 2021; Ferraro *et al.*, 2021).

8 For each of the three sites, we obtained annual precipitation and monthly average  
9 temperature of the study period from the closest meteorological station (municipality of  
10 Mandurí-SP), using the CIIAGRO platform (Agrometeorology Information Centre) (Supporting  
11 Information, Fig. S1). Soil characteristics (texture, chemical composition, and moisture content)  
12 of the top 20 cm were measured in 10 samples from each study site (for details see the  
13 supplementary information, Table S1).

#### 14 ***Effect of disturbance history***

15 We first assessed the effects of different disturbance histories (sites NCE, UPI, and CER)  
16 by measuring key morphometric parameters in 3 to 10 adult individuals of each species at each  
17 site (the different number of individuals was due to sampling difficulties). The following traits  
18 were measured in each plant: plant height – vertical extent of aerial biomass along its natural  
19 growth angle (n=10), total leaves (n=10), total leaflets (three leaves per plant; n=5; *S. loefgrenii*),  
20 genet crown diameter (n=5; *S. loefgrenii*), and total ramets (n=10; *S. loefgrenii*). Belowground  
21 traits were assessed by excavating entire plants, including the full extent of their root systems,  
22 using a backhoe (Fig. 1D, E). Specifically, we unearthed three individuals per species at each  
23 site. For each excavation, we first delineated a circular area with a radius of at least 150 cm from  
24 the centre of the plant to ensure the complete removal of the roots while reducing the impact on  
25 nearby vegetation. Then we measured the following parameters: belowground bud bank, total  
26 roots, root length, root occupied area, root diameter, and total non-structural carbohydrates  
27 (NSC). To sample the belowground bud bank and anatomical traits, the collected belowground  
28 systems were fixed in FAA 50 (1:1:18; formaldehyde, glacial acetic, 50% ethanol) (Johansen,  
29 1940) for 48 h, stored in 70% ethanol, and further analysed in the laboratory.

1 For the quantification of NSC, fragments of fresh rhizomes were frozen immediately after  
2 collection. For each plant in each area, three analytical replicates were obtained by sampling  
3 three distinct regions of the same rhizome. Each replicate was manually macerated, and 1 g of  
4 the macerated tissue was dissolved in ultrapure water and vacuum-filtered using a cellulose  
5 nitrate membrane. Total NSC contents were measured by the phenol-sulphuric method (DuBois  
6 *et al.*, 1956). The absorbance was read in a Shimadzu UV-visible spectrophotometer UV mini-  
7 1240 (Shimadzu, Kyoto, Japan) at 415 nm. The curve was made with glucose as a standard, and  
8 the results were expressed as g of NSC per 100 g of rhizome. To identify the type of storage  
9 compounds, fixed rhizome samples were cross-sectioned using a sliding microtome (Leica  
10 M2000R). These sections (20–30  $\mu\text{m}$  thick) were stained with zinc chloride iodine (Strasburger,  
11 1913) and Lugol (Gerlach, 1984) to detect starch grains and subsequently examined under a  
12 Leica DMLB microscope equipped with a digital camera.

### 13 ***Response to the removal of aboveground biomass***

14 In February 2019, at the end of the fruiting season, we removed all aboveground biomass  
15 at ground level from 10 adult individuals of each species at each site (with different disturbance  
16 history; NCE, UPI, CER) (Fig. 1F–H). Resprouting was monitored bi-monthly for one year by  
17 measuring the number of leaves and plant height for both species, as well as the number of  
18 ramets, which was recorded only for *S. loefgrenii*. Then, we compared the final values of each  
19 parameter with those obtained in the pre-removal state. Statistical analysis was performed using  
20 analysis of variance (Two-way ANOVA) and Tukey's test using the R software (R Core Team,  
21 2025).

22 *Insert Figure 1*

### 23 ***Acaulescent palms database (APALM) and meta-analysis***

24 We compiled the first global database on acaulescent palms (APALM database). APALM  
25 is composed of two tables, the first includes all the recognised species (n= 216), a brief  
26 description of the species, distribution, type of belowground systems, conservation status,  
27 whether it grows in a disturbance-prone environment, and the type of disturbance (Table S4,  
28 sheet 1). To better understand the global distribution of the acaulescent palms, we extracted

1 species occurrence using GBIF plugin (ver. 2.0) in QGIS 3.40 LTR (QGIS Development Team,  
2 2025), removed duplicate records, excluded records associated with botanical gardens or  
3 cultivated settings, and then computed species richness in a gridded global map of 2 degrees of  
4 resolution. This was performed with the R software (R Core Team, 2025) using the following  
5 libraries: *terra* (Hijmans, 2025), *sf* (Pebesma, 2025), *rnaturalearth* (South, 2025)  
6 and *RColorBrewer* (Neuwirth, 2025).

7 To create the database for the meta-analysis, we searched Web of Science and Google  
8 Scholar between April and June 2022, with no restriction on publication year, using  
9 combinations of the terms: (*disturbance*) AND (*acaulescent* OR *acaulescent palm\** OR *trunkless*  
10 *palm\** OR *palm species\** OR *hypogeous rhizome\** OR *rhizome*) AND (*fire\** OR  
11 *harvesting\** OR *logging\** OR *deforestation\** OR *freezing\**)\*\*. After removing duplicates, we  
12 screened titles and abstracts to exclude irrelevant studies (e.g. not containing data on *acaulescent*  
13 *palms* or *disturbance*). We then assessed the full texts and considered any study with the focus on  
14 *acaulescent palm species*; effects of *disturbance*; and quantitative comparisons between control  
15 and disturbed conditions with mean and variability data (SD or SE). A total of 16 studies fulfilled  
16 the inclusion criteria and accounted for 67 comparisons.

17 To perform the meta-analysis, we used 200 comparisons, comprising all quantitative data  
18 compiled from the literature (67 comparisons) as well as the results from our comparisons (effect  
19 of disturbance history) and from our experiment (response to aboveground biomass removal)  
20 (Table S4, sheet 2). Effect sizes were calculated using Hedges' *d*, the standardised mean  
21 difference, across all experiments and studies. We then performed hierarchical mixed-effects  
22 meta-analyses, incorporating moderators in a model with species and studies as random effects.  
23 The following qualitative parameters were included as moderators: fire intensity (none, medium,  
24 high), type of disturbance (one fire, two fires, or other disturbance), type of sampling (direct:  
25 comparisons before and after disturbance; indirect: comparisons between disturbed and  
26 undisturbed sites or individuals), and time since disturbance (short-term: 1 year; long-term: more  
27 than 1 year). We also grouped response variables into seven categories: traits related to  
28 belowground systems (carbohydrate content and root size), number of ramets, number of leaves,  
29 leaf size, plant height, growth, and cover (including plant density). An effect was considered

1 significant if the 95% confidence interval (CI) of Hedges'  $d$  did not overlap zero (Rosenberg *et*  
2 *al.*, 2013). All analyses were performed using the "metafor" package in R (Viechtbauer, 2010).

3

## 4 **Results**

### 5 ***Effects of disturbance history on target plant traits***

6 Plants shaded by pines (UPI) were taller than in the other areas, especially for *A.*  
7 *campestris* (Fig. 2A, Table S1). They also presented a greater area occupied by roots in the soil  
8 (Fig. 2E) and longer roots in *S. loefgrenii*. In both species, plants from the regenerating Cerrado  
9 (CER) presented a greater number of roots and thicker roots (Fig. 2C, D, Table S1). In *A.*  
10 *campestris*, while the shade of pines (UPI) decreased the number of leaves, the removal of the  
11 trees followed by a fire treatment (CER), stimulated the production of leaves compared to the  
12 plants from the natural Cerrado (NCE; Fig. 2B, Table S1). Both species stored carbohydrates in  
13 the form of starch grains in the rhizome (Fig. 3A–F). The content of non-structural carbohydrates  
14 in the rhizome of plants from NCE was lower in *A. campestris* than *S. loefgrenii* (Fig. 2F, Table  
15 S1). Starch grains were not observed either in *S. loefgrenii* roots from CER (Fig. 3I) or in *A.*  
16 *campestris* roots from any area. Additional results of morphometric measurements are shown in  
17 Supplementary Material, Fig. S2 and Table S1.

18 *Insert Figure 2*

19 *Insert Figure 3*

### 20 ***Response to the removal of aboveground biomass***

21 Most individuals of both species resprouted from belowground buds during the first two  
22 months after the aboveground biomass removal (Fig. S3, S4, Table S2). Only two individuals of  
23 *A. campestris* (one from NCE and another from CER) died after the biomass removal. Both  
24 species showed a gradual growth over the 12 months post-disturbance (Fig. S3, S4, Table S2).

25 In both species, the morphological traits returned to the pre-removal state after 12 months  
26 of growing (Fig. 4, Table S3). Moreover, in *S. loefgrenii*, the number of leaves and ramets  
27 remained higher in NCE (Fig. 4C, E) and the plant's height was similar in the individuals from

1 NCE and UPI. In *A. campestris*, the number of leaves remained higher in the plants from CER  
2 and the plant's height remained higher in the plants from UPI (Fig. 4B).

3 *Insert Figure 4*

#### 4 **Global analysis**

5 Acaulescent palm species are heterogeneously distributed across the world, with a higher  
6 concentration in South America and Southeast Asia (Fig. 5A). Among the 216 acaulescent palms  
7 surveyed, we identified a range of different belowground system forms (Table S4, sheet 1),  
8 which we divided into non-ramified and ramified. For some species, this trait is variable,  
9 probably depending on growing conditions and disturbances ('both' in Fig. 5B). Non-ramified  
10 rhizomes varied in size, ranging from very short to long, even in adult plants with complete  
11 phenological stages. Based on rhizome ramification, species habits were categorised as solitary  
12 (non-ramified rhizomes) and clustered (ramified rhizomes). A complete description of these 216  
13 species is found in the APALM database (Table S4, sheet 1).

14 The overall response to the disturbances observed in the study performed with *A.*  
15 *campestris* and *S. loefgrenii* (Fig. 6, left) was negative. These negative effects refer mainly to the  
16 number of leaves and plant height under a short temporal scale (less than a year), under high-  
17 intensity disturbances (more than one disturbance), and in direct experiments (before vs. after  
18 disturbance comparisons). In contrast, belowground traits exhibited significant positive effects,  
19 suggesting compensatory investment in belowground biomass.

20 Only non-significant overall effects were found in the data from the literature (Fig. 6,  
21 centre). The overall response was also not significant when analysing all data together (Fig. 6,  
22 right). However, the effects on root traits, number of ramets, and leaf size traits were positive.  
23 The effects of fire were also positive, but only when applied in isolation, and not when fires were  
24 applied recurrently or together with other disturbances.

25 *Insert Figure 5*

26 *Insert Figure 6*

27

## 1 Discussion

### 2 *Distribution and variability of belowground structures in acaulescent palms*

3 Our compilation (APALM) shows that the greater diversity of acaulescent palms is in  
4 tropical zones, especially in Brazil and Malaysia, with 29% and 9% of the acaulescent palms,  
5 respectively. In Brazil, although acaulescent palms occur in different habitats, they are especially  
6 adapted to seasonal and dry environments (Cássia-Silva *et al.*, 2022). Their belowground  
7 systems, mainly composed of rhizomes, show considerable variability, including ramified or  
8 non-ramified systems. The distinction between these types is important for understanding  
9 species' spatial occupation and clonal growth dynamics, which remain poorly studied (Herben  
10 and Klimešová, 2020), especially in palms. Ramified rhizomes may provide ecological  
11 advantages such as greater resilience to disturbance, enhanced propagation capacity, and more  
12 effective ramet production following damage (Kouassi *et al.*, 2014). Additionally, these  
13 structures play a central role in processes such as carbon storage and ramet interactions  
14 (Klimešová *et al.*, 2018; Fidelis *et al.*, 2014). Acaulescent palms are commonly associated with  
15 seasonal and dry environments, where disturbances such as fire and herbivory are frequent. In  
16 these habitats, clonal regeneration likely plays a critical role in enhancing survival after  
17 disturbance and, thus, in the long-term persistence. Understanding how disturbance regimes  
18 influence clonal strategies in acaulescent palms is therefore essential for advancing our  
19 knowledge of their adaptive strategies and for clarifying their functional roles in tropical  
20 ecosystems.

### 21 *Different disturbance histories modify plant morphological traits*

22 The environmental disturbances produced by the afforestation of Cerrado ecosystems  
23 altered the morphological features of the two studied palms. While *S. loefgrenii* produced less  
24 leaves in the shaded area (UPI) compared to plants from the natural Cerrado (NCE), *Allagoptera*  
25 *campestris* presented longer and more slender leaves when growing in pine plantations (Barbosa  
26 *et al.*, 2022). According to the authors, *A. campestris* performed such leaf adjustments to suit the  
27 light environment generated by the canopy changes (UPI and CER).

28 For the two studied species, the habitat fully exposed to sunlight (CER) is the one that  
29 displayed more differences in belowground organs, i.e. the number and the diameter of roots

1 were greater. Structural modifications such as an increase in root biomass allocation as well as in  
2 the diameter of roots are related to responses to the disturbed environment, especially in dry  
3 environments or when soil resources are limited (Callaway *et al.*, 2003; Phillips and Leger, 2015;  
4 Reynolds and D'Antonio, 1996). The soil temperature in CER is significantly higher in the  
5 hottest hours of the day compared to the other studied areas (Apezzato-da-Glória *et al.*, 2024).  
6 Due to the lower vegetation cover, the soil was more exposed to solar radiation in this area, thus,  
7 becoming drier and warmer (Lozano-Parra *et al.*, 2018).

8 Besides the complex belowground organs that enhance survival after disturbances,  
9 ramifications can be stimulated by aboveground injuries (Menezes and Araujo, 2004) as verified  
10 in *Syagrus loefgrenii*, which showed a higher number of ramets in NCE and CER areas (Fig.  
11 S2E). It is worth noting that the length of the roots and the area occupied by the roots are greater  
12 in the UPI. Changes that increase the belowground occupation area are important to plant  
13 survival under a range of different ecological conditions, because the increase in horizontal space  
14 may increase the number of buds, amplify the acquisition of nutrients, and strengthen the  
15 competition for space (Klimešová *et al.*, 2018 and the cited literature).

16 We propose that the lower temperature and higher soil moisture in the UPI can be  
17 attributed to the shade and presence of a thick layer of pine needles on the soil surface. The lower  
18 number of ramets in *S. loefgrenii* plants growing in UPI and CER compared to those growing in  
19 NCE can be related to resource constraints imposed by the long period of living under a pine  
20 plantation.

## 22 ***Regeneration after aboveground biomass removal***

23 Our results showed that plants of both species rapidly regenerated aboveground biomass  
24 following disturbance. Both species fully recovered their pre-disturbance morphology within one  
25 year, demonstrating that their trait modifications confer persistence in anthropogenically altered  
26 environments (effect of disturbance history) without compromising their capacity to withstand  
27 subsequent disturbances (effect of biomass removal). The regenerated plants from the disturbed  
28 areas (UPI and CER), however, remained smaller, less branched, and had fewer leaves compared  
29 to plants in the control area (NCE).

1           The meristematic tissues of the two studied species were strongly protected by a dense  
2 cover of leaf bases and by their location below the soil surface. Besides the protective role of the  
3 soil (Vesk and Westoby, 2004), acaulescent palms have a protective layer of relatively non-  
4 flammable mature leaf bases that insulate the meristems. This allows the emergence of new  
5 leaves that regenerate the aboveground biomass (McPherson and Williams, 1998). For this  
6 specific reason, there is a notable disturbance resilience, especially against fire, in species with  
7 this protective strategy, which allows them to regenerate remarkably fast (Abrahamson and  
8 Abrahamson, 2006). There are other examples of Cerrado acaulescent palms surviving  
9 aboveground biomass injury (Endress *et al.*, 2004; Abrahamson and Abrahamson, 2006;  
10 Higashikawa *et al.*, 2019), including *Astrocaryum campestre*, *Syagrus glazioviana* (Dammer)  
11 Becc. (Antar *et al.*, 2022), and *Allagoptera campestris* (Loiola *et al.*, 2010). It is important to  
12 note, however, that the protective traits described here are not exclusive to adult acaulescent  
13 palms. Some caulescent palms exhibit a prolonged acaulescent or rosette phase during  
14 establishment that is crucial for survival against disturbances, such as *Ceroxylon quindiuense*  
15 (H.Karst.) H.Wendl. (Sanín *et al.*, 2013) and *Sabal palmetto* (Walter) Lodd. ex Schult. &  
16 Schult.f. (McPherson and Williams, 1998). These palms can persist for decades under recurrent  
17 disturbances, as the meristem remains protected belowground, offering resilience advantages  
18 similar to those of the acaulescent species studied here. This strategy reminds of the grass stage  
19 in some pines under surface fires (Keeley and Zedler, 1998).

20           The regrowth of the aboveground biomass requires the mobilisation of reserves stored  
21 belowground (de Moraes *et al.*, 2016). In *Syagrus loefgrenii*, the plants from the undisturbed area  
22 had non-structural carbohydrates that were twice the amount found in the plants from the  
23 disturbed areas. The content of non-structural carbohydrates is similar to that found in Cerrado  
24 species with resprouting strategies from belowground organs (Silva *et al.*, 2020, da Silva *et al.*,  
25 2021; Faleiro *et al.*, 2022; Ferraro *et al.*, 2021). In addition, in these undisturbed plants, the  
26 number of ramets and leaves after biomass removal was two times as high as in plants from the  
27 disturbed areas (Fig. 5). After 12 months of the aboveground biomass removal, *S. loefgrenii*  
28 plants reached the pre-removal number of ramets. This may indicate that, in undisturbed areas,  
29 the amount of energy stored in the rhizome is sufficient not only for the plant to return to its pre-  
30 disturbance state, but also to stimulate the increase of aboveground biomass in this species.

1

## 2 *Global plant responses to different disturbance history*

3 Our meta-analysis contributes to reduce the knowledge gap surrounding how acaulescent  
4 palms respond to disturbance. Although the number of studies available for comparison remains  
5 limited, the patterns that emerge offer important insights. For our two target species, the overall  
6 effect of disturbance was negative (Fig. 6, left), yet the response of belowground traits was  
7 significantly positive. This result underscores the importance of belowground structures in  
8 recovery processes and highlights a major gap in the literature. Comparable belowground data  
9 for other acaulescent palms is virtually non-existent. This absence is likely related to the  
10 methodological challenges of excavating palm rhizomes in natural environments, where the use  
11 of large machinery (e.g. backhoes) is either impractical or environmentally damaging. Therefore,  
12 our study provides rare and valuable information on belowground traits across different  
13 disturbance histories in the Cerrado.

14 When synthesising responses from broader literature, most disturbance effects were non-  
15 significant, except for a clear positive effect after a single fire event (Fig. 6, center). The non-  
16 significant results may reflect a combination of limited sample sizes, variation in disturbance  
17 intensity and timing, and genuine differences in species responses. Some individual studies  
18 report neutral or even positive effects, such as root biomass increase and ramet production as a  
19 response to fire (Fig. 6, left). Liesenfeld and Vieira (2018) found that juvenile *Attalea maripa*  
20 (Aubl.) Mart. recovered 91.7% of individuals after fire; and other studies report similarly  
21 positive responses for *Astrocaryum campestre* Mart. and *Syagrus glazioviana* (Antar *et al.*,  
22 2022). Species with similar belowground structures also tend to benefit from fire, as seen in  
23 *Chamaerops humilis* (Ladd *et al.*, 2005) and *Serenoa repens* (W. Bartram) Small (Abrahamson &  
24 Abrahamson, 2006).

25 Taken together, the experimental findings and the meta-analysis reveal a more nuanced  
26 scenario than simple resilience or vulnerability responses of palms to disturbances. With limited  
27 but growing evidence, acaulescent palms do not appear to be negatively affected by disturbance;  
28 rather, it depends on the trait (see below- vs above-ground traits) and the disturbance regime  
29 (Fig. 6). Continued efforts to investigate and integrate above- and belowground traits among

1 acaulescent palms will be essential for understanding how this group responds to environmental  
2 pressures in ecosystems worldwide.

3

#### 4 **Final remarks**

5 Despite the inherent challenges of studying belowground structures in large, long-lived  
6 plants, which limits sample sizes, our study provides novel insights into the resilience and  
7 adaptive strategies of acaulescent palms. Widely distributed across the tropics, these species  
8 exhibit a diverse array of belowground structures.

9 In the Cerrado, acaulescent palms demonstrate remarkable plasticity in both above- and  
10 belowground traits, allowing them to persist in disturbed habitats with contrasting light regimes  
11 while maintaining the capacity to resprout following disturbances. Although the tested  
12 individuals in our study showed some degree of recovery across all treatments, ecological filters  
13 in the disturbed areas, such as reduced light under pine plantations and variable conditions in the  
14 regenerating habitat, shaped trait expression, resulting in distinct structural and functional  
15 differences compared to plants in undisturbed habitats. These differences do not compromise the  
16 palms' ability to resprout after subsequent disturbances. These observations enhance  
17 understanding of plant adaptation and resilience, offering relevant insights for conservation  
18 efforts in tropical ecosystems.

19

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## 7 Author contributions

8 This study was designed and conceived by B. Appezzato-da-Glória, G.S. da Silva and J.G. Pausas.  
9 G.S. da Silva, L.H.S. Barbosa, and B. Appezzato-da-Glória performed the field sampling. G.S. da  
10 Silva analysed the data, performed the statistical analysis, collected and curated species occurrence  
11 data and computed species density. G.S. da Silva and J.G. Pausas elaborated the APALM database  
12 and designed and plotted the gridded global map. J.G. Pausas performed the meta-analysis. G.S.  
13 da Silva wrote the manuscript, and all authors actively contributed to the edition and revision.  
14

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9

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11



Figure 1  
162x229 mm (DPI)

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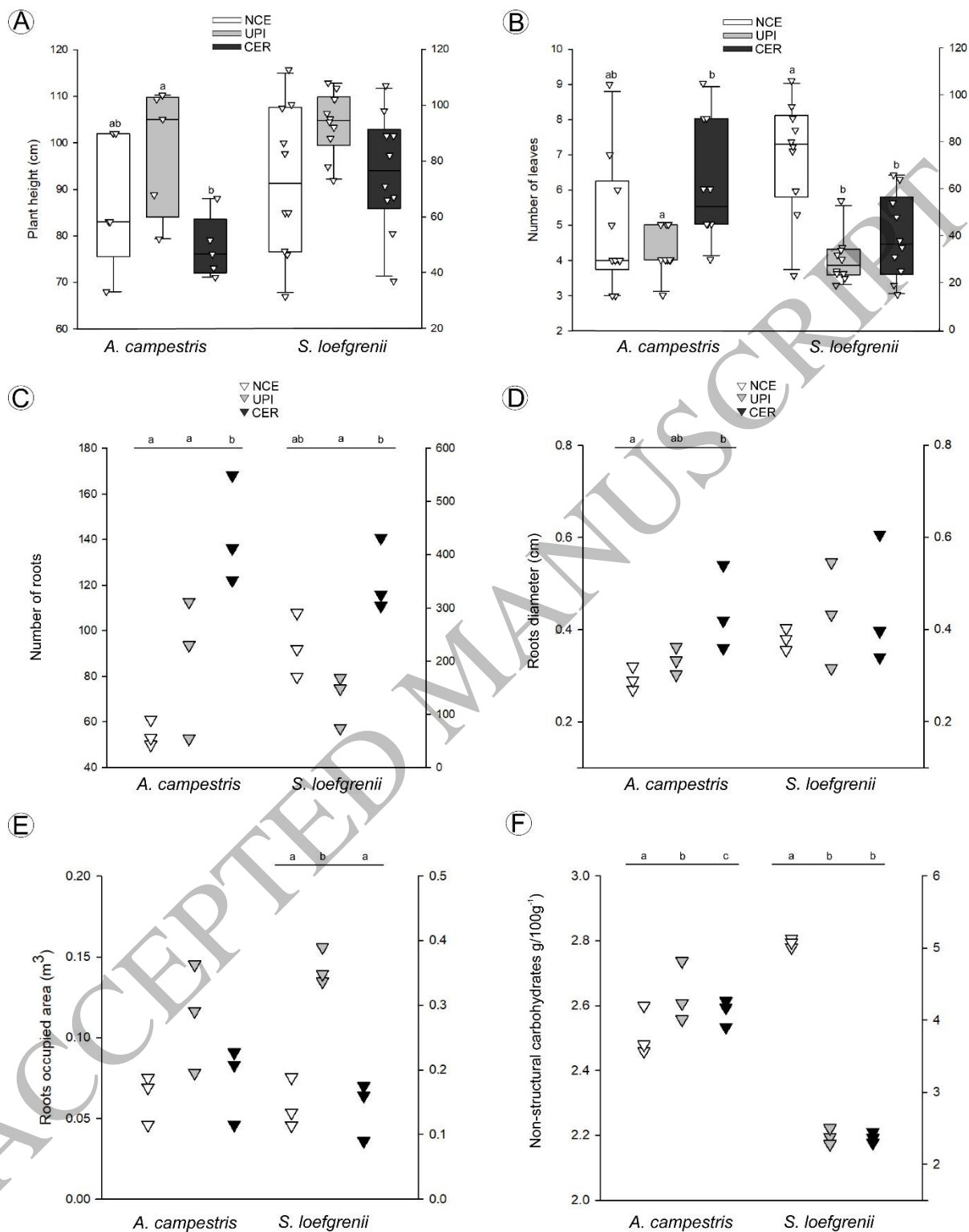


Figure 2  
158x201 mm (DPI)

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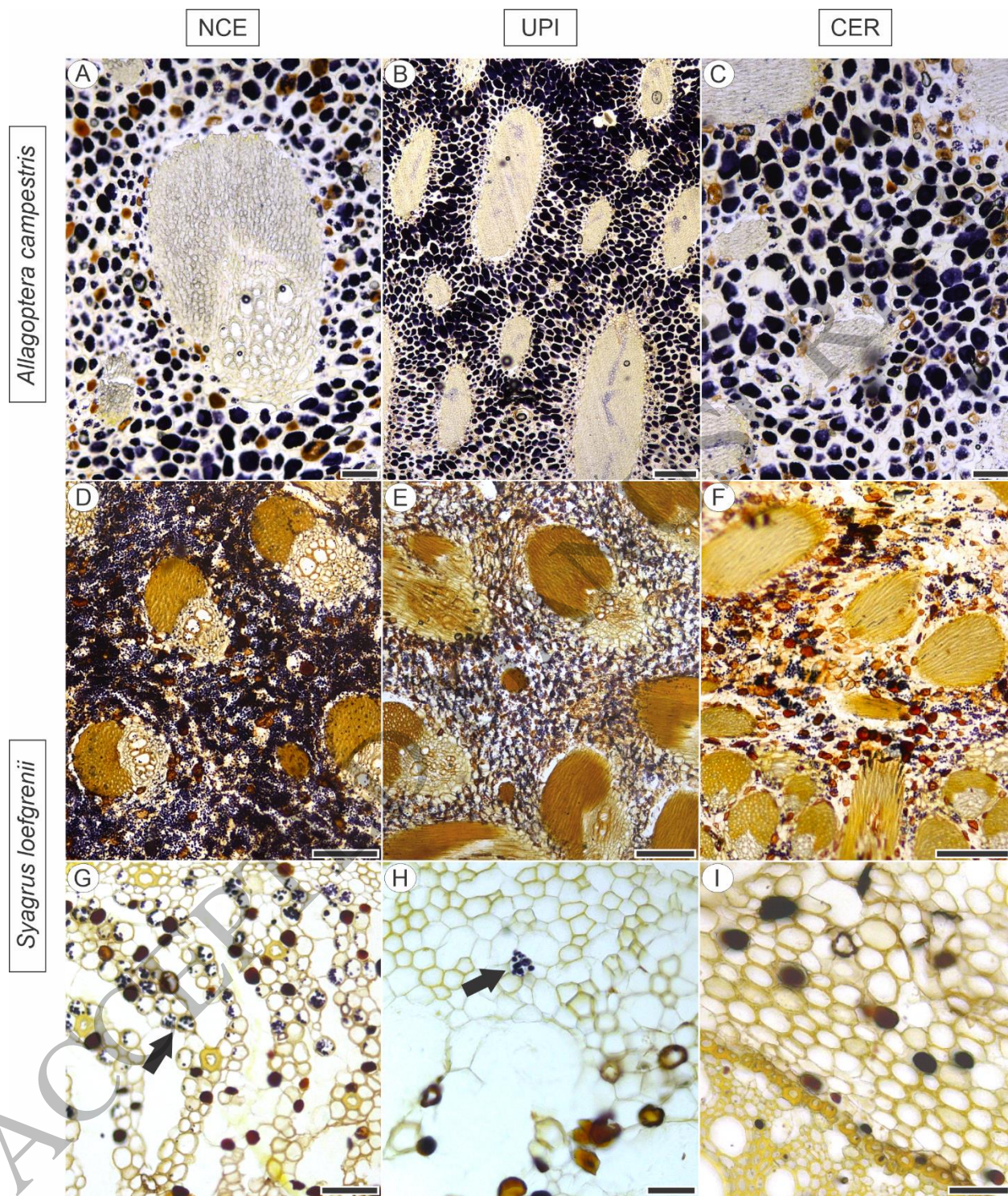


Figure 3  
165x196 mm (DPI)

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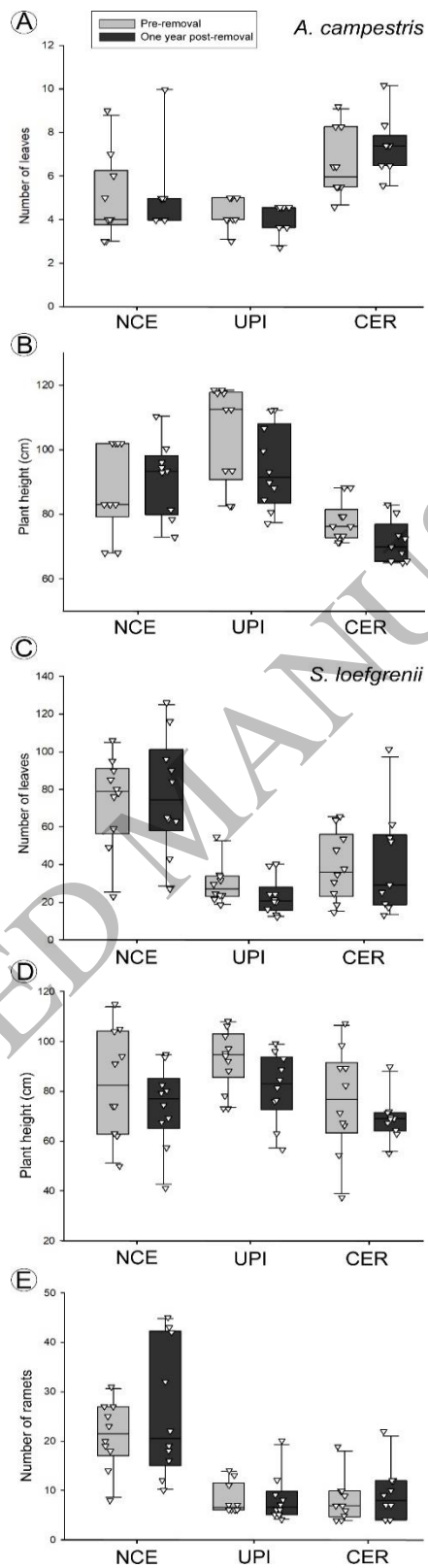


Figure 4  
56x229 mm (DPI)

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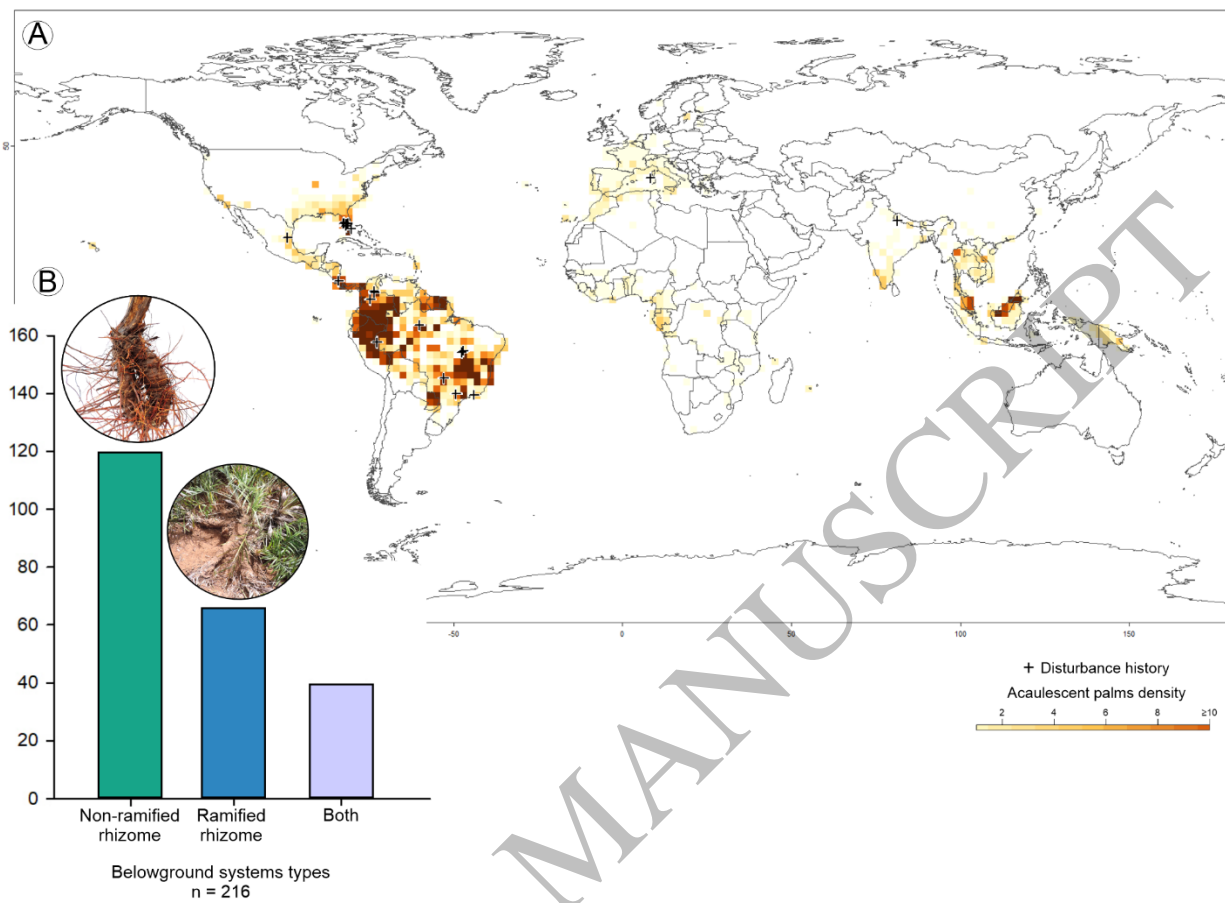


Figure 5  
165x119 mm (DPI)

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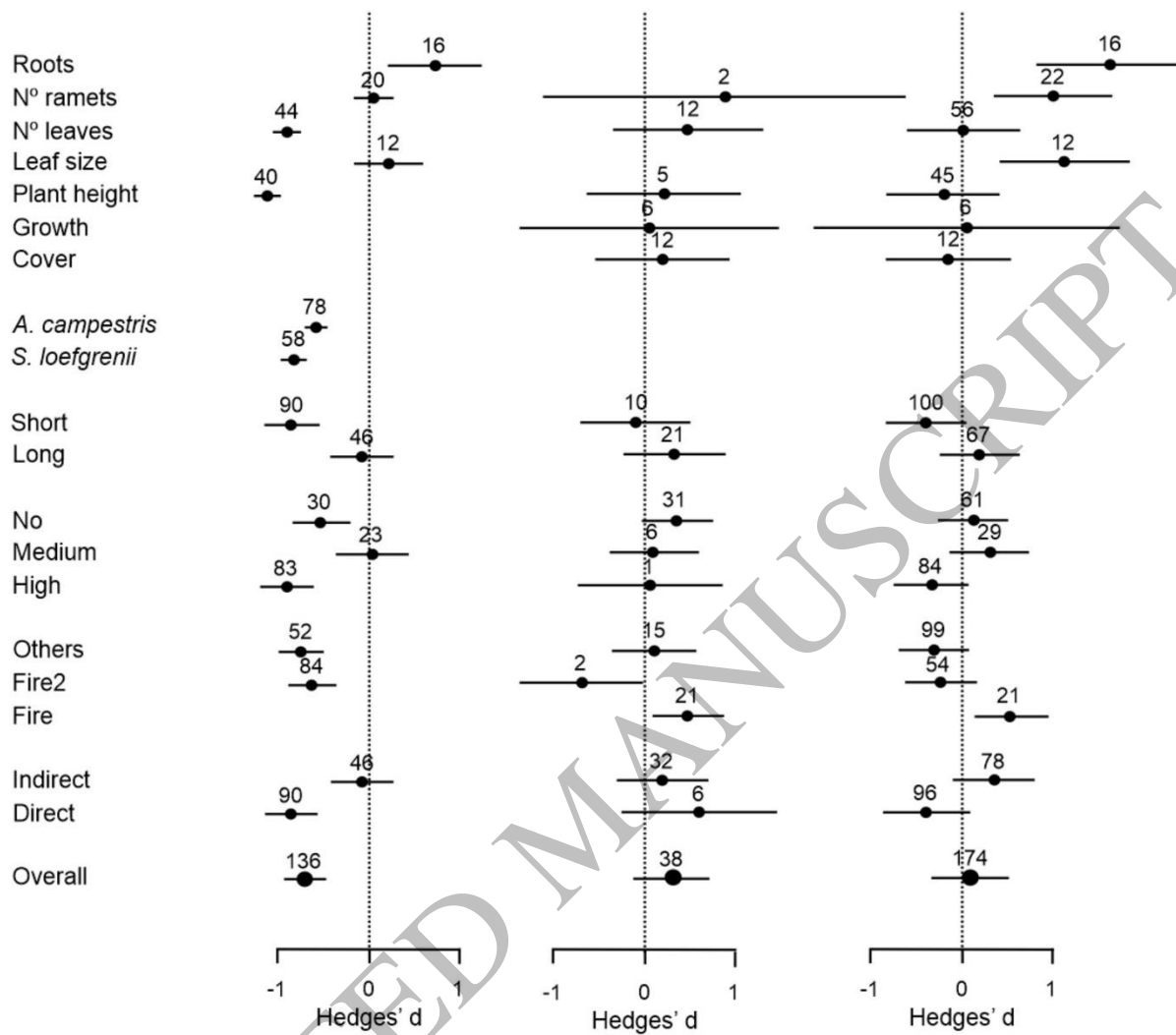


Figure 6  
165x150 mm (DPI)

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