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Original Paper

Population ecology and conservation status of *Parodia carambeiensis* (Cactaceae)

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Abstract

Parodia carambeiensis is a rupicolous, small-sized species, with globose cladode and showy flowers, and is the only endemic Cactaceae species in Paraná State (Brazil). Changes in natural landscapes and fragmentation isolate populations, increasing their vulnerability to local extinctions. Our aim was to verify the spatial distribution of *P. carambeiensis*, reviewing its conservation status and main threats in the distribution area. Expeditions were carried out in the Campos Gerais region to record the abundance, density and spatial distribution of *P. carambeiensis* populations. Local landscape and climatic variables as well as the joint effect of these with geographical distance, were analyzed. Our findings highlighted that population density differs among the studied sites and was driven by distinct levels of anthropic threats such as livestock, tourism, wildfires and their proximity to highways, along with the climatic variables evaluated (temperature range and precipitation). The models jointly explained 56% of the variation in the population density, which was mostly influence by climatic factors. *Parodia carambeiensis* is currently classified as (LC) least concern, however, our results provide strong evidence in favor of updating its status to (EN) endangered due to the elevated extinction risk of natural populations.

Key words: anthropic actions, cactus, endemism, vulnerability.

Resumo

Parodia carambeiensis é uma espécie rupícola de pequeno porte, com cladódio globoso e flores atrativas, sendo a única Cactaceae endêmica do estado do Paraná. As alterações das paisagens naturais e a fragmentação tem levado ao isolamento das populações deixando-as mais vulneráveis a extinções locais. Nosso objetivo foi verificar a distribuição espacial desta espécie, revisar seu status de conservação e principais ameaças ao longo da área de distribuição. Foram realizadas expedições na região dos Campos Gerais, relatando a abundância, densidade e distribuição espacial das populações. Foram conduzidas as análises das variáveis locais do ambiente e climáticas, bem como o efeito conjunto destas variáveis e a distância geográfica. Os resultados indicam uma variação da densidade populacional entre as localidades, e pode ser resultante das ações antrópicas locais como pecuária, turismo, queimadas e a proximidade com rodovia, além do clima considerando-se a amplitude térmica e precipitação. Os modelos avaliados em conjunto explicaram 56% de variação na densidade populacional, sendo os fatores climáticos os principais determinantes da distribuição desta espécie. Atualmente a espécie está classificada como pouco preocupante, entretanto sugere-se a mudança da categoria do status para em perigo, baseado na revisão dos dados atuais e alto risco de extinção na natureza.

Palavras-chave: ações antrópicas, cactus, endemismo, vulnerabilidade.

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Introduction

Cactaceae is represented by 129 genera and 1.450 species with neotropical distribution. According to current systematics, it is composed of four subfamilies: Pereskioideae, Maihuenioideae, Opuntioideae and Cactoideae (Hunt *et al*. 2006; Zappi & Taylor 2020). In Brazil, 81 genera and 484 species of Cactaceae have been recorded so far, of which 208 species are endemic (Zappi & Taylor 2020).

Species of Cactaceae are mostly distributed in the American continent, except for *Rhipsalis baccifera* (Muell.) Stearn which occurs in Africa, being known by the success to colonize hostile environments that are generally not suitable for other plants, for example, those with substrates scarce in nutrients and water (Silva *et al*. 2011; Cavalcante *et al*. 2013). They play important roles in ecosystems with low production and may contribute significantly to local food webs. Such plants provide succulent fruits, nectar and pollen, which are vital resources in xeric environments, supplying water and nutrients to a wide variety of animals (Cavalcante *et al*. 2013).

The genus *Parodia* Speg. is distributed along Argentina, Paraguay, Uruguay, Bolivia and Brazil, being comprised by of 48 species, 18 of which are restricted to the south of Brazil, mainly in the States of Santa Catarina and Paraná with the higher levels of species richness observed in Rio Grande do Sul, in the Pampa and Atlantic Rainforest biomes (Carneiro *et al*. 2016; Zappi & Taylor 2020). *Parodia carambeiensis* (Buining & Brederoo) Hofacker, is commonly known as "cactus-ball" globose stem, flowers with yellow tepals and pink stigma (Fig.1 a-b). Soller *et al*. (2014) conducted a taxonomic study of Cactcaeae in the state of Paraná and found the occurrence of 12 genera and 26 native species, most epiphytes, inhabiting Atlantic Rainforest and Araucaria Forest, being *P. carambeiensis* the only endemic species of Cactaceae in the state of Paraná.

Campos Gerais region is located in the second plateau of Paraná, where the vegetation is part of the Atlantic Rainforest domain, but comprises a mosaic of forest fragments, grasslands and savanna remnants, combining the ecotones in a very particular way (Moro & Carmo 2014). Despite the unique vegetational mosaic, these ecosystems have been severely threatened by forestation with exotic species, conversion of natural fields into monoculture, livestock, wildfires, excessive and illegal collections, as well as the impacts of tourism (Ziller & Galvão 2002; Linsingen *et al*. 2006).

On a broad scale, the distribution of *P. carambeiensis* is limited by patches of rocky outcrops, featured by shallow soils with water deficiency, for which this species' morpho-anatomy is well adapted to (Moro & Carmo 2014). On a local scale, like most Cactaceae, *P. carambeiensis* presents clumped distribution as consequence of concentrated resource allocation within heterogeneous environments (Godínez *et al*. 2003) (Fig. 1c). This species is also associated with species of the genus *Calea* L. (Asteraceae), *Andropogon* L. (Poaceae), *Dyckia* Schult. & Schult.f (Bromeliaceae) and mosses, which inhabit rocky outcrops in the Campos Gerais. Such plants are usually called "nurse plants" since they support the development of cacti and other plants in the outcrops by providing a more suitable microenvironment, with improved water supply and limited solar exposition (Flores & Jurado 2003; Oliveira 2009).

Cactaceae is the fifth most threatened plant family in Brazil, mainly due to its high endemism, endemic distribution and ornamental value, leading to a large number of vulnerable or threatened species (Hinostrosa & Hernandez 2000; Ortega & Godínez 2006; Silva *et al*. 2011; Goettsch *et al*. 2015). Currently, *Parodia carambeiensis* is categorized as Least Concern (LC) according to IUCN criteria (Larocca & Machado 2017), although a recent review suggested a new classification as Vulnerable (VU) (Anceschi & Magli 2018).

The current IUCN classification considers the presence of *P. carambeiensis* subpopulations in protected areas, which in turn decreases extinction risks. However, small and isolated populations are more vulnerable to local extinctions over time due to lower genetic variability, with barriers to dispersion and pollination causing low reproductive success (Ricklefs 2010). Therefore, preserving sustainable populations in diverse habitat patches can increase the capacity for recolonization and rescue populations that occasionally become more vulnerable (Begon *et al*. 2007).

In order to review the current conservation status and threats of *P. carambeiensis*, we aimed to report the main anthropogenic threats influencing the distribution and density of this species throughout the Campos Gerais area, how well conservation units protect it, as well as the influence of climatic factors and geographic distance on its distribution and density.

Figure 1 – a-f. Characteristics of *Parodia carambeiensis*, Campos Gerais, PR (Brazil). – a. flowers; b. lanugo as an indication of maturity; c. a local subpopulation; d. influence of *Pinus* spp; e. occurrence of recent wildfire in one study site; f. agriculture.

Material and Methods

Study area

The research was conducted within the Campos Gerais domain, encompassing 22 municipalities spread over the second plateau of Paraná, with total extension of 11,741.41 km², lying between 23°45'S and 26°15'S latitude and 49°15'W and 50°45'W longitude (Melo *et al*. 2014) (Fig. 2).

To assess populational distribution and density, the surveys were performed on 12 plots distributed in five municipalities in the area names as Campos Gerais, a geographic region restricted between Escarpa Devoniana and Escarpa da Esperança (Maack 2012). This region is characterized by extent areas of grassland, comprised by Atlantic Rainforest and Cerrado biomes, with open fields and rocky outcrops associated with forest remmants and savannah formations (Moro & Carmo 2014; Sema 2018). The soil is composed by sedimentary rocks, arenites and shales, classified as shallow and poor (Sá 2014). Ponta Grossa, Lapa, Palmeira, Carambeí and Tibagi are the municipalities covered in the study, which also included private and public conservation units such as "Parque Estadual do Canyon Guartelá" and "RPPN Sonho Meu" (Tibagi), Parque Estadual de Vila Velha (Ponta Grossa), and Parque Estadual do Monge (Lapa), as well as plots located on private lands (Tab. 1). Most localities are located within the environmental protection area of Escarpa Devoniana and some are inside Parque Nacional dos Campos Gerais.

In order to redraw the new conservation status, a distribution map was developed based on data records from herbaria collections and field samples, totaling 26 occurrence sites in Paraná state (Tab.1).

Samplings

Field expeditions were performed in the Campos Gerais region between March and August 2017. The studied sites were defined based on prior cacti occurrence reports, thus several surveys were conducted in habitats that are suitable for cacti development, *e.g.*, rocky outcrop, between

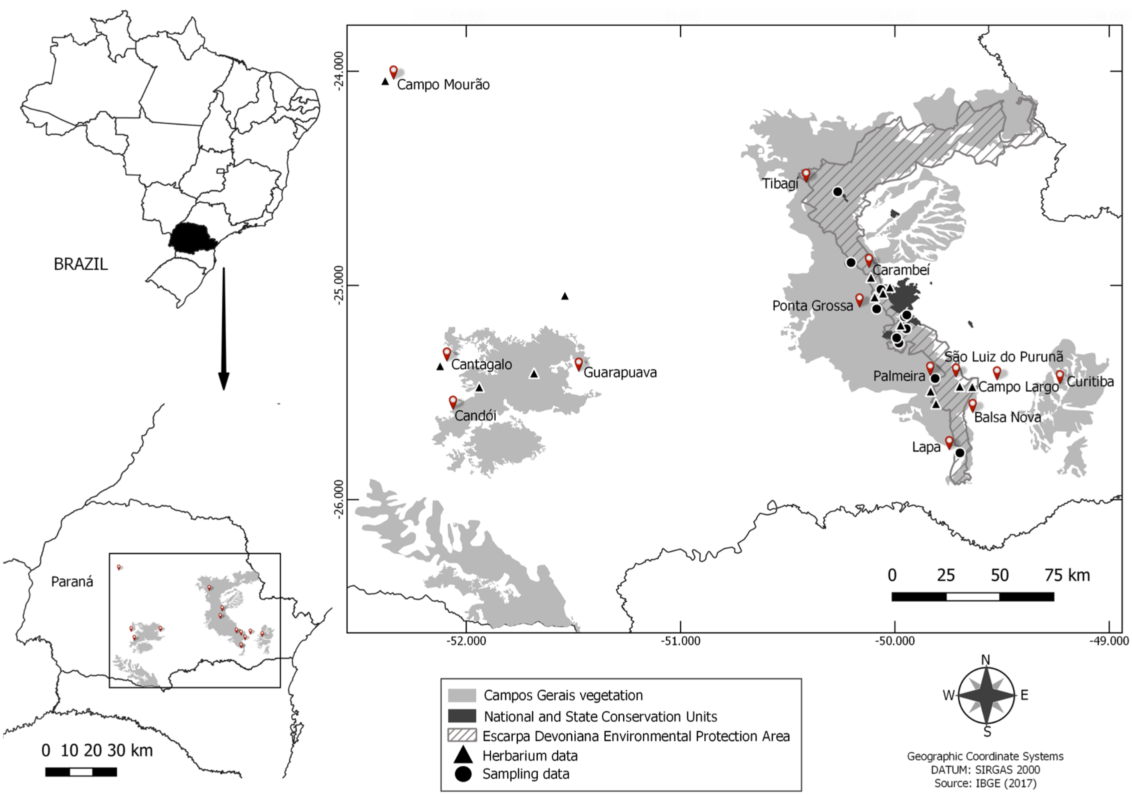

Figure 2 – Distribution and occurrence maps of *Parodia carambeiensis* based on the sampling sites and herbaria data from the Paraná State. The municipalities of the studied sites are also indicated on the map.

Table 1 – Distribution and occurrence sites of *Parodia carambeiensis* based on herbarium data and field expeditions in the Campos Gerais region, state of Paraná, 2017.

Municipality	Site	Data	Latitude	Longitude
Balsa Nova	Balsa Nova	Herbarium	-25.49370	-49.83258
	Ponte de Arcos	Herbarium	-25.55197	-49.80789
Campo Largo	Campo Largo	Herbarium	-25.49370	-49.83258
Campo Mourão	Campo Mourão	Herbarium	-24.04366	-52.37811
Candói	Fazenda Capão Redondo	Herbarium	-25.47423	-51.93931
Canta Galo	Canta Galo	Herbarium	-25.37546	-52.12174
Carambeí	Fazenda São Daniel	Herbarium	-24.96229	-50.11127
	Rio São João	Sampling	-24.89316	-50.20420
Guarapuava	Turvo	Herbarium	-25.04621	-51.53946
	Fazenda 3 Capões	Herbarium	-25.40940	-51.68356
Lapa	Parque Estadual do Monge	Sampling	-25.78195	-49.69609
Ponta Grossa	Alagado	Herbarium	-25.00734	-50.02262
	Buraco do Padre	Herbarium	-25.18533	-49.97293
	Fazenda Vila Velha	Sampling	-25.26903	-49.98079
	Fazenda Modelo	Sampling	-25.10982	-50.08444
	Furnas Gêmeas	Sampling	-25.14623	-49.95397
	Cachoeira Mariquinha	Sampling	-25.20248	-49.94657
	Pedra Solitária	Sampling	-25.13801	-49.94397
	Parque Estadual de Vila Velha	Sampling	-25.24478	-49.99133
	Rio São Jorge	Herbarium	-25.03648	-50.05506
	Tacinha	Sampling	-25.01887	-50.06458
	Usina Pitangui	Herbarium	-25.05395	-50.09404
Palmeira	Colônia Witmarsum	Sampling	-25.43443	-49.81172
São Luiz do Purunã	Fazenda Paraíso	Herbarium	-25.47111	-49.69694
	Mirante	Herbarium	-25.47257	-49.63865
Tibagi	RPPN Sonho Meu	Sampling	-24.56235	-50.26641

rock crevices, (rupicolous) and soil patches. During the expeditions, a specimen was collected and deposited into the Herbarium of the State University of Ponta Grossa (HUPG) as voucher material.

The field surveys were performed at 11 sites where the cactus was recorded in the five municipalities previously cited. In each area, six (6) 10 m × 10 m parcels were defined, with a total scanning area of 600 m^2 per site. At each site, the parcels were distributed according to an active search of the populations, with mature forms counted inside a given parcel, based on Ribeiro (2011).

Mature individuals were determined based on size, with height higher than 50 mm, presence of white fluff on the top (indicating the beginning of the reproductive phase) (Fig. 1c), remnants of floral structures and presence of fruits (Soller *et al*. 2014).

In each parcel, a set of local environmental factors that could influence the distribution and density of cacti were recorded, listed as follows: the presence of native vegetation, exotic plants, farming, deforestation, livestock, litter from ecotourism, recent wild fires, presence of roads nearby, presence of rivers and lakes nearby. The choice of the set of local variables was based on previous literature and studies referring to anthropic actions on cacti species (Silva *et al*. 2011), and about the local threatens to the native vegetation (Moro & Carmo 2014).

Climatic variables

Climate data from each site was obtained from the Worldclim website (<http://www.worldclim.org/>), with a resolution of 30 seconds (1km^2) (Fick & Hijmans 2017). The set of climatic variables included variations in temperature and precipitation data for each site (annual monthly average temperature, maximum and minimum temperature, temperature range, total annual precipitation, average monthly precipitation, driest monthly precipitation, precipitation in wettest month, among others with a total of 19 bioclimatic variables). These variables were evaluated for collinearity among themselves (correlation between variables). Therefore, the VIF values (variance inflation factor) for each variable were estimated, only retaining variables with values of < 2 VIF for analysis, i.e. those with little or no correlation to each other (Zuur *et al*. 2010), such as annual mean temperature (BIO1), mean diurnal range (mean of monthly (max temp – min temp)) (BIO2), temperature annual range (max temperature of warmest month – min temperature of coldest month) (BIO7) and annual precipitation (BIO12).

Data analysis

In order to compare the average abundance of individuals in the study areas, we conducted an analysis of variance (ANOVA one way), followed by Tukey test a posteriori for pairwise differentiation. To evaluate the effect of local environmental variables (presence of rivers, conservation units, presence of invasive plants (e.g. Pinus spp.) (Fig. 1d), highways, ecotourism, livestock, agriculture and wildfires (Fig.1 e-f) an ANOVA was performed for each of the factors assessed. For example, the average number of individuals in sites where invasive plants were present and sites without this influence were recorded.

The effects of local and climatic variables on *P. carambeiensis* were evaluated by developing generalized linear models (GLMs), making it possible to assess which set of variables drive distribution and density of the cacti. In this sense, explanatory models were developed with different sets of variables, using those with the lowest akaike (AIC) values and highest degree of explanation (delta weight) (Burnham & Anderson 1998).

In order to check the relative importance of each set of variables on different spatial scales, we carried out a partial variation partitioning analysis (RDA redundancy analysis). This verified the partial effect of geographical distance (considering latitude and longitude as variables, macro-scale sense), climate factors (meso-scale), and local elements of the landscape (presence of invasive plants, agriculture, ecotourism (micro-scale) on the distribution and population densities of *Parodia carambeiensis*. Before the analysis of variance (ANOVA), the normality of variables was checked using the Shapiro-Wilk test. Besides the ANOVA, the GLM and RDA analyzes were performed in the R Software (2014).

Distribution pattern

The spatial distribution pattern of *Parodia carambeiensis* (as aggregated or clumped, random and uniform) was calculated from the coefficient of dispersion (CD) and Green Index (GI), which evaluates the ratio between the variance and mean abundance values. A CD equal to one (= 1) denotes a population with random distribution, CD <1 indicates population with uniform distribution, while CD >1 indicates an aggregate (or clumped) distribution (Brower *et al*. 1998). Considering the Green Index (GI), positive values indicate aggregate distribution, negative ones indicate random distribution and those equal to zero indicate uniform distribution (Ludwig & Reynolds 1988).

Conservation status

The spatial distribution map was created using data from the field surveys and assembled from the following herbaria collections in the Paraná State: UTFPR- HCF (Herbarium of Universidade Tecnológica Federal do Paraná Campus Campo Mourão), MBM (Botanical Museum Municipal de Curitiba), UFPR- UPCB (Herbarium of Universidade Federal do Paraná), HUPG (Herbarium of Universidade Estadual de Ponta Grossa), online version available Taxonline (<https://taxonline.bio.br/specieslink.php>).

The risks of extinction were estimated considering the criteria established by the International Union for Conservation of Nature-IUCN on a regional and national context (IUCN 2019). The following factors were considered: population reductions, extent of occurrence, degree of isolation, area of occupancy, extent of anthropic impact on the number of populations, as well as the population density and spatial distribution map.

Thus, to reassess the conservation status of *P. carambeiensis*, we estimated the Extent of Occurrence (OE) and its Occurrence Area (OA) based on the recent dataset assembled by field surveys and available herbaria data. For OE, the entire (shortest) perimeter of the distribution area, including all occurrence points of *P. carambeiensis* records, was estimated. The occupancy area (OA) was estimated using Quantum GIS Program 2.0.1, by putting a mesh grid (4km^2 area) on top of a species distribution map. This area corresponds to the sum of the checkered areas where the species can be found.

Results

Population density

The average abundance of *P. carambeiensis* differed among sites, with the highest densities found in Tacinha - Ponta Grossa (45.3 cacti/m^2), and RPPN Sonho Meu – Tibagi (38.0 cacti/m^2), near the Parque Estadual do Cânion Guartelá, and Cachoeira da Mariquinha - Ponta Grossa (26.5 cacti/m^2). At other sites, the average density ranged from 1.4 to 10.0 cacti/m^2, with the smallest average found in the Parque Estadual do Monge (Tab. 2).

Although *P. carambeiensis* was found within the boundaries of some conservation units e.g., RPPN Sonho Meu, Parque Estadual de Vila Velha, and Parque Estadual do Monge, the highest population densities were still found on private properties in the areas surrounding the conservation units. The sites located in private domains have been experiencing intense anthropogenic pressure, enhancing the risks of local extinction, with isolation and fragmentation of habitats also increasing these chances.

Most populations of *P. carambeiensis* presented clumped distribution patterns since CD values ranged from 2.87 to 36.70 (Tab. 2). Only two sites fit in the uniform distribution pattern: Fazenda Modelo (CD=0.89), and Pedra Solitária (CD=0.98). However, considering the Green Index (GI), which complements the dispersion coefficient (CD), all the populations evaluated fit in a clumped pattern, except those from Fazenda Modelo which remained uniform.

Local and climatic variables

Populations of *P. carambeiensis* have been affected by changes in the natural landscape driven by anthropogenic actions (Fig.1 d-f). We found that the presence of roads nearby had a strongly negative effect on population densities, in addition, tourism and exotic or invasive species also tended to contribute negatively to cacti density (Tab. 3). On the other hand, presence of livestock, light wildfires, and lakes and rivers nearby seemed to contribute positively to population density (Tab.3).

Table 2 – Abundance of *Parodia carambeiensis* for each parcel (100m^2), with mean ± standard error (SE) and dispersion index per site.

Municipality	Site	P1	P2	P3	P4	P5	P6	Mean ± SE	CD	ID
Ponta Grossa	Tacinha	686	764	544	176	180	368	453 ± 102.9 [a]	19.25	1.23
Tibagi	RPPN Sonho Meu	281	556	410	41	319	675	380±90.8 [a]	21.98	1.25
Ponta Grossa	Cachoeira da Mariquinha	198	279	175	214	329	395	265±34.8 [b]	21.98	1.25
Palmeira	Colônia Witmar-sum	123	29	43	151	143	131	103±21.7 [b]	21.98	1.25
Ponta Grossa	Fazenda Modelo	77	175	70	57	83	62	87±17.9 [b]	21.98	1.25
Ponta Grossa	Fazenda Vila Velha	87	101	0	210	71	33	83±29.4 [b]	2.87	1.22
Ponta Grossa	Furnas Gêmeas	177	23	18	54	12	0	56±28.2 [b]	22.27	2.33
Carambeí	Rio São João	255	43	32	0	0	0	55±40.7 [b]	14.53	3.11
Ponta Grossa	Pedra Solitária	46	40	56	42	51	49	47±2.41 [b]	0.98	1.00
Ponta Grossa	PEVV	246	118	1	2	6	0	62±41.3 [b]	36.70	2.98
Lapa	Parque Estadual do Monge	84	0	0	0	0	0	14±14.0 [b]	18	6.00

P (Parcels), CD (Dispersion Coefficient), ID (Dispersion Index). Distinct letters ([ab]) indicate differentiation of means by *a posteriori* Tukey test.

Table 3 – Mean abundance ± standard error of *P. carambeiensis* according to the presence or absence of a given effect. Means were compared by a variance analysis (ANOVA).

Effect	Presence	Absence	$F_{1, 64}$	p
Agriculture	125.75 ± 5.59	156.50 ± 20.21	0.437	0.510
Exotic/invasive plants	119.82 ± 32.97	172.41 ±29.49	0.732	0.395
Rivers/lakes	212.54 ± 39.81	101.62 ± 24.08	6.413	0.014
Livestock	233.83 ± 62.43	125.65± 22.88	3.653	0.060
Wildfires	211.42 ± 53.23	118.60 ± 21.96	3.709	0.058
Protection area	152.17 ± 50.49	142.75 ± 21.43	0.035	0.852
Tourism	103.05 ± 29.53	162.40 ± 28.71	1.466	0.230
Roads	48.33 ± 14.93	181.69 ± 28.45	7.086	0.007

Considering the influence of the climatic variables on the distribution and density of *P. carambeiensis*, we observed that annual average temperature (BIO1), annual thermal amplitude (BIO2) and annual average precipitation (BIO12) were the main drivers for population. Additionally, according to the generalized linear models (GLMs), the populational density was best explained by the model that accounts for the combined effect of local and climatic variables, including recent wildfires ($Z = 49.97$; $p < 0.001$) (Fig. 3a), the occurrence of rivers/lakes near the sampling sites ($Z = -25.87$; $p < 0.001$) (Fig. 3b), annual thermal amplitude ($R^2 = 0.29$; $Z = 55.46$; $p < 0.001$) (Fig. 3c) and average precipitation ($R^2 = 0.03$; $Z = 25.03$; $p < 0.001$) (Fig. 3d).

Combined effects on macro, meso and micro scales

The variation partitioning analysis (RDA) highlighted that 56% ($R^2 = 0.56$) of the variation in *P. carambeiensis* density could be explained by the set of variables evaluated in the study. The total explanation percentage considers the importance of structuring components on a local scale (*e.g.*, presence of roads, lakes and rivers, livestock and wildfires), which accounted for 14% of the explanation ($R^2 = 0.14$), while macro-scale components (geographical distance among the sites) accounted for 18% of the explanation ($R^2 = 0.18$). Finally, the meso-scale components (represented by the climatic variables) accounted for 24% ($R^2 = 0.24$) of explanation.

Conservation status

According to IUCN criteria and the dataset about geographical distribution and occurrence of *P. carambeiensis*, this species fits into category B, which corresponds to taxa with restricted geographical distribution in fragmentated habitats, and declining or fluctuating populations. The species is distributed over an extension area of 23,276 km^2, however, only occupies 168 km^2. Notwithstanding, the results indicate that *P. carambeiensis* must be considered an Endangered species (EN), since it presents restricted distribution and is threatened by anthropic influences (IUCN criteria: EN: B2ab, iii, iv, v).

Discussion

The results demonstrate that populational density and spatial distribution of *P. carambeiensis* are ruled by a set of variables including local anthropic influences, climate variables and geographic distance.

Anthropic threats such as deforestation, fragmentation and conversion of natural lands for agriculture and livestock use are the leading causes of species extinction (Pimm *et al.* 1995; Gurevitch *et al.* 2009). Cultivation of exotic species such as *Eucalyptus* spp. and *Pinus* spp. affects at least 27 native plant species in the southern Brazil, including threatened species such as *Parodia muricata* (Otto *ex* Pfeiff.) Hofacker (Goettesch *et al.* 2015). Pine cultivation is one of the main crops in the Campos Gerais region, and, in addition to the conversion of natural areas, the seeds of this species are easily dispersed by the wind, making it a harmful invasive species in natural areas where it competes with native vegetation and increases extinction risks and native biodiversity loss (Neto & Rocha 2014; Rocha & Neto 2014).

Furthermore, areas of scenic natural beauty within the Campos Gerais region intrigue tourists and increase visitation in the region, which could have a negative effect on endangered species, especially *P. carambeiensis*, as highlighted. Whenever tourism and visitation are not regulated and sustainable, they can threaten natural ecosystems by decreasing populations, which is what was observed for this cactus. The main threats may be caused by direct impacts as trampling, crushing and uprooting, or indirect impacts such as environmental degradation, fires, the activities and behavior of native animals, pollinators, changes in soil biota including fungi and nutrients, and hydrology (Liddle 1997; Buckley 2004; Pickering & Hill 2007). The presence of highways near the areas also had a negative effect on these populations, since they facilitate human access and tourism in the sites, as well as act as barriers between habitat patches, hindering seed dispersion and pollination (Forman *et al*. 2003).

Nevertheless, our data agrees with Ortega et al. (2010) & Méndez *et al*. (2004), who highlighted that some anthropic actions may also enhance the occurrence and densities of Cactaceae. For example, the presence of livestock in areas near the studied sites had a peculiar influence and positively affected *P. carambeiensis* population densities. Studies by Martorell & Peters (2009) on the genus *Mammillaria* Haw. (Cactaceae) indicated that most species of this genus present high densities in areas near pastures. These studies help understand *P. carambeiensis* better because the RPPN Sonho Meu (Tibagi) is associated with cattle breeding sites, which could be providing an extra source of nutrients for the cacti and favoring population increase.

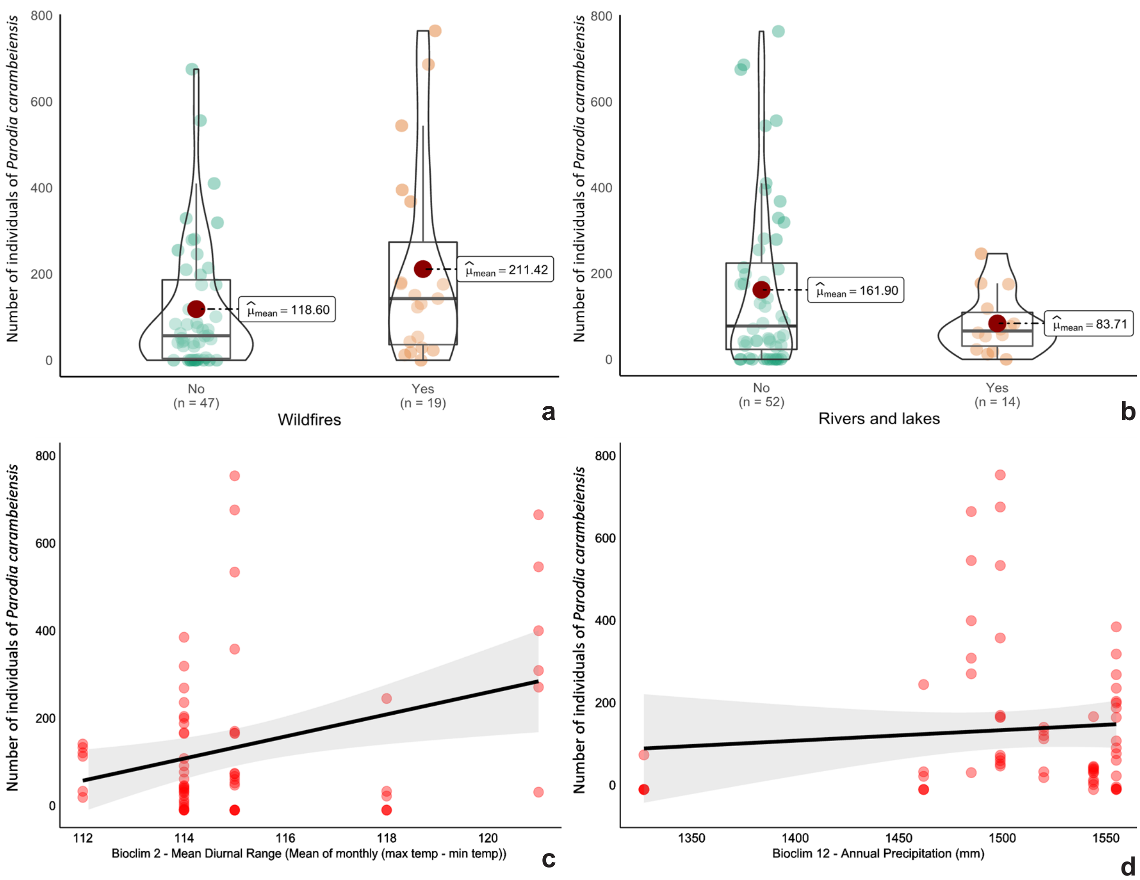

Figure 3– Variation in the observed abundance of *Parodia carambeiensis* according to climatic and local influences as a result of the general linear model test (GLM).

Similarly, we also found out that past wildfires also positively affected *P. carambeiensis* density, which could be due to the elimination of competitors and exotic species such as Melinis minutiflora P. Beauv. (Poaceae) (Martins *et al.* 2011), which is one of main threatens to the local vegetation (Moro & Carmo 2014). However, studies by Silva et al. (2011) report that sites with high intensity and frequent fires are negatively correlated to native Cactaceae populations, as they impair reproduction and survival in the environment. Bowman *et al.* (2009) and Durigan & Ratter (2015) also highlight the unknown effect of fire on the ecosystem processes mainly when it is not managed. Hence, more studies about how population dynamics of *P. carambeiensis* and entire ecosystems are influenced by wildfire occurrences are needed.

The results of the General Linear Models (GLM) corroborated the importance of some local influences from analysis of variance (ANOVA) in addition to climatic variables (meso-scale elements). According to studies of plant communities, the outputs highlighted that the thermal amplitude and rainfall were important for modeling population density (Santos & Oliveira 2008). The seasonal variation in temperature was important in the models, with higher temperature variation throughout the year correlated to higher density of *P. carambeiensis*. Cactaceae are adapted to environments with wide thermal ranges (Steenbergh & Lowe 1977), with *P. carambeiensis* seeming to follow such same pattern, presenting higher densities in sites with wider temperature ranges throughout the year. Associated to this, rainfall had a weak positive influence on the populations, where sites with higher precipitation presented a slightly higher cactus density.

Data comprising meso and macro scale variables (climatic effect and geographic points) accounted for 24 and 18% of explanation about the variation in *P. carambeiensis*, density, respectively. This dataset is vital for modeling the distribution and occurrence of this species throughout the Campos Gerais region, since understanding the main drivers of spatial distribution allow the occurrence limits to be precisely defined. Such information is important to guide the action and conservation efforts in wide landscapes and to integrate occurrence patches.

Micro-scale or local elements explained 14% of *P. carambeiensis* density, being related to anthropic effects on the landscape. Notwithstanding, anthropic effects seem to have a relatively small effect on the cacti population and could be managed at local scales, resulting in the preservation of local populations with small densities. Considering our results, the main efforts must be focused on conserving isolated populations outside the conservation units and in the private areas, since they shelter most abundant populations and are more susceptible to anthropic threats. Meanwhile, it is important to develop strategies to enhance the connectivity between population patches, reducing the chances of local extinction and allowing dispersion and recolonization of empty areas, as well as for conservation measures such as species reintroduction and local management (Hanski & Gaggiotti 2004; Salazar & Moreira 2019).

The clumped distribution of *P. carambeiensis*, typical of most Cactaceae, may be associated with the heterogeneous habitat found in Campos Gerais and also with the presence and type of soil in the rocky outcrop areas, these factors may be important for the occurrence of the species (Godínez *et al.* 2003). This distribution pattern, along with the high degree of endemism, make *P. carambeiensis* more vulnerable (Ortega *et al*. 2010; Menezes & Silva 2015).

According to the IUCN, *P. carambeiensis* is currently considered unconcerned (LC), which is used for taxon that present wide distribution or restricted distribution without significant threats. However, our outcomes highlighted that *P. carambeiensis* suffers from significant anthropogenic actions, with negative influences on their densities. Therefore, since most populations are distributed in sites without environmental protection and with high negative anthropic effects, suggesting that the species should be recategorized as endangered (EN). Goettsch et al. (2015) studied more than 1478 species of Cactaceae and reported a high concern about their current conservation status since it is among the most threatened plant families, being the habitat losses, invasive species and illegal collection the main causes of extinction.

In general, a major concern about the conservation status of Cactaceae is the combined effects of negative anthropic actions that lead to population isolation, increasing the vulnerability and extinction risks for this species (Hinostrosa & Hernández 2000; Contreras & Valverde 2002; Tapia *et al.* 2005). The new conservation status of *P. carambeiensis* arises from increased fragmentation in Campos Gerais, which in turn affects the populational conservation. Fragmentation and modification of a habitat can threaten local populations, drastically affecting the surviving, nutrients cycling, evapotranspiration and gene flow, with negative consequences to populations (Grilli *et al.* 2015; Martorell & Peters 2009).

Conclusions

Overall, our work provides an overview of the influences and threats that affect *Parodia carambeiensis* and suggests updating its conservation status to Endangered. Such update in conservation status reinforces the need to implement management measures that aim to protect this species and preserve Campos Gerais region, as this species is endemic and a symbol within this region.

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