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Abstract *Partamona rustica* is a stingless bee that occupies dry forests of Brazil, such as the cerrado (savanna-like biome) and *caatinga* (xeric shrubland and thorn forest), ranging from the northern portion of the state of Minas Gerais to the southwestern portion of the Bahia state. As this bee is endemic to these environments and its biology is poorly known, the aim of the present study was to investigate aspects of its natural history and biogeography. Moreover, the potential distribution of the species is analyzed through ecological niche modeling. Sampling was performed in the full range of distribution of the species. Nesting sites for 145 colonies, plants visited, and termite nests hosts were identified. Most of the termite nests in which the species nested were active (83 %) and corresponded to Constrictotermes cyphergaster. Pollen analyses revealed 62 pollen types from 30 families of angiosperms visited by P. rustica, the most common of which were from

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the families Leguminosae-Mimosoideae (11.1 %) and Myrtaceae (7.9 %). *Partamona rustica* occurs in areas at 500 ± 187.30 m above sea level with semi-arid climates. The climatic niche model revealed a very realistic range for *P. rustica*, contouring the *Chapada Diamantina* National Park by the east, where there are no records of the species. Given the ecological importance of bees as pollinators, the intense pressure exerted by bee hunters and environmental changes caused by human activities, the present findings underscore the importance of concentrating efforts on the conservation of dry areas and the endemic species that inhabit these forests.

Keywords Conservation · Constrictotermes

cyphergaster · Ecological niche modeling · Nesting sites · Pollen analysis · Stingless bee

Introduction

Brazil has a considerable diversity of bees, with 1678 species distributed among the families Apidae (n = 913), Halictidae (n = 251), Colletidae (n = 104), Andrenidae (n = 82), and Megachilidae (n = 328) (Silveira et al. 2002). The stingless bees are an important group, with 417 species considered valid in the Neotropical region (Camargo and Pedro 2013).

Stingless bees of the genus *Partamona* Schwarz, 1939 have a broad geographical distribution, occurring from southern Mexico to southern Brazil (Camargo and Pedro 2003). *Partamona rustica* Camargo and Pedro 2003 is an endemic bee to the Brazilian biomes known as the *cerrado* (savanna) and *caatinga* (xeric shrubland and thorn forest), ranging from northern portion of the state of Minas Gerais to the southwestern portion of the state of Bahia and nesting in

active arboreal termite nests (Camargo and Pedro 2003). The lack of studies on nesting sites, plants visited, natural enemies, and environmental constraints on its geographic distribution means that little is known of the natural history of *P. rustica*.

Bees play an important role as pollinators and are therefore key elements in the maintenance and conservation of natural ecosystems (Slaa et al. 2006; Ollerton et al. 2011; Wratten et al. 2012). Studies on plants and animals in dry forests in Brazil have shown that these environments harbor high levels of endemism, species richness, and insect–plant interactions (Klink and Machado 2005; Zanella and Martins 2008; Giannini et al. 2013). Therefore, investigations involving organisms in these forests are important, especially due to the fact that such organisms have been largely excluded from discussions on conservation (Klink and Machado 2005).

The *caatinga* biome is a highly exploited, modified environment that accounts for nearly 11 % of Brazil, with only 53 % of its original area intact (MMA 2014; Giulietti et al. 2006; Castelletti et al. 2003). The *cerrado* biome accounts for more than 20 % of country, with only 20 % of its original area intact. These changes are associated with agricultural needs, which lead to deforestation and pose serious threats to biodiversity (Myers et al. 2000).

Knowledge on the geographical distribution of a given species is an initial step to the establishment of conservation policies. Given the difficulty in determining a realistic distribution range for any organism, ecological niche modeling constitutes a viable alternative for the construction of potential distribution maps. The aim of this method is to determine non-randomized relationships among sampling points and bioclimatic data by building models that depict a potential geographic distribution with the greatest likelihood of finding favorable environmental conditions for a species to occur (Corsi et al. 1999; Peterson et al. 2011; Svenning et al. 2011).

Habitat fragmentation, competition for nesting sites due to deforestation, and predation by bee hunters are serious pressures imposed on stingless bees, which could result in the decline or also extinction of populations of these bees (Klein et al. 2007; Knight et al. 2009). Information on the natural history and biogeographic aspects of a given species provide the basis for studies on the interactions between bees and plants and assist in the establishment of management and conservation policies (Silva et al. 2010; Giannini et al. 2013).

The aim of the present study was to investigate aspects of the natural history and biogeography of the stingless bee P. *rustica* and establish the potential geographic distribution of this species using ecological niche modeling.

Materials and methods

Study area and sampling efforts

Adult *P. rustica* were sampled between May 2012 and January 2014. Thirty-two sites were visited in southwestern Bahia state and northern Minas Gerais state. *Partamona rustica* was found at 11 of these sites (1–11 in Table 1 and in Fig. 1), totalizing 145 nests (mean = 13 per site). However, no nests were found at 21 sites (12–21, red triangles in Fig. 1): Santo Estevão, Itatim, Itaberaba, Amargosa, Brejões, Cravolândia, Irajuba, Maracás, Jequié, Barra da Estiva, Mucugê, Andaraí, Anagé, Vitória da Conquista, Bom Jesus da Lapa, Serra do Ramalho, Carinhanha, Guanambi (in Bahia), Espinosa, Janaúba, Januária (in Minas Gerais).

Data collection

Nests were located through active searches of at least 16 h per site, to standardize sampling efforts. The nests were photographed, geo-located, and measured, and the site was characterized (identification of the substrate in which the termites were found). Five workers were collected from each nest and kept in dry conditions for identification, and 15–20 workers were preserved in 70 % alcohol for pollen analysis. Fifteen termites were also sampled and preserved in 70 % alcohol for taxonomic identification.

In addition, 37 farmers, beekeepers or bee hunters, from 27 sites were informally interviewed to determine their knowledge on the occurrence, exploration, and conservation of *P. rustica*, based on three questions: (1) "Do you know the "cupinheira" stingless bee (*Partamona rustica*)?"; (2) "Have you ever used or removed honey, wax or pollen from the nests of this bee?"; (3) "Have you seen this bee nests recently?" The answers were recorded and tabulated.

Pollen analysis

Five *P. rustica* nests were selected at random from each of the 11 sites sampled. From each nest, the pollen load of 15–20 adult workers (about 825 workers in all) was extracted for analysis. In the laboratory, the workers were placed in test tubes, which were shaken gently. The workers were then removed and the remaining material was centrifuged for 15 min at 2000 rpm (Silva et al. 2014). The alcohol was discarded and glacial acetic acid (4 mL) was added to the pellet. The material was acetolyzed (Erdtman 1960) and placed on slides (two per sample) prepared with Kisser gelatin. Pollen types were analyzed by comparisons to material in the collection of the Palynology Laboratory of the Biology Department of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto of Universidade de São

	Localities	Abbreviation	S	W	Altitude	N
1	Ruy Barbosa-BA	RBA	-12.2279	-40.3109	314	12
2	Boa Vista do Tupim-BA	BVT	-12.5021	-40.4709	328	14
3	Milagres-BA	MIL	-12.9311	-39.7197	365	20
4	Iramaia-BA	IRA	-13.8617	-40.0814	392	15
5	Manoel Vitorino-BA	MVT	-13.9393	-40.5634	256	16
6	Contendas do Sincorá-BA	CSI	-13.7937	-41.0165	300	12
7	Ituaçu-BA	ITU	-13.8823	-41.3246	586	11
8	Tanque Novo-BA	TNO	-13.5949	-42.5211	900	14
9	Macaúbas-BA	MAC	-12.243	-40.2499	756	11
10	Cocos-BA	COC	-14.1579	-44.4031	587	10
11	Conego Marinho-MG	СМА	-15.3143	-44.3819	632	10
Total						145

Table 1 Sites at which Partamona rustica nests were sampled

N = number of nests sampled



Fig. 1 Map illustrating sites visited during field expeditions. *Black triangles* represent 11 sites with active *P. rustica* colonies (Table 1). *Red triangles* (12–32) refer to sites where the species was not found. Plateaus and hills of *Chapada Diamantina* are represented by *diagonal*

Paulo (FFCLRP-USP), and the specialized literature (Silva et al. 2010, 2014; Bauermann et al. 2013). Voucher specimens were deposited in the aforementioned collection.

Pollen analyses were conducted with the aid of a binocular microscope. Digital pictures of the pollen grains were obtained using a Leica DFC280 photodocumentation system. Quantitative analyses were conducted to evaluate the richness of the first 400 pollen grains of each sample (Montero and Tormo 1990). Shannon–Wiener diversity (H') (Shannon and Weaver 1949) and uniformity per site (J') (Pielou 1966) were estimated using the PAST program

lines. Serra do Espinhaço is represented by horizontal lines. *Chapada do Rio Irecê* and *Utinga* are in grid shape. São Francisco River is indicated by the dotted line (color figure online)

(Hammer et al. 2001), to evaluate the trophic niche of *P. rustica*.

Ecological niche modeling

A potential distribution model for *P. rustica* was constructed using the maximum entropy algorithm implemented in MaxEnt3.3.3k (Phillips et al. 2006; Phillips and Dudík 2008). The model was obtained after different tests using 21 occurrence records and 19 bioclimatic variables obtained from Worldclim (http://www.worldclim.org). Two important databases on the occurrence of Meliponini in Brazil were consulted to compile the complete records of occurrence of *P. rustica*. One was the Moure Collection of the Federal University of Paraná and the other was the Camargo Collection of FFCLRP-USP. Ten sites at which *P. rustica* was previously sampled were identified (Table S1). For samples on which no coordinates were available, geo-location was performed based on the sample labels using Google Earth. The occurrence data for the species were supplemented with the 11 sites at which active nests were found in the present study (Table 1).

Ecological niche modeling was conducted with grids edited in DIVA-GIS 7.5.0.0 (http://www.diva-gis.org/) containing the minimum area for the known range of occurrence of the species to prevent the effect of possible bias in the output of the model resulting from background extension and niche expansion (Anderson and Raza 2010). The potential distribution map was edited in Arc-Gis 10.1.

Area under the curve (AUC) values higher than 0.9 are considered reliable in recent analyses (Giannini et al. 2012, 2013). However, alternative analyses may be more efficient when calibrating and improving niche models. Such analyses can be carried out using different regularization multiplier values ranging from 0.5, 1, 1.5, ... to 4, with two sets of MaxEnt features (quadratic + product + threshold + hinge and quadratic + product + hinge), totaling 16 calibrations. These combinations were employed in the present study based on the amount of sampling sites for P. rustica. It is expected that such combinations of features generate different AUC values and the 10 percentile training omission (OR_{10 %}). The latter parameter indicates the likelihood of finding favorable conditions for the species to occur when using the lowest value attributed to any of the 90 % occurrence records with the highest scores. In summary, the most reliable potential distribution model for the species is expected to present a high AUC value and the lowest $OR_{10\%}$ value. Moreover, 30 % of the occurrence sites (n = 6) were randomly chosen to test the predictability of the models for determining non-sampled areas where the species could occur (Rosauer et al. 2009).

Results and discussion

Characterization of nests and sites used by P. rustica

The entrances of the *P. rustica* nests were located mostly in the lower-middle portion of the termite nests. The conical shape of the entrances is simple compared to other species of this genus, such as *Partamona ailyae* Camargo (1980), *Partamona helleri* Friese (1900), and *Partamona gregaria* Pedro and Camargo (2003) (Camargo and Pedro 2003), measuring 3.0 cm in entrance, built with mud and slightly detached from the surface of the substrate. Unlike other sites, in which the mud of the entrances had the same color as the nests, the nests at Manoel Vitorino had reddish mud at the entrances (Fig. 2a, b).We also observed color variation in the wax envelope that ranged from reddish in Tanque Novo and Cocos to brown in Iramaia, Ruy Barbosa, Macaúbas and Boa Vista do Tupim (Fig. 2c, d).

Most termite nests with colonies of *P. rustica* were active (83 %; n = 144). One colony was found in a crack in the wall of a house made of mud in Macaúbas, Bahia. This demonstrates that *P. rustica* builds nests preferentially in active arboreal termite nests, but not exclusively.

Nearly all colonies of this stingless bee were associated with Constrictotermes cyphergaster Silvestri (Isoptera, Termitidae) (90 %; n = 144). Only two colonies were associated with nests of Nasutitermes spp. (Ruy Barbosa and Boa Vista do Tupim). The genus Constrictotermes is endemic to South America, with five known species, most of which build arboreal nests (Godinho et al. 1989; Melo and Bandeira 2004). C. cyphergaster is commonly found not only in the central savanna of Brazil as well as Paraguay, Bolivia, and northern Argentina, but also in the Atlantic Forest (Araújo 1970; Constantino 1998). Studies report the occurrence of C. cyphergaster in the caatinga, which is the main species of termite that builds conspicuous nests in this biome (Godinho et al. 1989; Melo and Bandeira 2004). Lorenzon et al. (1999) report the association of the bee genus Partamona with this species of termite.

The present data suggest a strong preference by P. rustica to build nests in the nests of C. cyphergaster, although nests of genus Nasutitermes were found at all the sites analyzed. Studying the nesting ecology of P. rustica and P. cupira in Milagres (state of Bahia, Brazil), Barreto and Castro (2007) also found this preference, despite the presence of other arboreal termite nests in the area, as 90 % (n = 28) of the stingless bee colonies were built in nests of C. cyphergaster. In this study, only one nest of P. rustica was associated with another termite species (Nasutitermes corniger Motschulsky). Termite nests hosting colonies of P. rustica had a mean length and circumference of 71.22 ± 13.17 cm and 139.95 ± 25.26 cm, respectively. Barreto and Castro (2007) report a similar mean length (63.45 \pm 24.04 cm; n = 25) in the nests of C. cyphergaster hosting colonies of P. rustica and P. cupira.

Termite nests were mostly attached to *umburana* (*Commiphora leptophloeos* Mart. J. B. Gillett) and *umbuzeiro* (*Spondias tuberosa* Arruda) trees, with 44 and 13 records, respectively. Barreto and Castro (2007) reported the same preference. According to the authors cited, species of the genus *Partamona* build nests in preexisting cavities made by the cactus parakeet (*Aratinga cactorum* Kuhl, 1820) in the *caatinga*. However, although termite nests with such hollows were found during the field trips in the present

Fig. 2 Different coloration

P. rustica

recorded for nest entrances (**a**, **b**) and envelopes (**c**, **d**) of



Table 2 Number of pollen types collected by *Partamona rustica* per site, pollen diversity (H' Shannon index), and pollen uniformity (J'). The results were obtained based on the analyses of pollen

collected from workers at 11 sites in the states of Bahia and Minas Gerais. The sites are described in Table 1

Localities	BVT	COC	СМА	CSI	IRA	ITU	MAC	MVT	MIL	RBA	TNO
Number of pollen types	19	16	28	14	8	7	11	15	15	27	27
Η'	1.089	2.058	2.731	1.094	1.018	1.123	1.835	1.743	2.174	2.304	2.411
J'	0.376	0.780	0.838	0.426	0.522	0.577	0.835	0.679	0.823	0.707	0.758

study, no nesting activity of *P. rustica* in cavities made by this bird was observed.

Trophic resources and plants visited by P. rustica

The pollen analysis revealed 62 types (Table S2), with 17.0 ± 6.0 pollen types per site. Pollen from *Anacardium* sp. was found at 10 of the 11 sampled sites, while pollen from *Senna sp., Mimosa tenuiflora* (Wild.) Poir., and

Syagrus sp. were found at 9, 8, and 8 sites, respectively (Table 2). These results may be attributed to the fact that these plants are found throughout the *caatinga* biome and some flower both in dry and rainy periods (Maia-Silva et al. 2012).

Although flowers of the genus *Senna* have poricidal anthers, it is common to find pollen from species of this genus among the material collected by stingless bees that do not vibrate, as observed for *Scaptotrigona depilis* Moure (1942) and *S.* aff. *depilis* (Ferreira et al. 2010; Faria et al. 2012). Novais et al. (2013) also observed pollen from *Senna* in pots and honey of *Tetragonisca angustula* from *caatinga* sites, reinforcing the importance of these plant species in the diet of these bees. They obtain pollen by plundering material that falls on the petals after vibrations made by other bees and by accessing the resource through openings made by species of *Trigona* on the anthers of flowers. The same occurs with other poricidal anther plant species of the genera *Solanum, Tibouchina*, and *Miconia* (Marques-Souza et al. 2007; Ferreira et al. 2010; Faria et al. 2012).

The greatest pollen diversity was found in colonies from Conego Marinho (CMA), Tanque Novo, and Ruy Barbosa (TNO RBA. respectively) and $(H'_{\rm CMA} = 2.73;$ $H'_{\rm TNO} = 2.41$, and $H'_{\rm RBA} = 2.30$). The lowest degree of pollen diversity was found in colonies from Iramaia and Ituaçu (IRA and ITU) ($H'_{IRA} = 1.02$ and $H'_{ITU} = 1.12$) (Table 2). These findings may be explained by the fact that surveying in CMA, TNO, and RBA was conducted in the rainy season and these regions are composed of different ecotones, such as transitional areas of the *caatinga*, *cerrado*, and seasonal semi-deciduous forests. On the other hand, surveying was conducted in the dry season at IRA and ITU, when few plant species flower.

Different degrees of pollen diversity were found in samples from CMA, Macaúbas (MAC) and Milagres (MIL) (Table 2). However, similar uniformity was found at these sites (J' = 0.838; J' = 0.835 and J' = 0.823, respectively). This indicates that colonies of P. rustica from these sites did not exhibit selectivity for a given source of pollen, i.e., there was no dominant pollen type (when a pollen type represents more than 45 % of total). Dominance was only recorded at IRA (Anacardium sp., 81.3 %), ITU (Pityrocarpa moniliformis (Benth.) Luckow and Jobson, 60.7 %), Boa Vista do Tupim (BVT; Myrcia sp., 67.5 %), and Contendas do Sincorá (CSI; Mimosa caesalpiniaefolia Benth (69.3 %) (Table S2). Among these four sites, surveying was conducted mostly in the dry period. At CSI, surveying was conducted in the rainy season, when M. caesalpiniaefolia flowers (Maia-Silva et al. 2012). It is therefore evident that P. rustica is a generalist regarding food sources, as described for most stingless bees studied (Ramalho 1990; Marques-Souza et al. 2007; Ferreira et al. 2010; Faria et al. 2012; Aleixo et al. 2013).

Factors such as nest proximity, high protein content, and the dominance of flowering plant species may explain the high frequency of plants visited by bees (Kleinert et al. 2009). Antonini et al. (2006) found that *Melipona quadrifasciata* Lepeletier (1836) visited only 19.3 % of flowering plants in its habitat. Despite the generalist classification (Faria et al. 2012; Aleixo et al. 2013), this finding may be attributed to the fact that these bees concentrate foraging activities in plants close to the nests that offer greater yields, as predicted by the theory of optimal foraging (MacArthur and Pianka 1966).

The pollen analysis revealed that *P. rustica* visited 30 families of plants (Table S2). The most visited families were Leguminosae-Mimosoideae (11.1 %) and Myrtaceae (7.9 %), which were present at all sites. Previous studies also describe these plant families as the most visited by bees from the tribes Meliponini and Apini (Cortopassi-Laurino and Ramalho 1988; Imperatriz-Fonseca et al. 1989; Ramalho 1990; Faria et al. 2012; Aleixo et al. 2013). According to Ramalho (1990), social bees are expected to visit species of Leguminosae, Malvaceae and Myrtaceae more frequently. Moreover, species of family Myrtaceae have flowers with many stamens and longitudinally opened anthers, which facilitates the acquisition of pollen (Ferreira et al. 2010).

Information on plant species that bees visit allows the determination of niche overlap and bee–plant interactions, which can contribute to the drafting of management and conservation policies (Eltz et al. 2001; Silva et al. 2010). Thus, analyses were performed to determine the most common pollen sources for *P. rustica* at all sites.

Biogeographical aspects and potential distribution of *P. rustica*

Partamona rustica was found at a mean altitude of 500 ± 187.30 m. The highest altitude was recorded at TNO (900 m) on the Espinhaço hills and the lowest was recorded at Manoel Vitorino (256 m), both in the state of Bahia (Table 1). The species apparently occurs in semi-arid environments.

The calibration of the model indicated that the QPTH-1 (1 refers to the regularization multiplier) set of features is the ideal combination for predicting potential areas with favorable conditions for *P. rustica* (AUC = 0.949; $OR_{10\%} = 0.493$) (Figure S1). This set of features was used to construct the potential distribution map for the species (Fig. 3). Suitable areas for the occurrence of *P. rustica* were identified in the Cerrado biome of northwestern Minas Gerais to the *caatinga* biome in southwestern Bahia, contouring the plateaus and hills of the Chapada Diamantina and Chapada do Rio Irecê and Rio Utinga by the east (Fig. 3). Indeed, there are no records of the species in these areas in museum collections and no specimens were found during surveys conducted in Mucugê, Andaraí, and Barra da Estiva (state of Bahia) between December 2012 and January 2013.

The data indicated that the environmental conditions, such as low temperatures in winter and rock vegetation in the Chapada Diamantina National Park, constrain the occurrence of *P. rustica*. Moreover, the termite mounds in which *P. rustica* nests have a low potential of occurrence in



Fig. 3 Potential geographic distribution of *P. rustica. Black diamonds* represent the 21 records for the species used to build the potential distribution map through niche modeling. *White circles* with a *black point* indicate sites at which no *P. rustica* colonies were found. *Legend*

refers to the likelihood of finding suitable conditions for the species to occur. *Chapada Diamantina* (*CD*) is shown as an area of low potential for the occurrence of the species (color figure online)

this region (Schmidt 2007). These data corroborate the niche modeling results for *P. rustica* and may explain the absence of the species in such locations.

According to Pedro and Camargo (2003), *P. rustica* is endemic from northern Minas Gerais to Espinhaço hills in Maracás in the state of Bahia. In the present study, however, colonies were found in Ruy Barbosa and Boa Vista do Tupim, which are 150 km to the north of Maracás, demonstrating a larger distribution range for *P. rustica*. The species has its distribution discontinued by the São Francisco River in northern Minas Gerais (Fig. 1).

A case of predation, imminent dangers, and conservation

A colony of *P. rustica* was found being attacked by the ant *Camponotus rufipes* Fabricius (1775) in Boa Vista do Tupim. Besides feeding on honey and pollen, this ant also predated the larvae of the bees. According to Nogueira-Neto (1953), some ants build nests in preexisting hollows in hives, resulting in little injury to the bees. It is also possible

that ants may drive off other predators, secondarily defending the bee colony (Nogueira-Neto 1953). In the present study, however, ants were only found predating the *P. rustica* colony.

The field observations suggest that bee hunters are the most serious threat to *P. rustica*. These hunters use honey, pollen, and wax for commercial and pharmacological means as well as for folk remedies. Due to the honey, non-aggressive nature and the ease of locating *P. rustica* nests, the species has been intensively exploited and nests have become rare or even absent from some areas of its distribution. Indeed, no nests were found at previously sampled sites, such as Maracás, Anagé, Vitória da Conquista, Jequié, Guanambi, Amargosa, Iaçu and Itaberaba (in the state of Bahia), and Espinosa (in the state of Minas Gerais). The niche model predicted some of these areas as highly suitable for the species to occur, but the intense human pressure is likely the main cause of the current situation.

Most (70 %) of the farmers, beekeepers and bee hunters interviewed, knew *P. rustica*; 88 % of these interviewees had used resources obtained from this species (honey, wax, or pollen), and most had seen the species rarely (58 %) or had not seen (31 %) this bee nests currently. Exploitation has reduced the number of swarms, and colonies have become more susceptible to natural enemies, such as birds, ants, and phorids (e.g., *Pseudohypocera* spp.). Additionally, the harmful effects of bee hunters place strong pressure on stingless bees (Klein et al. 2007; Knight et al. 2009).

The intense deforestation of the *caatinga* biome also likely exerts an influence on the decline in the population size of these bees, as reported by Neves and Castro (2006) for *Melipona mandacaia* Smith (1863). Indeed, stingless bees are becoming increasingly rare in some semi-arid regions, as deforestation diminishes the density of trees in which the species nests.

In conclusion, the intense exploitation of *P. rustica* by bee hunters and the loss of habitat due to deforestation for agricultural purposes threaten populations of this endemic species, which is restricted to dry forests in Brazil. Given the ecological value of bees and the constant pressures placed on the *caatinga* and *cerrado* biomes, the present findings underscore the importance of the conservation of these environments and the endemic species such environments harbor.

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