Floristic patterns of the neotropical forests, savannas and scrublands with *Trithrinax campestris* (Arecalesae) in central Argentina

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Abstract

**Aims:** *Trithrinax campestris* is one of the palm species with the southernmost distribution in the Neotropics. Despite that the vegetation types in which *T. campestris* occurs are nowadays heavily threatened by land use and land cover changes, their floristic composition and structure are still to be documented. In order to characterize *T. campestris* habitats, the aim of this study was to describe the floristic composition of the vegetation types in which this palm occurs and their relationships with different environmental factors.

**Study area:** The survey was conducted in central Argentina in an area comprising the southern extreme of the distribution of *T. campestris* in the following phytogeographic areas: Espinal, Lowland and Mountain Chaco.

**Methods:** Following the Braun-Blanquet approach we collected 92 floristic relevés recording a total of 601 vascular plant species. Vegetation was classified through the ISOPAM hierarchical analysis. Bioclimatic and elevation data were related to the floristic data through the ISOMAP ordination. Remote-sensed images (Landsat TM, ETM+ and OLI) were used to characterize the fire frequency in the 92 stands.

**Results:** Four vegetation types that differed in floristic composition and in diagnostic species were discriminated: 1.1 *Celtis tala*/Sida rhombifolia closed forest; 1.2 *Aspidosperma quebracho-blanco*/Prosopis kuntzei open forest; 2.1 *Jarava pseudoichu*/Vachellia caven open savanna; and 2.2 *Acalypha variabilis*/Nassella cordobensis scrubland. The ISOMAP ordination showed that differences in floristic composition were related to elevation, topography and climatic variables. Out of the 92 stands, only 21 showed the occurrence of fires during the period 1999–2018.

**Conclusions:** Our results evidenced that vegetation types (forests, savannas and scrublands) comprising *T. campestris* developed in a wide range of environmental conditions. This is the first study that focuses on all vegetation types in which *T. campestris* occurs in central Argentina and it is relevant for conservation and sustainable management of the only native palm species in the flora of this part of the country.

**Taxonomic reference:** Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar).

**Abbreviations:** ISOMAP = isometric feature mapping; ISOPAM = isometric partitioning around medoids.
Introduction

*Trithrinax* Martius is a neotropical genus of palms (*Arecaceae*) distributed in the subtropical and warm temperate region of South America, from almost sea level up to an elevation of 1,500 m (Cano et al. 2013). It belongs to the subfamily Coryphoideae and to the tribe Cryosophileae (Dransfield et al. 2005, 2008), and occurs in Brazil, Argentina, Bolivia, Paraguay, and Uruguay (Henderson et al. 1995; Dransfield et al. 2008; Pintaud et al. 2008; Zuloaga et al. 2008; Gaiero et al. 2012). *Trithrinax* comprises three species (*T. brasiliensis*, *T. schizophylla* and *T. campestris*), widely distributed in different habitats and vegetation types. The northern limit of its distribution lies in Santa Cruz Department, Bolivia, where *T. schizophylla* occurs, while in the southern extreme of its range, in central Argentina and Uruguay, *T. campestris* is found (Cano et al. 2013). *Trithrinax* species are more tolerant to drought and lower temperatures than other species of palms (Boyer 1992; Riffle and Craft 2003; Meerow 2005). Particularly, it has been documented that *T. campestris* may resist even less than -10°C (Meerow 2005), which may explain its distribution at higher latitudes.

The distribution area of *T. campestris* is mainly restricted to central Argentina (Cano et al. 2013) where the vegetation types in which the palm occurs, belong to the Espinal and Chaco phytogeographical provinces (Cabrera 1976). Previous studies report the presence of this species in various vegetation types with different soil and climatic conditions and different disturbance histories (Sayago 1969; Luti et al. 1979). In each habitat the importance of *T. campestris* ranges from some scattered, isolated individuals, to locally dense populations where the species becomes dominant in the community (Sayago 1969). From the phytogeographic point of view, Kurtz (1904), Sayago (1969) and Cabido et al. (2018) reported the occurrence of *T. campestris* in forests, grasslands or in savannas of the Lowland Chaco area, while Giorgis et al. (2017) recognized the presence of the palm as a co-dominant and subordinate species across different vegetation types in the Mountain Chaco. Within the Espinal phytogeographic province, Lewis and Collantes (1973) identified a floristic district based in part on the occurrence of this species. More recently, Lewis et al. (2009) also reported the occurrence of some isolated patches of Espinal forests comprising *T. campestris* in the eastern area of Córdoba province, central Argentina. However, none of these studies performed on Chaco or Espinal reported the complete floristic composition of the patches in which this palm occurs. Moreover, the effect of those factors that have been previously reported as major drivers influencing the distribution of palm vegetation types worldwide (Eiserhardt et al. 2011) such as climatic (e.g., water and temperature seasonality related variables), edaphic and anthropic (e.g., agriculture, fire and herbivory) have not been explored comprehensively for this palm species (Sayago 1969; Luti et al. 1979). Therefore, the vegetation types in which *T. campestris* occurs, their composition and structure, as well as the relationship with the main environmental variables are still to be documented.

As many palms worldwide, *T. campestris* is a keystone species for local people that traditionally use the leaves and spines to make handicrafts such as baskets and a variety of objects (Moraes 2001; Cano 2014). Moreover, this palm is being evaluated for the production of biofuels. At the same time, vegetation types with *T. campestris* are threatened because many habitats previously occupied by communities with palms are currently replaced by soybean and corn crops and also by pastures (Cano 2014; Mendoza et al. 2016; and personal observation by the authors). Knowledge of the effects of human activities (i.e., fire and grazing) on the population dynamics of *T. campestris*, as well as its germination ecology, is still preliminary. Cano (2014) reported an evident lack of seedlings and saplings due to anthropogenic fires and cattle grazing, while Mendoza et al. (2016) highlighted the lack of new palm seedlings related to extremely low seed germination observed in field and laboratory experiments. The persistent leaf-sheaths protect the stems of adult individuals what may be an adaptation to anthropogenic originated fires (Cano et al. 2013). Individuals of *T. campestris* seen in the field frequently show fire marks in the naked stems which lose their sheath layers (Cano et al. 2013 and personal observations by the authors). However, seedlings are not resistant to fire episodes, showing that fire may represent an important threat for the long-term survival for *Trithrinax* wild populations (Cano et al. 2013). In the last decades mature specimens have been exported to European countries for use in gardening (in 2003 the exportation of *T. campestris* generated an income of 600,000 USD; SENASA, Argentina, http://www.senasa.gob.ar/senasa-comunica/noticias/). Furthermore, the invasion by exotic species represents an additional potential threat for the vegetation types in which *T. campestris* occurs (Giorgis et al. 2017; Cabido et al. 2018; Zeballos et al. 2020). Cano et al. (2013) defined the conservation status of *T. campestris* as vulnerable, mainly due to habitat destruction and conversion to agriculture, and further insights on vegetation types with *T. campestris* are urgently needed to develop proper conservation and management strategies.

This study aimed to describe for the first time the whole floristic composition of vegetation types of the main habitats in which *T. campestris* occurs in central Argentina. Since disturbance may have introduced dramatic changes...
in the physiognomy of vegetation, we also explored the patterns of life forms distribution. In addition, and taking into account that the habitats in which *T. campestris* occurs involve different phytogeographic units, we also establish the proportion of chorotypes and endemic species present, as well as the origin of all the taxa recorded in each vegetation type. Finally, the association between the floristic composition and the main environmental variables (i.e., bio-climatic, topographic and edaphic) and fire frequency, were assessed.

**Methods**

**Study area and vegetation survey**

The survey was conducted in central Argentina, Córdoba province, covering ca. 161,000 km² (Figure 1). Sampling sites were distributed in habitats where the presence of *T. campestris* had been reported in previous works by Kurtz (1904), Sayago (1969), Lewis and Collantes (1973) and Luti et al. (1979), as well as in sites where specimens deposited in the Herbarium of the National University of Córdoba (CORD) had been collected. The study area is partially included in the Espinal phytogeographic province and the Western (Lowland) and Mountain Chaco districts according to the phytogeographic scheme of Argentina (Cabrera 1976). Following the Biogeographic Map of South America by Rivas-Martínez et al. (2011), our vegetation types are mainly included in the South Chacoan Province within the Chacoan Region (Chaqueña), and in the Xerophytic Pampean Region. The eastern extreme of the study area belongs to the Espinal (Lewis and Collantes 1973; Cabrera 1976; Zeballos et al. 2020), and is characterized by seasonally dry subtropical forests and woodlands distributed on lowlands with deep and well to imperfectly drained soils, in the proximity of the Pampean phytogeographic province. The northern extreme occupies part of the Lowland Chaco ecosystem (Western Chaco District sensu Cabrera, 1976) with xerophytic forests on welldrainable soils, in the proximity of the Pampean phytogeographic province. The northern extreme occupies part of the Lowland Chaco ecosystem (Western Chaco District sensu Cabrera, 1976) with xerophytic forests on well to excessively drained soils and part of the Mountain Chaco District (Cabrera 1976) occupying low hillsides and slopes with shallow and rocky substrates and small valley bottoms with deeper soils. Finally, the western extreme of the study area also belongs to the Mountain Chaco District; the landscape is dominated by open woodlands and scrublands on dry gentle and steep slopes alternating with flat areas (“pampas”) with deeper soils and narrow valley bottoms likely to suffer occasional flooding. At the beginning of the 20th century, the study area (Figure 2). Sampling followed the Zürich-Montpellier School of phytosociology (Braun-Blanquet 1932), and comprised 92 georeferenced 20 × 20 m² plots. In each plot, all vascular plants were recorded and species cover was estimated using the cover-abundance scale of Braun-Blanquet (1932) (+ = <1% cover; 1 = 1–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–100%). The height and cover of the tree, shrub and herb layers were visually estimated. Species nomenclature,
their distributional range and species origin (i.e., native or exotic) followed the catalogue of vascular plants of the Southern Cone (Zuloaga et al. 2008) and its online update (http://www.darwin.edu.ar/). Endemic taxa at the national and local levels followed Giorgis et al. (under review). Endemic at the local levels means endemic species restricted to the study area and surrounding provinces (mainly Córdoba and San Luis). Fourteen out of the 92 vegetation plots are registered in the Global Index of Vegetation-Plot Database (Dengler et al. 2011; http://www.givd.info) under ID SA-AR-002.

To assess the main trends of species distribution patterns and their representation in the study area, species chorotypes (groups of species with a similar distribution), were assigned following the criteria proposed by Cabido et al. (1998) and Zeballos et al. (2020): Southern-Brazilian (1), Chaquenian (2), Low Mountain Chaco (3), Arid Chaco and Monte (4) and Exotic (5). Additionally, the mean percentage of each chorotype per plot as well as the mean species richness and number of exotics per relevé were calculated. Life forms followed Zeballos et al. (2020) thus sorted as: cactus (c), climber (cl), epiphyte (e), fern (f), grass (g), graminoid (gr), herb (h), parasite (p), palm (pl), shrub (s) and tree (t).

Environmental variables

Bioclimatic variables and elevation were interpolated from the WorldClim database (http://www.worldclim.org; Fick and Hijmans 2017), at a spatial resolution of 30 seconds (ca. 1 km²) for continental South America. As the main bioclimatic variables that constrain the distribution of palm species and communities worldwide are related to water availability and temperature (Eiserhardt et al. 2011) the following variables were selected: Precipitation of the Wettest Quarter (PWeQ), Minimum Temperature of the Coldest Month (MTCM), Precipitation Seasonality (PS), Precipitation of the Wettest Month (PWeM), Annual Precipitation (AP), and Precipitation of the Driest Quarter (PDQ) (see O’Donnell and Ignizio 2012 for details concerning all the bioclimatic variables). To obtain data on topographic and edaphic variables for each plot (slope and organic matter content of the surface soil layer), all the 92 relevés were plotted on digitalized maps of the soils of Córdoba province provided at two different scales (i.e., 1:500,000 and 1:50,000) (Gorgas and Tassile 2006; http://visor.geointa.inta.gob.ar/?p=857). The 1:50,000 scale was preferentially used, but some information gaps at this
scale were completed with data provided by the map at 1:500,000. Both maps depict soil cartographic units and describe the internal heterogeneity of each unit through representative soil profiles providing an analysis of their chemical and physical properties.

Following Argañaraz et al. (2015a) and Argañaraz et al. (2020) the fire history frequency was characterized for the 92 sampling sites. Time series of Landsat TM, ETM+, and OLI images (30 m of spatial resolution), covering the study area, acquired between 1999 and 2018 were used. This fire database was derived automatically using ABAMS (Automatic Burned Area Mapping Software), a tool based on the algorithm proposed by Bastarrika et al. (2011) and updated versions implemented in Google Earth Engine. We considered any continuous burned patch as a single fire event except when the intensity of the burned signal was markedly different. Specifically, fire frequency is the number of times that a plot was burned for the period of time considered. The minimum mapping unit of the fire database is of 5 ha (Argañaraz et al. 2015a). We converted vector layers of burned areas to raster format as binary layers (burned or unburned) and determined the fire frequency for the 92 sites.

Data analyses

The ISOmetric feature mapping and Partition Around Medoids (ISOPAM) ordination and classification method were employed to analyze the 92 relevés. This analysis was used to detect the major vegetation types and their corresponding diagnostic species groups (Schmidtlein et al. 2010; Černý et al. 2015; Cabido et al. 2018). Hierarchical ISOPAM was run on the Bray-Curtis dissimilarity matrix. This matrix was constructed with the floristic table after Braun-Blanquet scores were transformed to the central class values (Kent 2012). The maximum number of clusters on each hierarchical level was arbitrarily set to ten and standardized G statistics to five. For each vegetation type, diagnostic species were selected using the phi coefficient of fidelity (Chytrý et al. 2002). Those species with phi ≥ 0.1 and a statistically significant association (p < 0.001) with a particular vegetation type according to Fisher’s exact test, were considered as diagnostic. These analyses were performed in the JUICE 7.0 program (Tichý 2002).

Each vegetation type was named after the first two species, (12), shrubs (88), climbers (46), trees (27) and cacti (22). The most prominent chorotype was the Southern-Brazi (56.08 ± 1.13% of all species, mean plus standard deviation), followed by the Chaquenian (29.67 ± 13.15%), the Low Mountain Chaco (11.08 ± 5.65%), and the Arid Chaco and Monte (0.12 ± 0.43%) chorotypes. Exotics were represented by 3.05 ± 3.19% of all species. The overall cover of T. campestris in the 92 relevés ranged from less than 1% to almost 40%.

Results

Floristic composition

A total of 601 vascular plant species and infraspecific taxa (555 natives, including 68 endemics and 46 exotics), distributed among 77 families and 333 genera, were recorded in the 92 relevés (Table 1 and see also Suppl. material 1: Table S1.1). The most common families were Poaceae (108 species), Asteraceae (104), and Fabaceae (43), which together accounted for 42.4% of all species. Other common families were Euphorbiaceae (27 species), Solanaceae (26), Malvaceae (24), Cactaceae and Verbenaceae (22 species each). The most common genera were Baccharis, (13 species), Euphorbia (12), Solanum (11), Tillandsia (10), Nassella and Croton (8 species each). The predominant life forms were herbs (264 species), followed by grasses (108), shrubs (88), climbers (46), trees (27) and cacti (22). The most prominent chorotype was the Southern-Brazilian (56.08 ± 11.73% of all species, mean plus standard deviation), followed by the Chaquenian (29.67 ± 13.15%), the Low Mountain Chaco (11.08 ± 5.65%), and the Arid Chaco and Monte (0.12 ± 0.43%) chorotypes. Exotics were represented by 3.05 ± 3.19% of all species. The overall coverage of T. campestris in the 92 relevés ranged from less than 1% to almost 40%.
Table 1. Synoptic table of the vegetation types classified by ISOPAM analysis showing the percentage constancy, mean Braun-Blanquet cover (as superscript) and phi values based on 92 relevés collected in Córdoba province, central Argentina. Species are sorted by decreasing fidelity within each vegetation type. Dark, medium and light grey indicate phi ≥ 0.3, phi ≥ 0.2 and phi ≥ 0.1, respectively. Vegetation type codes: 1.1 Celtis tala/Sida rhombifolia closed forest; 1.2 Aspidosperma quebracho-blanco/Prosopis kuntzei open forest; 2.1 Jarava pseudoichu/Vachelia caven open savanna; 2.2 Acaryla variabilis/Nassella cordobensis scrubland. Life forms (LF): c: cactus; cl: climber; e: epiphyte; f: fern; g: grass; gr: graminoid; h: herb; p: parasite; pl: palm; s: shrub; t: tree. Chorotypes (CT): (1) Southern-Brazilian, (2) Chaqueñian, (3) Low Mountain Chaco, (4) Arid Chaco and Monte, (5) Exotic. Symbols: #: endemic at local level; #: endemics at the national level.

| Vegetation type                        | LF | CT | Cluster 1 | Cluster 2 |
|----------------------------------------|----|----|-----------|-----------|
| Trithrinax campestris                  | pl | 2  | 100*      | 100*      |
| Sida rhombifolia                       | 1  | 66.7| 11.1*     | 7.5*      |
| Celtis tala                            | t  | 1  | 100*      | 77.8*     |
| Nassella hyalina                       | g  | 1  | 40*       | 5*        |
| Rivina humilis                         | h  | 1  | 66.7*     | 11.1*     |
| Diclera squarrosa                      | h  | 1  | 53.3*     | 12.5*     |
| Melavirgation terebrata                | t  | 1  | 73.2*     | 22.2*     |
| Holmbergia tweedia                     | s  | 2  | 33.3*     |           |
| Schinus longifolius                    | s  | 2  | 46.7*     | 10*       |
| Capsicum characensis                   | s  | 2  | 40*       | 7.5*      |
| Cyperus hermophroditus                 | g  | 1  | 26.7*     |           |
| Araujia odorata                        | cl | 1  | 53.3*     | 22.2*     |
| Prosopis kuntzei                       | t  | 2  | 88.9*     |           |
| Sarcarphalus mistol                    | t  | 2  | 6.7*      | 88.9*     |
| Jarava ichu var. ichu                  | g  | 3  | 55.6*     | 10*       |
| Aspidosperma quebracho-blanco          | t  | 2  | 13.3*     | 100*      |
| Vachelia avara                         | s  | 2  | 66.7*     | 7.5*      |
| Senegalia praecox                      | t  | 2  | 13.3*     | 88.9*     |
| Mimosa detinera                       | s  | 2  | 55.6*     |           |
| Daesichardia urbanovar                 | c  | 2  | 6.7*      | 88.9*     |
| Monteverdale spinosa                   | s  | 2  | 6.7*      | 77.8*     |
| Nicotiana glauca                      | s  | 1  | 44.4*     |           |
| Gouinia paraguayensis                  | g  | 2  | 44.4*     | 3.6*      |
| Croton lechonstachys                   | s  | 3  | 33.3*     | 77.8*     |
| Tillandia aizoides var.               | e  | 2  | 13.3*     | 55.6*     |
| Castello coccinea                     | t  | 2  | 55.6*     |           |
| Opuntia quimila                       | c  | 2  | 66.7*     | 3.6*      |
| Cleistocactus baumanni                | c  | 2  | 44.4*     |           |
| Atamisquea emarginata                 | s  | 2  | 44.4*     |           |
| Passiudulion petlonculatum             | h  | 2  | 13.3*     | 66.7*     |
| Leptochloa crinita                     | g  | 2  | 6.7*      | 44.4*     |
| Harrisia pomeranensis                 | c  | 2  | 44.4*     | 3.6*      |
| Syngrellia var. gisebachii            | h  | 2  | 66.7*     | 5*        |
| M. melia argyrea                       | g  | 1  | 55.6*     |           |
| Jarava pseudoichu                      | g  | 3  | 46.7*     | 80*       |
| Prosopis campestris                   | t  | 2  | 32.5*     | 3.6*      |
| Cordalia microphylla var.             | s  | 2  | 33.3*     | 100*      |
| Lippia turbinata var. f. turbinata    | s  | 2  | 20*       | 11.1*     |
| Vachelia caven                          | s  | 1  | 53.3*     | 11.1*     |
| Acalypha variabilis                   | h  | 1  | 26.7*     | 45*       |
| Nassella cordobensis                   | g  | 3  | 55.6*     | 15*       |
| Krapovickia flavescens                | h  | 1  | 6.7*      | 11.1*     |
| Aristida cimicula                      | g  | 1  | 25.9*     |           |
| Sporobolus indicus                     | g  | 1  | 6.7*      | 17.5*     |
| Aristida cimiculosa                    | g  | 2  | 11.1*     | 40*       |
| Cordalia montana                       | t  | 3  | 20*       | 11.1*     |

Vegetation classification

The vegetation matrix was classified by the ISOPAM analysis into two main clusters (C1 and C2) and each cluster was further partitioned into two vegetation types (Table 1). Species constancy and average cover data are reported in synoptic Table 1 and also in the extended Suppl. material 1: Table S1.1. Cluster 1 comprised relevés collected mainly in the plains located to the east and north of the study area (Espinal and the Lowland Chaco, respectively), while Cluster 2 included relevés distributed predominantly, but not exclusively, in low mountain ranges and valley bottoms located to the north and west of the area (Lowland Chaco and the Mountain Chaco, respectively). Although the sample-size-based rarefaction showed that the curves of the four vegetation types had not yet reached the asymptote (Figure 3A), the observed species richness reached a high percentage of the species estimated using the non-parametric estimators (Table 2). The coverage-based rarefaction curves suggested that the four vegetation types identified were well represented since the sample coverage percentage showed values equal or higher than 0.85 in all types (Figure 3B, C; Table 2).

Table 2. Species observed (S) and non-parametric estimators of species richness plus standard error for incidence data for each vegetation type. Vegetation type codes: 1.1 Celtis tala/Sida rhombifolia closed forest; 1.2 Aspidosperma quebracho-blanco/Prosopis kuntzei open forest; 2.1 Jarava pseudoichu/Vachelia caven open savanna; 2.2 Acalypha variabilis/Nassella cordobensis scrubland. Estimators: Chao2-bc: a bias-corrected form for the Chao2 estimator; Jackknife 1: Estimator that use the frequency of unique; Jackknife 2: Estimators that use the frequencies of unique and duplicates, and C: hat: Sample coverage index.

| Vegetation type                        | LF | Cluster 1 | Cluster 2 |
|----------------------------------------|----|-----------|-----------|
| Tripogonella spicata                   | g  | 1         | 11.1*     | 5*       |
| Baccharis linearifolia                 | s  | 1         | 15*       | 53.6*    |
| Microchla indica var. indica           | g  | 1         | 11.1*     | 4.6*     |
| Schizachyrium salmianii                | g  | 1         | 2.5*      | 25*      |
| Andropogon ternatus                    | g  | 1         | 2.5*      | 25*      |
| Eustachys retusa                       | g  | 1         | 11.1*     | 60*      | 78.6* |
| Gomphrena perennis var. perennis      | h  | 1         | 6.7*      | 10*      | 42.9* |
| Glendandula peruviana                  | h  | 1         | 11.1*     | 45*      | 71.4* |
| Margrincarpus pinnatus                 | s  | 1         | 15*       | 57.1*    |
| Glendandula venturi                    | h  | 2         | 15*       | 57.1*    |

Descriptions of the vegetation types are given below:

Cluster 1: Comprises two vegetation types distributed mainly in the lowlands of the Espinal phytogeographical
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Vachellia caven, Nassella cor, and Prosopis kuntzei.

Cluster 2: This Cluster includes two vegetation types distributed mainly in low mountain slopes and valley bottoms located in the Mountain Chaco District in the north and west of the study area.

2.1 Jarava pseudoichu/Vachellia caven open savanna. Open savannas with a high grass and herb cover (average cover and height of the herbaceous layer were 78.28 ± 3.59% and 0.74 ± 0.02 m, respectively). The average cover...
of the tree and shrub layers was low (14.15 ± 2.16% and 34.3 ± 2.69%, respectively) while their height also showed low values (4.64 ± 0.33 and 3.31 ± 0.1 m, for the tree and shrub layers, respectively). *Trithrinax campestris* density varied from only scattered individuals to denser patches in almost pure stands, reaching an average cover of 14.44 ± 2.11%. The *C.* grass *Jarava pseudeoichi* and the shrubs *Prosopis campestris*, *Condalia microphylly*, *Lippia turbinata* fo. *turbinata* and *Vachellia caven* were diagnostic species for this vegetation type (Table 1).

This vegetation type was widely distributed across gentle slopes and valley bottoms mostly in the mountains of the northern part of the study area though some stands are located to the west, on both gentle relief and more steep topography. In some stands, the dominant vegetation was an open scrubland dominated by *Vachellia caven*, while on slopes of the mountains to the west of the area remnants of Low Mountain Chaco Forest, dominated by *Schinopsis marginata*, *Lithraea molleoides* and *Ruprechtia apetala*, with only sparse individuals of *T. campestris* were found. A total of 406 (375 natives and 31 exotic species) species were recorded of which 39 are endemics (31 at the national and eight at the local levels). The mean species richness per relevé was 64.3 ± 2.28. Herbs (197 species, 44.3%), grasses (87 species, 19.5%) and shrubs (68 species, 15.3%) were the most common life forms.

### 2.2 *Acalypha variabilis/Nassella cordobensis* scrubland.

Open scrubland with an almost continuous grass and herb cover (the average cover of the herbaceous layer was 70.68 ± 4.73% with a height of 0.71 ± 0.05 m). Despite that in some stands on rocky substrate the shrub cover may increase, the average cover and height of this layer were medium to low (35.18 ± 3.30% and 2.34 ± 0.14 m, respectively). Tree cover and height were the lowest among the four types described (5.54 ± 2.65% and 3.46 ± 0.5 m, respectively). *Trithrinax campestris* was present generally with sparse individuals and showed the lowest average cover reported in this study (3.78 ± 0.92%). Among the diagnostic species, the small shrub *Acalypha variabilis* showed the highest constancy and average cover (Table 1). The list of diagnostic species is completed with the *C.* grass *Nassella cordobensis*, the *C.* grasses *Aristida circina* lis, *Sporobolus indicus*, *Eustachys retusa*, *Microchloa indica*, *Tripogonoma spicata*, *Schizachyrium salzmannii*, *Andropogon ternatus*, *Euchalyx retusa* and some shrubs and herbs.

This vegetation type was distributed on gentle to steep slopes in the mountains of the northern part of the study area, though a few stands were also recorded in the mountains to the west. Soils were shallow and the percentage of bare rock was generally considerable. A total of 400 (385 natives and 15 exotics) species were recorded in this community, of which 47 are endemic (35 at the national and 12 at the local levels). The mean species richness per relevé was 76.5 ± 3.06. Herbs (181 species, 45.2%), grasses (77 species, 19.25%) and shrubs (53 species, 13.2%) were the most abundant life forms.

### Richness and chorotype patterns among vegetation types

The total number of vascular plant species per relevé ranged between 29 and 103, and the mean species richness per relevé differed significantly among vegetation types (F<sub>3,38</sub> = 15.04; p = 0.001). The *Acalypha variabilis/Nassella cordobensis* scrubland showed the highest mean species richness per relevé (Table 3), while the *Celitis tala/Sida rhombifolia* closed forest had the lowest richness; the other two vegetation types showed intermediate values. We recorded 52 endemic species at national level and 16 at local level; only 5 endemic species (*Gymnocalycium mostii*, *Gymnocalyicium capillifelle*, *Apurimasia dolichocarpa*, *Alantarneura pumila* and *Trichocline plicata*) were restricted to the study area and surroundings. Significant differences in the representativeness of the different chorotypes were observed among the vegetation types, with the exception of the Arid Chaco and Monte chorotype (Table 3). The vegetation types differed significantly in their Southern-Brazilian chorotype representativeness (F<sub>3,38</sub> = 23.34; p = 0.001) as well as in the Chaquenian chorotype (F<sub>3,38</sub> = 40.73; p < 0.001). The Southern-Brazilian chorotype was the best represented with the exception of the *Aspidosperma quebracho-blanco*/*Prosopis kuntzei* open forest in which the Chaquenian chorotype exhibited the highest percentage of species (Table 3). Species of the Southern-Brazilian chorotype showed the highest proportion in the two vegetation types of Cluster 2 and in *Celitis tala/Sida rhombifolia* closed forest. The Arid Chaco and Monte chorotype was less represented in the four vegetation types (i.e., less than 1% on each one), and without significant differences between them (F<sub>3,38</sub> = 1.46; p = 0.23). The Low Mountain Chaco chorotype also showed differences between vegetation types (F<sub>3,38</sub> = 9.34; p < 0.001) with the highest values in both vegetation types of Cluster 2 (Table 3). The number of exotic species, as well as the proportion of exotics per relevé, showed significant differences between vegetation types (F<sub>3,38</sub> = 40.73; p < 0.001).

### Table 3. Species richness, number of exotics per plot and mean percentage of each chorotype per plot (plus standard error) for each vegetation types classified by ISOPAM analysis.

| Vegetation type | 1 | 1.1 | 1.2 | 2.1 | 2.2 |
|----------------|---|-----|-----|-----|-----|
| Species richness | 47.3 ± 3.3 | 44.8 ± 3.2 | 64.3 ± 2.8 | 76.5 ± 3.0 |
| Number of exotics per plot | 2.2 ± 0.5 | 1.1 ± 0.3 | 2.4 ± 0.3 | 1.07 ± 0.19 |
| Southern-Brazilian | 55.5 ± 3.4 | 34.3 ± 2.7 | 56.8 ± 3.8 | 62.6 ± 3.2 |
| Chaquenian | 31.6 ± 3.3 | 58.2 ± 2.9 | 28.3 ± 1.7 | 21.9 ± 1.2 |
| Low Mountain Chaco | 7.7 ± 1.5 | 5.6 ± 0.7 | 11.3 ± 0.7 | 14.2 ± 1.0 |
| Arid Chaco and Monte | 0.2 ± 0.0 | 0.3 ± 0.0 | 0.0 ± 0.0 | 0.0 ± 0.0 |
| Exotic | 4.0 ± 1.3 | 1.4 ± 0.7 | 3.4 ± 0.7 | 1.1 ± 0.2 |
Vegetation Classification and Survey

Vegetation types, environmental variables and fire frequency

The ISOMAP ordination (Figure 4) showed that differences in floristic composition were related to elevation (Elev; $r^2 = 0.44, p = 0.001$), minimum temperature of the coldest month (MTCM; $r^2 = 0.40, p = 0.001$), precipitation of the driest quarter (PDQ; $r^2 = 0.37, p = 0.001$), precipitation of the wettest month (PWeM; $r^2 = 0.37, p = 0.001$), annual precipitation (AP; $r^2 = 0.37, p = 0.001$), precipitation seasonality (PS; $r^2 = 0.33, p = 0.001$), precipitation of the wettest quarter (PWeQ; $r^2 = 0.31, p = 0.001$), organic matter content of the topsoil (OM; $r^2 = 0.29, p = 0.001$) and slope ($r^2 = 0.28, p = 0.001$). Elevation was the most important factor in relation to composition, with both vegetation types included in Cluster 2 characterized by mean elevations higher than 900 m, while elevation ranged from 340 to 436 m in average in Cluster 1. This elevation gradient mirrored trends in temperature related variables (e.g., minimum temperature of coldest month). The vegetation types included in Cluster 1 occupied warmer areas with higher precipitations with ca. 100 mm difference respect to Cluster 2. Slope exhibited an appreciable range of variation between both Clusters and was steeper in low mountain areas (Cluster 2). Organic matter content of the surface soil layer showed higher average values in Cluster 1.

Out of the 92 stands, only 21 showed the frequency of fires during the period 1999–2018. Overall, the fire frequency was not related to the floristic composition ($r^2 = 0.04, p = 0.12$). Eighteen sites were burned only once while three sites were burned three times during the period analyzed. Those stands that belong to the vegetation types of Clusters 2 showed a higher fire frequency since 13 out of 40 stands were burned in the Jarava pseudoichu/Vachellia caven open savanna while 4 out of 28 stands were burned in the Acalypha variabilis/Nassella cordobensis scrubland. The vegetation types of Cluster 1 showed just two stands burned each. However, the four vegetation types did not differ in their fire frequency ($F_{3,84} = 2.16; p = 0.09$). Furthermore, the vegetation structure of stands (i.e., the percentage cover of each vegetation layer) of the different vegetation types did not show any significant differences between unburned and burned stands according to their tree ($F_{3,84} = 0.81; p = 0.49$), shrub ($F_{3,84} = 0.39; p = 0.76$) and herb ($F_{3,84} = 0.18; p = 0.9$) layers cover as well as in T. campestris cover ($F_{3,84} = 0.46; p = 0.71$).

Discussion

In this study we describe for the first time the complete floristic composition of the main vegetation types in which T. campestris occurs in central Argentina. Our results evidenced that either as isolated individuals intermingled in forests (Cluster 1), in savannas and scrublands (Cluster 2), or as denser populations (likely in both Clusters) (Table 1 and Figure 4), this palm is able to occupy sites with different topography and soils along a wide gradient of environmental conditions. This wide gradient of environmental conditions was already observed by former botanists who studied the flora in central Argentina more than one hundred years ago (Lorentz 1876; Kurtz 1904), and several decades before our survey (Sayago 1969; Luti et al. 1979); however, none of them included complete floristic inventories.

Richness, endemism and chorological patterns among vegetation types

Relevés included in Cluster 2 revealed higher mean species number if compared with Cluster 1. The higher species richness recorded in vegetation types of Cluster 2 (Jarava pseudoichu/Vachellia caven open savanna and Acalypha variabilis/Nassella cordobensis scrubland)
(Table 3), might reflect the topographic and edaphic heterogeneity observed in the Low mountain Chaco habitats occupied by these vegetation types. In mountain environments, topography may influence the distribution of plant species and vegetation types by modifying soil properties, exposure, and temperature, as well as vegetation physiognomy and dynamics (Svenning 2001; Eiserhardt et al. 2011). In contrast, both vegetation types included in Cluster 1 (Celtis tala/Sida rhombifolia closed forest and Aspidosperma quebracho-blanco/Prosopis kuntzei open forest), are distributed in more homogeneous landscapes found in the plains and flatlands of the Espinal and Chaco domains. Vegetation types in Cluster 2 are also richer in species than other woody communities of plains and low mountain habitats in central Argentina (Giorgis et al. 2017; Cabido et al. 2018; Zeballos et al. 2020). Similar patterns of higher species diversity reflecting habitat heterogeneity have been reported elsewhere in the world for different types of vegetation (Whittaker 1960; Coblentz and Rüters 2004; Kretz and Jetz 2007) and specifically for communities rich in palm species (Guimarães et al. 2002; Resende et al. 2013). An additional factor influencing local species richness may be the physiognomy of vegetation which, is the results of complex feedback between climate, topography and disturbance (i.e., fire and grazing) (Giorgis et al. 2017; Argañaraz et al. 2020). Vegetation types comprised in Cluster 1 exhibited higher tree canopy cover and the differences in their canopy openness could determine gradients of light affecting the distribution of species. Cluster 2, instead, comprised open savannas and scrublands allowing for more light availability at the shrub and herb layers (Figure 2), which may enhance plant species richness. Strong influence of light gradients through competition for light and shade tolerance has been reported elsewhere in other biomes, especially in tropical forests (Carson and Schnitzer 2008), but at the moment, our evidence is scarce and needs further research.

In addition to the variations in species richness among the vegetation types (Table 3), differences in the composition of endemic species were also observed. Vegetation types included in Cluster 2 showed the highest numbers of endemic species both at the national and local levels. Jarava pseudoichu/Vachellia caven open savanna and Acalypha variabilis/Nassella cordobensis scrubland comprised 8 and 12 endemicism at local level, respectively, which evidenced the high natural value of these vegetation types and their importance for biodiversity conservation. The valuable pattern of endemism reflected in our data could be explained through the isolating effect of mountains with respect to lowlands; recent studies report a clear correlation between plant endemism and mountain isolation (Steinbauer et al. 2016; Camacho-Sanchez et al. 2019). Despite our findings, the distribution of many taxa is still scarcely known in Argentina and further floristic and chorological studies could change the status of many plant species.

The Southern-Brazilian and Chaquenian chorotypes were dominant in all the four vegetation types described (Table 3). The same pattern has also been reported by Cabido et al. (1998) and Zeballos et al. (2020) for woody vegetation types from central Argentina including mainly lowland vegetation types. The predominance of these chorotypes is not surprising since our study area includes sedimentary plains and low mountain habitats. Moreover, there are not significant barriers to the dispersal of taxa distributed in the eastern and northeastern area of the country (Southern-Brazilian chorotype) and from the northern flatlands of the Great Chaco in the northern region of Argentina, but also Bolivia and Paraguay (Chaqueñian chorotype) (Fuentes and Navarro 2000; Steinerger et al. 2001; Navarro et al. 2006). Many of the species reported in our survey with a Southern-Brazilian distribution have also been mentioned by Rodriguez et al. (2017) as components of Butia yatay palm groves and gallery forests in northeastern Argentina, where T. campestris is a subordinate element.

The overall number of exotics in our survey is lower with respect to those reported in previous floristic studies from central Argentina (Giorgis and Tecco 2014; Cabido et al. 2018; Zeballos et al. 2020). The number of exotic species ranged from 7 to 31 among the four vegetation types, with Jarava pseudoichu/Vachellia caven open savanna showing the highest record, while the mean number of exotics per plot was maximum in Celtis tala/Sida rhombifolia closed forest. Note that in this vegetation type even some exotics are considered diagnostic species (e.g., the grass Chloris gayana and the tree Morus alba). This higher exotic occurrence may be explained by the earlier expansion of agriculture in this area in comparison with that of the Aspidosperma quebracho-blanco/Prosopis kuntzei open forest, where the introduction of intensive agriculture is more recent (Zak et al. 2008; Cabido et al. 2018; Zeballos et al. 2020).

Vegetation types and environmental factors

Within Cluster 1, trends in floristic composition were mainly related to annual rainfall, other precipitation parameters associated to it, and the minimum temperature of the coldest month (Figure 4). On the other side, in Cluster 2 composition was mainly driven by elevation and topography but also by precipitation seasonality. Celtis tala/Sida rhombifolia closed forest and Aspidosperma quebracho-blanco/Prosopis kuntzei open forest occurred at the warmest part of the study area where annual rainfall is higher, whereas Jarava pseudoichu/Vachellia caven open savanna and Acalypha variabilis/Nassella cordobensis scrubland occupied the highest and coldest habitats in premontane hills to the north and west of the study area. Areas at higher elevations are characterized not only by lower temperatures, but also by different topographic conditions and rocky soils that which may avoid the establishment of species from the lowland Espinal and Chaco areas (Cabido et al. 2018; Zeballos et al. 2020).

Despite of the environmental differences between the vegetation types described, our results showed that
**Conclusions and further perspectives**

This study provides a detailed analysis of the vegetation types comprising *T. campestris*, the only native palm species in the flora from central Argentina. Moreover, our study highlights that *T. campestris* can grow in a variety of community types with different environmental conditions. These results are essential to develop adequate conservation strategies and useful for the sustainable management of this endangered species. It is accepted that the current distribution of palms is limited by climatic conditions prevailing during the cold season (Walther 2002), and that under warming scenarios some palm species may be extending their ranges into higher latitudes and altitudes (Walther et al. 2007; Giorgis et al. 2015). However, to our knowledge, there is no information about the behavior that *T. campestris* may show under changing scenarios of temperature and rainfall neither about its regeneration niche. Preliminary field observations suggest that a high number of seedlings could be associated with higher tree canopy cover while in more open sites the lack of regeneration could be related to more vulnerable populations. Future studies should extend the floristic survey to other areas in which the vegetation types comprising *T. campestris* have been reported (Cano et al. 2013; 2014), especially in San Luis and Santiago del Estero provinces, also located in central Argentina (see Figure 1). Similarly, future successional and demographic studies should complement our survey in order to give a more complete picture of the real conservation status of the species and of the vegetation types in which it occurs.

**Data availability**

A subset of the plots is included in the database SA-AR-002 – Vegetation of Central Argentina (Dengler et al. 2011; http://www.givd.info). The remaining subset will be included in the same database in 2021. The data are also available from the Corresponding author upon reasonable request.

**Author contributions**

SRZ, MRC, MAG, designed the survey; MAG, MRC, JJC, ATRA, PIM, did the field work; SRZ, MRC performed data analysis; SRZ, MAG, MRC, ATRA, JJC wrote the original manuscript; JA analyzed fire data; MVP, JA, PIM, PAT, AF, GF, MVV, GC contributed substantially to the final writing of the manuscript and in the interpretation of results.

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Supplementary material

Supplementary material 1
Extended synoptic table
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