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PLANTS AT THE SUMMIT: CHARACTERIZATION OF GRASSLANDS ON CERROS CHATOS OF NORTHEASTERN URUGUAY

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Flat-top hills ("cerros chatos") stand out as distinct relief formations in northeastern Uruguay. These are elevations of about 300 m above mean sea level, generally formed by Jurassic sandstones, characterized by a flat top, a stone ledge of variable height, and a concave or stepped hillside. Little is known about the vegetation atop these hills, which consists mostly of sparse grasslands with little to no grazing. As such, the aim of this study is to make the first characterization of the vegetation at the top of flat-top hills. In order to achieve this, we describe the vegetation of three emblematic hills in the region: Del Medio Hill, Vigilante Hill and Miriñaque Hill. Plant species composition surveys were carried out in spring 2021 and autumn 2022, identifying and delineating distinct vegetation formations. 315 species belonging to 63 vascular plant families were identified, with Poaceae and Asteraceae ranking as the top two families in terms of species richness. Among the species found, 31 are included in the list of priority species for conservation in Uruguay. Furthermore, *Achyrocline marchiorii* represents a new record for the Uruguayan flora. Two vegetation formations were present in all three hills: the ledge formation, associated with the rocky outcrops around the perimeter of the hilltops; and the crest formation, associated with the deep soils and low rock cover at the center of the hilltops. A shoulder formation of colluvial origin was also identified in the Miriñaque Hill, showing moderate slope and rockiness. The uncommon flora found on top of these hills is threatened due to the rapid increase of afforestation in the region, and the presence of the alien species *Cynodon dactylon*, *Melinis repens* and *Pinus taeda*. Such evidences emphasize the need for urgent management plans to protect these hills, which are not covered by any conservation program on a national or global scale.

Keywords. Afforestation; conservation; flat-top hill; flora; sandstone.

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Los cerros chatos resaltan como un relieve característico del noreste de Uruguay. Son elevaciones de 300 m sobre el nivel del mar, generalmente formadas por areniscas Jurásicas, caracterizadas por una cima plana, una saliente de piedra de altura variable y una ladera escalonada o cóncava. Poco se sabe sobre la vegetación en la cima de estos cerros, donde dominan los pastizales con baja presión de pastoreo. El objetivo de este estudio es realizar la primera caracterización de la vegetación en la cima de los cerros chatos. Para conseguir esto, se describe la vegetación de tres cerros emblemáticos de la región: Cerro Del Medio, Cerro Vigilante y Cerro Miriñaque. Se realizaron muestreos de composición de especies de plantas en primavera de 2021 y otoño de 2022, identificando y delineando las distintas formaciones vegetales. Se encontraron 315 especies pertenecientes a 63 familias de plantas vasculares, donde Poaceae y Asteraceae tenían el mayor número de especies. De las especies registradas, 31 se encuentran en el listado de especies prioritarias para la conservación en Uruguay. Además, la especie

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Achyrocline marchiorii representa un nuevo registro para la flora uruguaya. Dos formaciones vegetales estaban presentes en los tres cerros: la formación de saliente, asociada a los afloramientos rocosos, formando un perímetro alrededor de las cimas; y la formación de cresta, asociada a suelos profundos con baja rocosidad, hacia el centro de las cimas. Una formación hombrera de origen coluvial también fue identificada en el Cerro Miriñaque, mostrando una pendiente y rocosidad moderada. La flora poco común encontrada en la cima de estos cerros se ve amenazada debido al rápido incremento de la forestación en la región, y la presencia de especies exóticas como *Cynodon dactylon*, *Melinis repens* y *Pinus taeda*. Esto enfatiza la urgente necesidad de planes de manejo para proteger estos cerros, que no se encuentran contemplados por ningún programa de conservación a nivel nacional o global.

Palabras clave. Arenisca; cerro mesetiforme; conservación; flora; forestación.

INTRODUCTION

Within the neotropics, the Río de la Plata grasslands comprise one of the largest areas of the grassland biome (Soriano et al., 1991; Dixon et al., 2014). The Río de la Plata grasslands are temperate to subtropical, dominated by C_4 and C_3 perennial grasses, and extend from east-central Argentina to southern Brazil, including all of Uruguay (Soriano et al., 1991). A total of 4864 vascular plant species are recorded for the region, representing 194 families, of which Asteraceae, Poaceae and Fabaceae are dominant. Uruguay has 2756 of these species, 126 of which are exclusive to this country (Andrade et al., 2018).

In the context of south American biogeography, Uruguay is included within the Pampean province, a part of the Chacoan dominion. This province is characterized by vast grasslands, with a variable coverage of shrubs, and the scarce presence of forests and other ecosystems (Cabrera & Willink, 1973; Morrone, 2014). Influences from other neighboring phytogeographic provinces, in terms of similarities in species composition and/or presence of dominant or characteristic species, have been detected on Uruguay's woody flora (Grela, 2004; Haretche et al., 2012). In particular, influences from the Chaco and Parana provinces (sensu Morrone, 2014) are evident in western Uruguay, along the Uruguay river corridor, while to the northeast ravine forests are heavily influenced by the Parana province. Furthermore, a possible influence of the Cerrado province on the woody vegetation associated with flat-top sandstone hills on the northeast has been proposed (Grela, 2004; Brussa & Grela, 2007). To our knowledge, there are no studies on possible phytogeographic influences on herbaceous vegetation in Uruguay.

Northeastern Uruguay is included in the 'Gondwanic sedimentary basin' ecoregion, characterized by undulating terrain with plains and hills, deep soils and a geological material mostly made up of diverse sandstones of Gondwanic origin, although basaltic and crystalline rocks also occur (Panario et al., 2015). The region sustains a high species richness and is considered a hotspot for woody flora (Grela, 2004; Brussa & Grela, 2007). This is partly due to the great diversity of landforms and habitats in a span of relatively few kilometers (Brussa & Grela, 2007). Among these formations, flat-top hills (locally known as "cerros chatos") stand out as one of the most conspicuous. These are elevations of about 300 m above mean sea level (rising between 100 m and 150 m with respect to ground level), generally formed by Jurassic sandstones, characterized (from top to bottom) by a flat top, a stone ledge of variable height and a concave or stepped hillside. In its upper layers, this sandstone generally has undergone a silicification process that makes it particularly hardy, resisting the surrounding erosion and leaving a well-defined flat-top (Chebataroff & Zavala, 1975; Grela & Brussa, 2005). Flat-top hills represent a distinctive feature of the Uruguayan landscape with particular cultural importance (Brussa & Grela, 2007).

Little is known about the vegetation at the top of these hills, which mostly consists of sparse grasslands, with a varying abundance of trees and shrubs. Previous studies on these formations have focused on woody species (which mainly grow on the slopes of the hills), highlighting their distinctive flora, with the occurrence of several rare or exclusive species within the country (Marchesi, 1997; Grela, 2004; Grela & Brussa, 2005; Brussa & Grela, 2007; Ramos, 2009).

Fig. 1. Map of the study sites. **A,** location of study sites in Uruguay. **B,** location of the Vigilante, Miriñaque and Del Medio hills in Rivera department, Uruguay.

However, the herbaceous vegetation, which is dominant in these landforms, has not been properly described to this date. Likewise, a comprehensive list of the species present at the top of these hills, or a description of the vegetation's structure is also lacking. Hence, the aim of this study is to make the first characterization of the vegetation at the top of flat-top hills, identifying distinct vegetation formations and their structure, as well as presenting a referenced list of the species present. In order to achieve this, we described the vegetation of three emblematic hills in the region.

MATERIALS AND METHODS

Study site and data collection

The study area is located at the southmost extreme of the Cuñapirú Hills ("Cuchilla de Cuñapirú"), within the Rivera department, Uruguay (Fig. 1A). Three flat-top hills were selected, based on their distinctive position within the landscape and known botanical interest (Figs. 1B and 2A): Del Medio Hill ("Cerro del Medio"; Fig. 2B), part of the three hills of Cuñapirú (Chebataroff & Zavala, 1975), located at 31°35'19.6"S 55°37'37.9"W, with an average height of 281 m a.s.l. and a surface of 4.4 ha at its top; Miriñaque Hill ("Cerro Miriñaque"; Fig. 2C), located at 31°32'00.7"S 55°37'58.6"W, with an average height of 263 m a.s.l. and a surface of 1.7 ha at its top; and Vigilante Hill ("Cerro Vigilante", also called "Cerro de los Chivos"; Fig. 2D), located at 31°31'26.0"S 55°39'04.8"W, with an average height of 284 m a.s.l. and a surface of 11.6 ha at its top.

Plant species composition surveys were carried out in spring (November) of 2021 and autumn (March) of 2022, above the stone ledge that defines the top of the hill. In each hill, the main vegetation stands present were identified as a function of the dominant species and vegetation structure (Mueller-Dombois & Ellenberg, 1974; Whittaker, 1978). In spring, for each stand, a 5x5 m sampling plot was placed in a relatively homogeneous area, where all vascular plant species were identified, and their aerial cover-abundance was visually estimated, along with rockiness, bare ground, and dry matter cover (Dengler et al., 2008).

Fig. 2. A, view from the top of Miriñaque Hill, looking at the three hills of Cuñapirú. **B,** panoramic view of Del Medio Hill. **C,** panoramic view of Miriñaque Hill. **D,** panoramic view of Vigilante Hill. Color version at https://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/1145/1310

Afterwards, an enrichment of the species list was carried out, taking 15 minutes to walk around the area of the stand unit to include species that were left out of the sampling plot. In autumn, the plots were revisited and the species list enrichment was carried out a second time, with the objective of including species that went unnoticed on the spring sampling, either due to a lack of reproductive structures that made them conspicuous, or because they were annual summer species. Epilithic plants growing on the sides of the stone cliffs (surrounding the top) were not considered for the vegetation surveys.

We collected vouchers for most species present in each location. When available, earlier exsiccates from those sites deposited at the MVFA and MVJB herbaria were also included as vouchers for the species list. Taxa were tentatively identified in the field, and later confirmed using pertinent taxonomic literature (Rosengurtt, 1970; Burkart et al., 2005; Lezama & Bonifacino, 2012; López, 2012; Zuloaga et al., 2012; Zuloaga et al., 2014; Silveira, 2015; Brazilian Flora Group, 2021) and herbarium specimens hosted at MVFA. All samples collected were deposited at MVFA herbarium. Plant species nomenclature follows Zuloaga et al. (2019). Herbaria acronyms follow Thiers (2022).

Lastly, a procedural drone flight was carried out, surveying the top of the hills. A total of three drone flights were made in March 2022, with a multicopter DJI Mavic 2 Pro (Da-Jiang Innovations, Shenzhen, China). All three flat-top hills were covered in each flight. The flights followed a simple grid designed in the mobile app Flight (Drone Deploy, United States). Flights were conducted at 120 m above the maximum elevation for each hill, with a 65% overlap which resulted in a 2.7 cm/pix image resolution. Images were assembled into an orthomosaic. Based on the location and appearance of the vegetation surveys and their surrounding landcover in the orthomosaic, a manual delineation of vegetation stands was done, resulting in maps for each vegetation stand in each hill.

Data manipulation

The vegetation stands were manually grouped between hills into formations as a function of their slope, vegetation structure (reflected in the shrub cover), bare ground, dry matter cover and rockiness (Mueller-Dombois & Ellenberg, 1974). These are described mentioning their topographic characteristics, species richness and most abundant species on average (>5% aerial cover).

All species were classified according to their origin (i.e., native or alien), their life form (Raunkiaer, 1934), their conservation status according to Uruguay's priority for conservation species list (Marchesi et al., 2013) and the IUCN Red List (IUCN, 2022), and whether they are endemic to the Río de la Plata Grasslands (Andrade et al., 2018). Total species richness averages were compared through ANOVA between formations (with *post hoc* Tukey comparison). Richness averages between Raunkiaer life forms for all species present were compared through ANOVA (with *post hoc* Tukey comparison), in order to know which life form is dominant across all hills. Analyses considered hills as a random factor. All statistical analyses were carried out in R (R Core Team, 2022).

RESULTS

A total of 315 species belonging to 63 vascular plant families were identified throughout seven surveys, 45 of which were found exclusively during autumn (Appendix). Some distinctive species are depicted in Fig. 3. Poaceae and Asteraceae, with 76 and 73 species respectively, were the two most species-rich families, comprising nearly 50% of the total richness. They were followed by Fabaceae (23 spp.), Cyperaceae (11 spp.), Euphorbiaceae (8 spp.), Apiaceae (6 spp.), and Iridaceae (6 spp.) (Fig. 4). The remaining 56 families were represented by five or less species each. The diversity found corresponds to 10.4% of the vascular plant species present in the Uruguayan flora (Fig. 4). The most abundant life forms were hemicryptophytes, representing close to half the species present (48%), followed by chamaephytes (26%) and cryptophytes (14%) (Fig. 4).

Of all the species found, 31 are considered priority for conservation in Uruguay (Fig. 5). Of these, *Oxypetalum aurantiacum* (Apocynaceae) stands out for not having been recorded in the country in the last 64 years. The species *Parodia ottonis* (Cactaceae), found on all three hills, is the only one from our surveys considered threatened by the IUCN Red List, falling into the "Vulnerable" category (Appendix). Additionally, 13 species are endemic to the Río de la Plata grasslands.

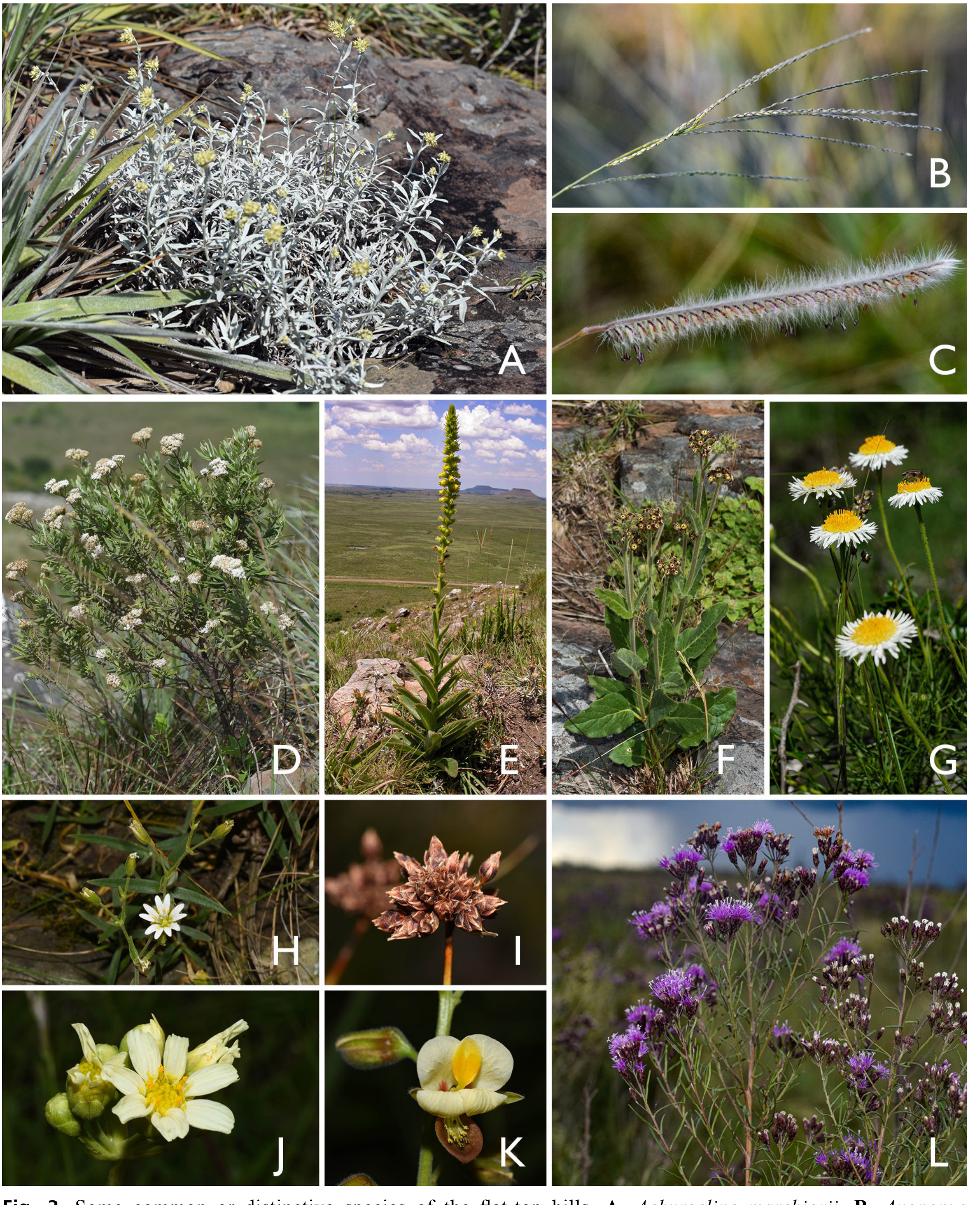

Fig. 3. Some common or distinctive species of the flat-top hills. **A,** *Achyrocline marchiorii*. **B,** *Axonopus siccus*. **C,** *Paspalum polyphyllum*. **D,** *Grazielia intermedia*. **E,** *Sinningia lutea*. **F,** *Oxypetalum arnottianum*. **G,** *Hysterionica chamomilloides*. **H,** *Cerastium dicrotrichum*. **I,** *Bulbostylis juncoides*. **J,** *Calea cymosa*. **K,** *Pomaria pilosa*. **L,** *Vernonanthura nudiflora*. Color version at https://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/1145/1310

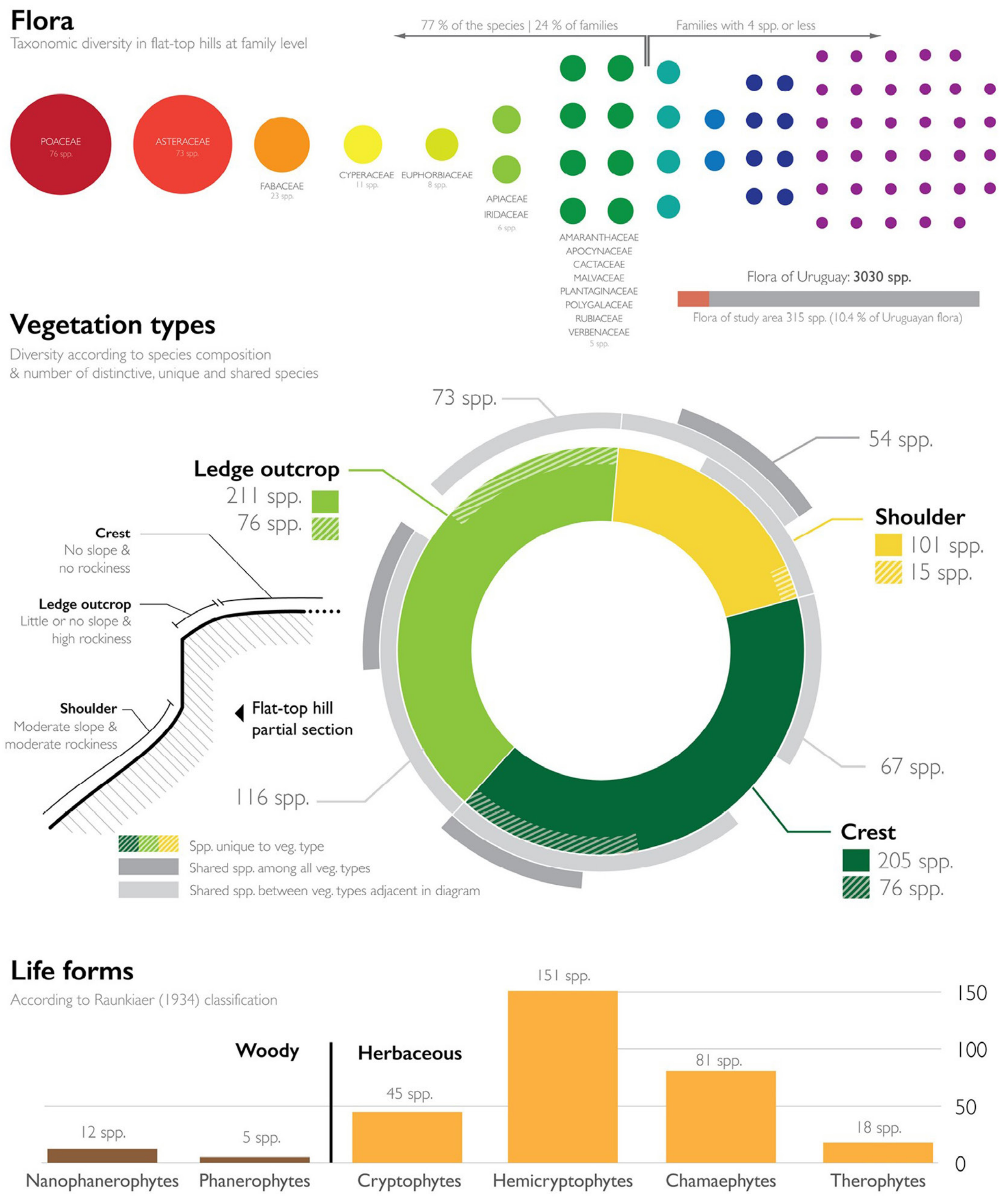

Fig. 4. Infographic showing vegetation and taxonomic diversity on flat-top hills. Families with four species or less include: Amaryllidaceae, Orchidaceae, Oxalidaceae, Solanaceae (four species); Caryophyllaceae, Convolvulaceae (three species); Acanthaceae, Anacardiaceae, Asparagaceae, Bromeliaceae, Campanulaceae, Linaceae, Passifloraceae, Pteridaceae (two species); Anemiaceae, Arecaceae, Aristolochiaceae, Bignoniaceae, Celastraceae, Cistaceae, Commelinaceae, Cucurbitaceae, Dioscoreaceae, Dryopteridaceae, Ericaceae, Eryhtroxylaceae, Gentianaceae, Gesneriaceae, Hypericaceae, Hypoxidaceae, Lamiaceae, Loganiaceae, Lythraceae, Malpighiaceae, Melastomataceae, Moraceae, Myrtaceae, Orobanchaceae, Pinaceae, Polypodiaceae, Primulaceae, Rhamnaceae, Salicaceae, Selaginellaceae, Smilacaceae, Thymelaeaceae, Urticaceae, Violaceae (one species). Color version at https://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/1145/1310

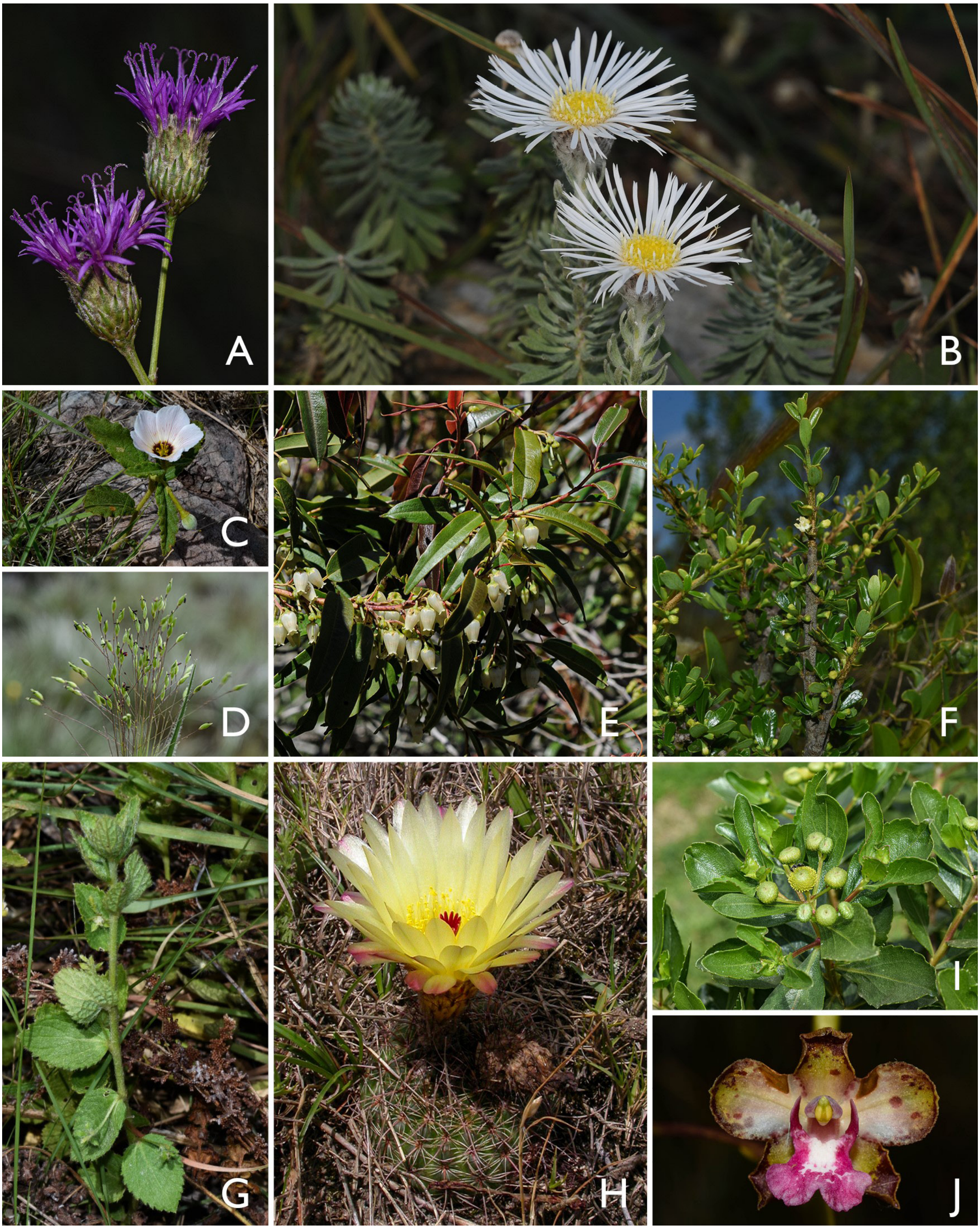

Fig. 5. Selection of priority species for conservation present in flat-top hills according to IUCN (2022) and Marchesi et al. (2013). **A,** *Vernonanthura pseudolinearifolia*. **B,** *Asteropsis megapotamica*. **C,** *Piriqueta taubatensis*. **D,** *Panicum olyroides*. **E,** *Agarista eucalyptoides*. **F,** *Erythroxylum microphyllum*. **G,** *Chiropetalum intermedium*. **H,** *Parodia ottonis*. **I,** *Baccharis psiadioides*. **J,** *Cyrtopodium brandonianum*. Color version at https://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/1145/1310

Fig. 5. (Continuation). Selection of priority species for conservation present in flat-top hills according to IUCN (2022) and Marchesi et al. (2013). **K,** *Butia paraguayensis*. **L,** *Schlechtendalia luzulaefolia*. **M,** *Eryngium eriophorum*. **N,** *Oxypetalum aurantiacum*. **O,** *Ceratosanthes multiloba*. **P,** *Eragrostis perennis*. **Q,** *Sommerfeltia spinulosa*. **R,** *Lessingianthus macrocephalus*. **S,** *Tragia melochioides*. Color version at https://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/1145/1310

Two alien species were registered: *Cynodon dactylon* and *Pinus taeda*. We also highlight the presence of *Melinis repens* (Willd.) Zizka along rocky outcrops at the ledges of Del Medio Hill, although it was not found in the surveyed area, therefore it is not a part of our list of species.

Lastly, we highlight a new formal record for the Uruguayan flora: *Achyrocline marchiorii* (Compositae: Gnaphalieae; *A. Mailhos et al. 133*; *A. Mailhos & P. Pañella 208*; *A. Mailhos et al. 251*, MVFA) (Fig. 3A).

Description of each formation

All floristic surveys were grouped into three distinct vegetation formations: crest, ledge outcrop, and shoulder (Fig. 4). Table 1 summarizes the main characteristics that defined each formation (slope, shrub cover, bare ground cover, dry matter cover and rock cover, along with the species richness of each formation). No statistically significant differences were detected in terms of the richness of each formation ($F_{2,6} = 0.02$, $p = 0.99$).

The crest formation was present in all three hills and was located in each case towards the middle of the flat tops (Figs. 6A and 7), occupying the most surface in each case. This formation is characterized by occurring on medium to deep soils, with an intermediate cover of bare ground (8.7 ± 14.2%) and dry matter (11.6 ± 2.6%), and no rockiness. Shrub cover was 0.9 ± 1%. A mean richness of 106 ± 13 species was recorded across sampling sites for this formation, with 76 species exclusively occurring in it (Fig. 4). Herbaceous vegetation (cryptophytes and hemicryptophytes) is the dominant component, with some isolated chamaephytes and nanophanerophytes (e.g., *Baccharis dracunculifolia*, *Butia paraguayensis*, *Myrsine coriacea*). The dominant species were *Schlechtendalia luzulifolia* (16.67 ± 17.56 %), and the grasses *Sorghastrum pellitum* (13.3 ± 11.55%), *Axonopus siccus* (8.5 ± 14.29%), *Axonopus argentinus* (8.3 ± 14.43%), and *Bromus auleticus* (6.67 ± 11.54%).

The ledge outcrop formation was also present in all three hills, and occurred mostly towards the rocky sandstone ledges that delimit the flat tops of the hills (Figs. 6B and 7). The soils on which this formation develops are superficial, with low bare ground and dry matter cover (0.7 ± 0.6% and 2 ± 2.6% respectively). and a high percentage of rock cover (53.3 ± 11.5%). Shrub cover was 3.3 ± 4%. The mean richness for this formation was of 104 ± 21.6 species, 76 of which were exclusive to it (Fig. 4). In a similar manner to the crest formation, herbaceous vegetation (cryptophytes and hemicryptophytes) is predominant, but in this case the proportion of chamaephytes and nanophanerophytes becomes larger (e.g., *Baccharis psiadioides*, *Erythroxylum microphyllum*, *Grazielia intermedia*, *Monteverdia ilicifolia*, *Xylosma tweediana*). A high heterogeneity in terms of species composition was observed within any given plot. As such, the only species that could be considered dominant was *Schlechtendalia luzulifolia*, and even so it had a relatively low cover percentage (5.3 ± 8.39%) and was absent in one of the plots.

Lastly, the shoulder formation was identified only on the Miriñaque Hill (Figs. 6C and 7B). This hill has the peculiarity of having a double sandstone ledge, which generates a ‘stepped top’, in which a lower and more pronounced ledge is followed by a moderate slope of colluvial origin, and this in turn is followed by a secondary ledge which surrounds the flat, central region of the hill. The shoulder formation occurs on the slope between the two rocky ledges.

Table 1. Information regarding each described formation: number of surveys performed for each, slope, bare ground cover (%), dry matter cover (%), rockiness (%), shrub cover (%) and species richness (n).

Formation	Crest	Ledge outcrop	Shoulder
Number of plots	3	3	1
Slope	Slight to null	Slight to null	Moderate
Bare ground (%)	8.7 ± 14.2	0.7 ± 0.6	0
Dry matter cover (%)	11.6 ± 2.6	2 ± 2.6	15
Rockiness (%)	0	53.3 ± 11.5	25
Shrub cover (%)	0.9 ± 1	3.3 ± 4	1.6
Species richness (n)	106 ± 13	104 ± 21.6	100

Fig. 6. Representative vegetation patches of each formation. **A,** crest. **B,** ledge outcrop. **C,** shoulder formation. Color version at https://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/1145/1310

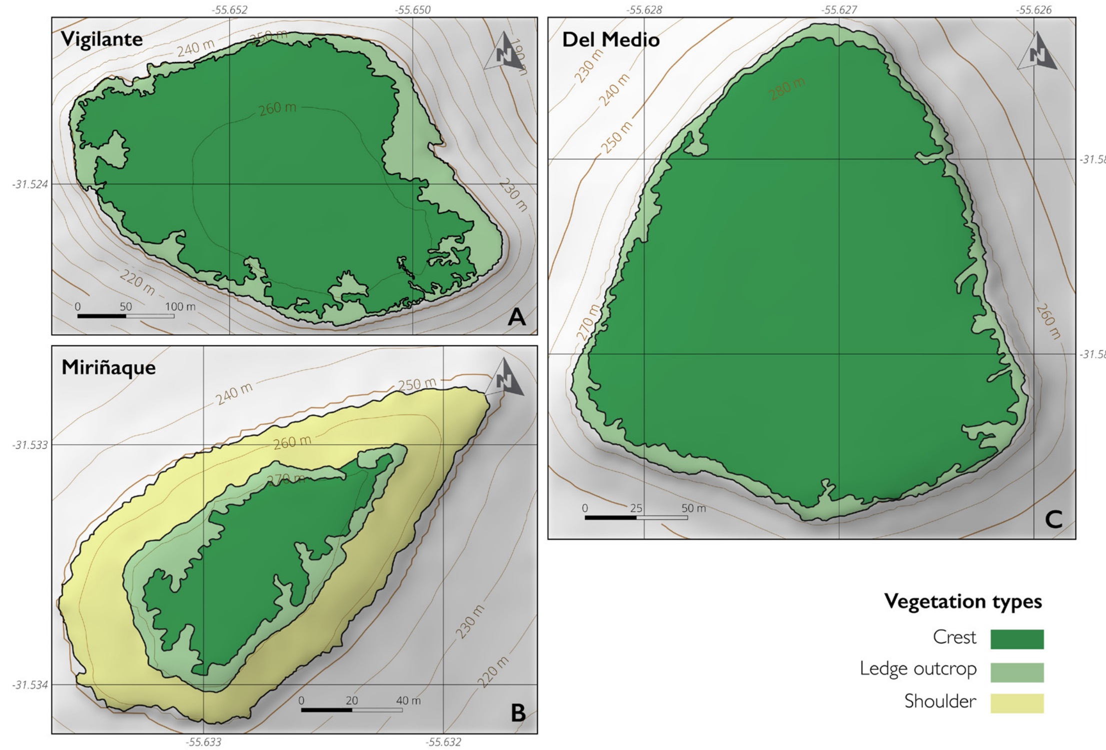

Fig. 7. Maps of the **A,** Vigilante; **B,** Miriñaque; and **C,** Del Medio hills, showing the distribution of each vegetation formation. Color version at https://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/1145/1310

No bare ground was evident, and it presents an intermediate dry matter cover and rockiness (15% and 25% respectively), while shrub cover was 1.6%. One hundred species were recorded in this formation, with 14 occurring exclusively on it (Fig. 4). This formation was also dominated by herbaceous cryptophytes and hemicryptophytes, with some isolated nanophanerophtes (*Agarista eucalyptoides* and *Butia paraguayensis*). The dominant species were: *Agenium villosum* (30%), *Axonopus siccus* (10%), *Axonopus suffultus* (10%), *Schlechtendalia luzulifolia* (10%), *Schizachyrium imberbe* (5%), *Schizachyrium tenerum* (5%), and *Sporobolus aeneus* var. *angustifolia* (5%).

Characteristics of each hill

With 205 species, Vigilante Hill had the highest richness of all three study sites. Of this total, 73 species were exclusive to this hill and 14 were priorities for conservation in Uruguay (Appendix). Three priority species were only found here. Some cattle feces were observed, which implies livestock have access to the top of this hill and grazing occurs. Additionally, field observations and interviews with the landowners revealed that the vegetation on top of this hill is periodically subjected to fire as a management practice.

A total of 173 species were present in the Del Medio Hill, 51 of which were exclusive to this site and 12 were priorities for conservation (Appendix). Only two priority species were also exclusively found on this hill. No evidence of cattle presence was found at this site, while at the same time large amounts of accumulated dry biomass were observed, which suggests that no grazing or regular burning occur.

On the Miriñaque Hill 171 species were recorded, 58 of which were exclusive to this hill. Of a total of 21 species considered priorities for conservation present on this hill's top, 13 were exclusive to this site (Appendix). Cattle feces were present at the site, suggesting livestock have access to the top of this hill and grazing occurs.

DISCUSSION

This is the first formal characterization of the vegetation of flat-top hills in Northern Uruguay, which are unique geoforms in the region, with great diversity and an uncommon flora. The sites visited hold a large number of species (315 spp.) in a relatively small total area (17.7 ha), many of which have a restricted distribution within the country and are considered priority for conservation (Marchesi et al., 2013). This description is also of particular interest because of the cultural importance of the Vigilante, Miriñaque and Del Medio hills (Brussa & Grela, 2007).

A pattern was found on the three hills sampled, where at least two vegetation types were present: the ledge associated with the rocky outcrops around the perimeter of the hilltop, and the crest associated with the deep soils and low rock cover at the center of the hilltops. Differences in flat-top hills' or plateaus' vegetation due to rock or stone abundance have been registered in the past (Winterringer, 1956; Smeins et al., 1974). In this case, these differences lead to a ring-like pattern due to the rocky ledges of the sandstone cliffs that circumscribe the top of the hill. It is important to note that although these formations can be recognized across all three study sites, with similar rockiness, vegetation structure and several species in common, they still show clear distinctions and a pronounced heterogeneity between hills. Additionally, a third formation was registered in the Miriñaque Hill, with soils that probably are of colluvial origin, derived from the erosion and detachment of rocks from the uppermost rocky ledge. The composition of this shoulder formation has few exclusive species, resembling both the crest and ledge outcrop formations, while also holding species common to the lower slope of the hill. The present study functions as a first approach into the characterization of the vegetation that exists on top of flat-top hills. Identified patterns are still just an insinuation of the great diversity of vegetation formations that exist in these ecosystems. More surveys are needed in order to provide a more robust classification of its different formations, with the identification of diagnostic species, something that should be tackled in future research endeavors.

Although the flora is mostly typical for the Río de la Plata grasslands (Appendix), it is clearly distinct from the surrounding grassland vegetation. Lezama et al. (2019) described most grasslands in the 'Gondwanic sedimentary basin' ecoregion as subassemblies of the following two communities: 'II Sparsely-vegetated grasslands *Trachypogon spicatus-Crocanthemum brasiliense*', which in the region have *Richardia humistrata*, *Paspalum notatum* and *Piptochaetium montevidense* as dominant species (Lezama et al., 2011); and 'IV Densely-vegetated grasslands *Eryngium horridum-Juncus capillaceus*', which in the region have *Paspalum notatum*, *Axonopus fissifolius* and *Saccharum angustifolium* as dominant species (Lezama et al., 2011). The dominant species from these and other communities described by Lezama et al. (2011) differ from those present in the formations described in our study. Also, the complete list of species is very distinct, showing several species that are rare or do not appear in the communities described by Lezama et al. (2019). Thus, species assemblies described here do not correlate to the expected communities for the region, nor do they correspond with other communities described for the country (Lezama et al., 2019). The differences observed on top of these hills may be due to the combination of two main factors: the low grazing pressure, and the particular geology and soils in these sites. In regard to the low grazing, this is likely due to the stone cliffs that circumscribe the top of these hills, limiting herbivore access, and allowing species that do not resist usual grazing levels to develop, such as two dominant species from the crest formation: *Sorghastrum pellitum* and *Bromus auleticus* (Lezama & Rossado, 2012). Regarding the geology, as we described, the silicified sandstones and uneven erosion that gave rise to these hills probably generated particular soils, which are linked to differences in vegetation communities. These two features, together with the isolated nature of flat-top hills, have led to unique species assemblies, distinct from the grassland matrix that surrounds them, as has been reported in other regions of the world (Burke et al., 2003).

Our results also suggest a possible convergence with Brazil's Cerrado biogeographic province for the herbaceous vegetation, similar to what other authors have suggested for the woody flora (Marchesi, 1997; Grela, 2004; Brussa & Grela, 2007). While several of the taxa present have an ample distribution, and no single one is considered as indicative of the Cerrado on its own, the herbaceous community ensemble as a whole does resemble this province, with genera such as the Asteraceae *Achyrocline* (Less.) DC., *Calea* L., *Dimerostemma* Cass., *Lessingianthus* H. Rob., *Porophyllum* Guett. and *Stevia* Cav.; the Fabaceae *Eriosema* (DC.) Desv. and *Galactia s.l.* P. Browne; the Orchidaceae *Cyrtopodium* R. Br. and *Habenaria* Willd.; the Poaceae *Andropogon* L., *Aristida* L., *Eragrostis* Wolf, *Paspalum* L. and *Setaria* P. Beauv.; the ferns *Anemia* Sw. and *Pleopeltis* Humb. & Bonpl. ex Willd.; and other genera such as *Bernardia* Houst. ex Mill. (Euphorbiaceae), *Eryngium* L. (Apiaceae), *Mandevilla* Lindl. (Apocynaceae), *Oxalis* L. (Oxalidaceae), *Piriqueta* Aubl. (Passifloraceae) and *Sisyrinchium* L. (Iridaceae). Particular species are worth pointing out, such as the grasses *Anthenantia lanata*, *Axonopus siccus*, *Panicum olyroides*, *Trachypogon spicatus*, and the palm *Butia paraguayensis* (Cole, 1960; Eiten, 1972; Cabrera & Willink, 1973; Marchesi, 1997; Batalha & Mantovani, 2001; Filgueiras, 2002). It should also be noted that, according to recent phytogeographic literature, both the Pampean and Cerrado provinces are placed within the Chacoan dominion (Morrone, 2014). The similarity between flat-top hills and the Cerrado can be partially explained by shared geologic and edaphic conditions (i.e., sandstones with deep, poor soils that are levelled and of pronounced age) (Ranzani, 1963; Eiten, 1972; Chebataroff & Zavala, 1975). That being said, the lower average temperatures and the presence of winter frost represent a clear limitation to the expression of actual Cerrado-like vegetation on these flat-top hills (Eiten 1972; INIA GRAS, 2022).

We also highlight the potential importance of fire in these ecosystems. The very low grazing intensity leads to a pronounced biomass accumulation that makes these systems prone to spontaneous or anthropic fires. In the case of the Vigilante Hill, the site had been burned shortly before our first visit as a management measure, leaving visible marks such as ashes and plants that were just resprouting, with charred dead leaves at the base of stems and tillers. While not recently burned, the Del Medio and Miriñaque hills showed a lot of dry biomass which had accumulated over time, which could burn easily. Several of the species present were cryptophytes and hemicryptophytes, showing a thick bark (e.g., *Agarista eucalyptoides*, *Pomaria pilosa*), and/or retaining leaf sheaths to protect buds (e.g., *Eragrostis perennis*, *Sorghastrum pellitum*), adaptations that are often associated with a resistance to fire damage in fire-prone environments (Archibald et al., 2019; Nolan et al., 2020). While fires may play a role in shaping these ecosystems, the magnitude at which they intervene is yet to be understood and requires further studies.

About 10% of the identified species are priorities for conservation at a national level, while only one species (*Parodia ottonis*) is classified as threatened by the IUCN Red List, falling into the 'Vulnerable' category (IUCN, 2022). It is important to take into account, however, that the vast majority of plant species native to Uruguay are yet to be diagnosed by the IUCN, so their global threat level is unknown. While five priority species were shared between all three hills (*Baccharis psiadioides*, *Galium atherodes*, *Mimosa rupestris*, *Piriqueta taubatensis*, *Vernonanthura pseudolinearifolia*), most were exclusive to just one of them, with Miriñaque holding the largest amount despite its smaller surface area.

Regarding management practices, these grasslands are under private administration, which means that they can be freely exploited leading to the loss of valuable ecosystems that should be conserved. In particular, the region in Uruguay where flat-top hills occur has seen a steady and rapid increase in afforestation in recent years (Baeza & Paruelo, 2020), and it is not unusual to find these hills completely surrounded by large afforested areas. In some extreme cases, the slopes and even the hilltops have been afforested. The hills could also be subject to other kinds of land degradation, such as overgrazing, uncontrolled fires and unregulated tourism.

At the same time, these sites are under threat due to the invasion of alien species. Three invasives were found on top of the hills: *Cynodon dactylon*, *Melinis repens* and *Pinus taeda*. *Cynodon dactylon* is a summer grass that tends to dominate the patches where it establishes, excluding native species (Rosengurtt et al., 1970; Holm et al., 1977). *Melinis repens* is a summer grass native to Africa that has colonized grasslands throughout America, establishing in shallow or rocky soils, hence its appearance at the ledge of the hilltops (Stokes et al., 2011; Melgoza Castillo et al., 2014). Finally, *Pinus taeda* is a tree native to the United States, which was introduced for industrial forestry in the last century, and has had a pronounced expansion in this region since 1985 (Porcile, 2007; Baeza et al., 2022; MapBiomas Pampa, 2022). Due to its large propagule production, anemochorous dispersal and broad range of tolerance to climatic and edaphic conditions, it has turned into an invasive alien species, impacting the soil and water cycles as well as the local biota (Richardson & Higgins, 1998; Pauchard et al., 2015). These invasive alien species could represent a threat to the conservation of these ecosystems and their diverse flora if they are not controlled.

Implications for conservation

The current work reports 10 % of the Uruguayan flora (315 species total) within 17.7 ha of land. Also, 10 % of the species found are priorities for conservation at a national level. Considering the large number of species within a relatively small surface area, and the numerous threats to their preservation, the need for urgent protection of these hills arises. This is further emphasized by the large proportion of priority species for conservation. Flat-top hills in Uruguay are not contemplated under any conservation programs at neither national (Sistema Nacional de Áreas Protegidas) (SNAP, 2022) nor global scales. The fact that most plant species native to Uruguay are not diagnosed by the IUCN limits the capacity for national or international aid and conservation policies. Given the lack of objective information, the preservation of these ecosystems and their species are not guaranteed, and their conservation status is likely more delicate than one might think. Actions should be taken to preserve these unique ecosystems and prevent their further degradation, where the main focus should be controlling the spread of invasive species. Also, management practices that allow for pastoral use without leading to overgrazing should be contemplated. Finally, fire regimes should be considered, where more research could help determine a periodicity and intensity compatible with the conservation of these ecosystems. Although the precise number of flat-top hills in the region is not documented, it is possible to estimate that there are tens to hundreds of them, scattered across a considerable area, with distinct geologic and edaphic characteristics that probably grant them particular vegetation features that need to be explored. Future research should focus on exploring more hills in the region and their vegetation, community patterns and biogeographic influences.

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Appendix. Species list of Del Medio, Miriñaque, and Vigilante hills. Origin: Co- Cosmopolitan, En-RPG- Endemic to the Río de la Plata grasslands, Re-Uy- Restricted to Uruguay, Ex-IAS- Exotic invasive alien species, N- Native to Uruguay. Conservation status: Pr- Priority species for conservation in Uruguay according to Marchesi et al. (2013); DD- Data deficient, LC- Least concern, VU- Vulnerable, according to IUCN (2022), blank spaces indicate species not evaluated. Lifeform,following Raunkiaer (1934): CH- Chamaephyte, CR- Cryptophyte, HC- Hemicryptophyte, NP- Nanophanerophyte, PH- Phanerophyte, TH- Therophyte. Formation: vegetation formations where species were found, Cr- Crest, LO- Ledge outcrop, Sh- Shoulder. Voucher: specimen deposited in national herbaria, when available.

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Acanthaceae					
Justicia axillaris (Nees) Lindau	N		CH	LO	A. Mailhos et al. 145 (MVFA)
Stenandrium dulce (Cav.) Nees	N		HC	Cr	-
Amaranthaceae					
Dysphania ambrosioides (L.) Mosyakin & Clemants	N		TH	LO	-
Gomphrena graminea Moq.	N		HC	Sh	M. Bonifacino & Wilson 2112 (MVFA)
Gomphrena perennis L.	N		HC	LO	A. Mailhos et al. 114 (MVFA)
Pfaffia gnaphalioides (L. f.) Mart.	N		HC	Cr, LO, Sh	-
Pfaffia tuberosa (Spreng.) Hicken	N		HC	Cr, LO, Sh	A. Mailhos et al. 146 (MVFA)
Amaryllidaceae					
Nothoscordum gaudichaudianum Kunth	N		CR	Cr, LO	A. Mailhos et al. 188 (MVFA)
Nothoscordum gracile (Aiton) Stearn	N		CR	LO	-
Nothoscordum sp.	N		CR	LO	-
Zephyranthes gracilifolia (Herb.) G. Nicholson	N		CR	Cr	-
Anacardiaceae					
Lithraea molleoides (Vell.) Engl.	N	LC	PH	LO	-
Schinus engleri F.A. Barkley	N	DD	NP	LO	A. Mailhos et al. 312 (MVFA)
Anemiaceae					
Anemia tomentosa (Savigny) Sw.	N		CR	LO, Sh	-
Apiaceae					
Eryngium eriophorum Cham. & Schltdl.	N	Pr	HC	Cr	A. Mailhos et al. 151 (MVFA)
Eryngium horridum Malme	N		HC	Cr, LO	-
Eryngium luzulaefolium Cham. & Schltdl.	N		HC	Sh	-
Eryngium megapotamicum Malme	N		HC	Cr, LO, Sh	A. Mailhos et al. 304 (MVFA)
Eryngium regnellii Malme	N		HC	LO	A. Mailhos et al. 215 (MVFA)
Eryngium sanguisorba Cham. & Schltdl.	N		HC	Cr	-
Apocynaceae					
Mandevilla coccinea (Hook. & Arn.) Woodson	N		HC	LO, Sh	-
Mandevilla longiflora (Desf.) Pichon	N		HC	Cr, LO, Sh	P. Davies & M. Bonifacino (MVFA 26053)
Oxypetalum arnottianum H. Buek ex E. Fourn.	N		HC	Cr, LO	A. Mailhos et al. 121 (MVFA)
Oxypetalum aurantiacum Malme ex Chodat & Hassl.	N	Pr	HC	Sh	A. Mailhos et al. 257 (MVFA)
Oxypetalum commersonianum (Decne.) Fontella & E.A. Schwarz	N		HC	Cr	A. Mailhos et al. 263 (MVFA)
Arecaceae					
Butia paraguayensis (Barb. Rodr.) L.H. Bailey	N	Pr	NP	Cr, LO, Sh	Carbonell (MVFA 8489)
Aristolochiaceae					
Aristolochia angustifolia Cham.	N		CR	LO	A. Mailhos et al. 94 (MVFA)
Asparagaceae					
Clara ophiopogonoides Kunth	N		HC	Cr	A. Mailhos et al. 229 (MVFA)

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Herreria montevidensis Klotzsch ex Griseb.	N		HC	Cr	A. Mailhos et al. 244 (MVFA)
Asteraceae					
Acanthostyles buniifolius (Hook. ex Arn.) R.M. King & H. Rob.	N		NP	Cr	A. Mailhos et al. 227 (MVFA)
Achyrocline flaccida (Weinm.) DC.	N		CH	Cr, LO, Sh	A. Mailhos et al. 245 (MVFA)
Achyrocline marchiorii Deble	En-RPG		CH	LO, Sh	A. Mailhos et al. 133 (MVFA)
Achyrocline saturejoides (Lam.) DC.	N		CH	Cr, LO	A. Mailhos et al. 132 (MVFA)
Acmella decumbens (Sm.) R.K. Jansen	N		HC	Cr, Sh	-
Aldama anchusifolia (DC.) E.E. Schill. & Panero	N		HC	LO	A. Mailhos et al. 210 (MVFA)
Aspilia pascalioides Griseb.	N		CH	Cr, LO, Sh	A. Mailhos et al. 221 (MVFA)
Asteropsis megapotamica (Spreng.) Marchesi, Bonif. & G. Sancho	En-RPG	Pr	CH	Cr	M. Bayce et al. (MVFA 17226)
Baccharis articulata (Lam.) Pers.	N		CH	Cr, LO, Sh	-
Baccharis cognata DC.	N		CH	Cr	A. Mailhos et al. 193 (MVFA)
Baccharis coridifolia DC.	N		CH	Cr	-
Baccharis dracunculifolia DC.	N		NP	Cr, LO, Sh	M. Bonifacino et al. (MVFA 26686)
Baccharis leptophylla DC.	N		NP	Cr, LO, Sh	A. Mailhos et al. 157 (MVFA)
Baccharis psiadioides (Less.) Joch. Müll.	N	Pr	NP	Cr, LO, Sh	C. Brussa & I. Grela (MVFA 29706)
Baccharis spicata Hieron.	N		CH	Cr	-
Baccharis trimera (Less.) DC.	N		CH	Cr, LO, Sh	A. Mailhos et al. 298 (MVFA)
Baccharis vernicosa W. Hook. & Arn.	En-RPG		NP	LO, Sh	-
Calea clematidea Baker	N		CH	LO	A. Mailhos et al. 110 (MVFA)
Calea cymosa Less.	N		CR	Cr	A. Mailhos et al. 228 (MVFA)
Calea uniflora Less.	N		CR	LO, Sh	-
Campuloclinium macrocephalum (Less.) DC.	N		CR	Cr	A. Mailhos et al. 166 (MVFA)
Chaptalia exscapa (Pers.) Baker	N		HC	Cr	-
Chaptalia integerrima (Vell.) Burkart	N		HC	Cr, LO	A. Mailhos et al. 233 (MVFA)
Chaptalia piloselloides (Vahl) Baker	N		HC	Cr, Sh	-
Chevreulia acuminata Less.	N		HC	Cr	-
Chromolaena caaguazuensis (Hieron.) R.M. King & H. Rob.	N		HC	Cr	A. Mailhos et al. 159 (MVFA)
Chromolaena hirsuta (Hook. & Arn.) R.M. King & H. Rob.	N		HC	Cr, LO	-
Chromolaena squarrulosa (Hook. & Arn.) R.M. King & H. Rob.	N		HC	Cr, Sh	A. Mailhos et al. 160 (MVFA)
Chrysolaena cognata (Less.) M. Dematt.	N		HC	Cr, LO, Sh	A. Mailhos et al. 246 (MVFA)
Chrysolaena flexuosa (Sims) H. Rob.	N		HC	Cr	A. Mailhos et al. 183 (MVFA)
Conyza blakei (Cabrera) Cabrera	N		TH	LO	-
Conyza bonariensis (L.) Cronquist	N		TH	LO	A. Mailhos et al. 111 (MVFA)
Conyza monorchis (Griseb.) Cabrera	N		CR	Cr	A. Mailhos et al. 283 (MVFA)
Conyza primulifolia (Lam.) Cuatrec. & Lourteig	N		HC	Cr	A. Mailhos et al. 182 (MVFA)
Conyza sp.	N			Cr	-
Dimerostemma grisebachii (Baker) M.D. Moraes	N		CH	Cr, Sh	A. Mailhos et al. 311 (MVFA)
Facelis retusa (Lam.) Sch. Bip.	N		TH	LO	-
Gamochaeta argentina Cabrera	N		TH	Cr, LO	A. Mailhos et al. 301 (MVFA)
Gamochaeta filaginea (DC.) Cabrera	N		TH	LO, Sh	A. Mailhos et al. 295 (MVFA)
Gamochaeta sp.	N		TH	Cr	-

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Grazielia intermedia (DC.) R.M. King & H. Rob.	N		NP	Cr, LO, Sh	A. Mailhos et al. 95 (MVFA)
Gyptis commersonii Cass.	N		HC	LO	-
Gyptis lanigera (Hook. & Arn.) R.M. King & H. Rob.	N		HC	Cr, LO	A. Mailhos et al. 155 (MVFA)
Gyptis tanacetifolia (Gillies ex Hook. & Arn.) D.J.N. Hind & Flann	N		HC	LO	-
Hieracium commersonii Monnier	N		HC	Cr, LO, Sh	A. Mailhos et al. 209 (MVFA)
Holocheilus brasiliensis (L.) Cabrera	N		HC	LO	-
Hypochaeris albiflora (Kuntze) Azevêdo-Gonç. & Matzenb.	N		HC	LO	-
Hypochaeris megapotamica Cabrera	N		HC	LO	-
Hysterionica chamomilloides Deble	En-RPG		CH	LO	A. Mailhos et al. 98 (MVFA)
Lessingianthus brevifolius (Less.) H. Rob.	N		HC	Cr, LO, Sh	A. Mailhos et al. 306 (MVFA)
Lessingianthus macrocephalus (Less.) H. Rob.	En-RPG	Pr	HC	Cr, LO, Sh	M. Bonifacino & P. Davies (MVFA 26057)
Lessingianthus sellowii (Less.) H. Rob.	N		HC	Cr	A. Mailhos et al. 156 (MVFA)
Lucilia acutifolia (Poir.) Cass.	N		CH	Cr, LO, Sh	-
Lucilia nitens Less.	N		CH	Cr, LO, Sh	A. Mailhos et al. 167 (MVFA)
Mikania anethifolia (DC.) Matzenbacher	N		CH	Cr, LO, Sh	.
Mikania thapsoides DC.	N		HC	LO	-
Podocoma hirsuta (Hook. & Arn.) Baker	N		HC	Cr	A. Mailhos et al. 190 (MVFA)
Porophyllum obscurum (Spreng.) DC.	N		TH	Sh	A. Mailhos et al. 262 (MVFA)
Porophyllum ruderale (Jacq.) Cass.	N		TH	LO	A. Mailhos et al. 117 (MVFA)
Pterocaulon angustifolium DC.	N		HC	Cr, LO	A. Mailhos et al. 165 (MVFA)
Schlechtendalia luzulaefolia Less.	En-RPG	Pr	HC	Cr, LO, Sh	A. Mailhos et al. 100 (MVFA)
Senecio leptolobus DC.	N		CH	LO	-
Senecio selloi (Spreng.) DC.	N		CH	Cr	-
Solidago chilensis Meyen	N		TH	Cr	A. Mailhos et al. 230 (MVFA)
Sommerfeltia spinulosa (Spreng.) Less.	N	Pr	CH	Sh	-
Stenachaenium megapotamicum Baker	N		HC	Cr	-
Stenocephalum megapotamicum (Spreng.) Sch. Bip.	N		CH	Cr, Sh	M. Bayce et al. (MVFA 17234)
Stevia cinerascens Sch. Bip. ex Baker	N		CH	Cr, LO	A. Mailhos et al. 199 (MVFA)
Stevia multiaristata Spreng.	N		CH	LO, Sh	A. Mailhos et al. 141 (MVFA)
Stevia satureiifolia (Lam.) Sch. Bip. ex Klotzsch	N		CH	LO, Sh	-
Trixis nobilis (Vell.) Katinas	N		CH	LO	A. Mailhos et al. 232 (MVFA)
Vernonanthura nudiflora (Less.) H. Rob.	N		CH	Cr, LO, Sh	-
Vernonanthura pseudolinearifolia (Hieron.) A.J. Vega & M. Dematt.	En-RPG	Pr	CH	Cr, LO, Sh	A. Mailhos et al. 180 (MVFA)
Bignoniaceae					
Dolichandra cynanchoides Cham.	N		CH	LO	-
Bromeliaceae					
Billbergia nutans J.C. Wendl.	N		HC	LO	S/C (MVFA 18424)
Dyckia remotiflora Otto & A. Dietr.	N		HC	Cr, LO, Sh	M. Bonifacino & Sytsma 840 (MVFA)
Cactaceae					
Cereus hildmannianus ssp. *uruguayanus* (R. Kiesling) N.P. Taylor	N	LC	CH	LO	-
Frailea sp.	N		CH	LO	-

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Parodia erinacea (Haw.) N.P. Taylor	N	LC	CH	LO	-
Parodia ottonis (Lehm.) N.P. Taylor	N	VU	CH	LO, Sh	R. Nyffeler 1538 (MVJB 22396)
Parodia sp.	N		CH	LO	-
Campanulaceae					
Triodanis biflora (Ruiz & Pav.) Greene	N		TH	LO	-
Wahlenbergia linarioides (Lam.) A. DC.	N		CH	LO, Sh	-
Caryophyllaceae					
Cerastium dicrotrichum Fenzl ex Rohrb.	N		CH	LO	A. Mailhos et al. 286 (MVFA)
Paronychia communis Cambess.	N		CH	LO	-
Spergula grandis Pers.	N		CH	LO	-
Celastraceae					
Monteverdia ilicifolia (Mart. ex Reissek) Biral	N		NP	LO	-
Cistaceae					
Crocanthemum brasiliensis Spach	N		CH	Cr, LO, Sh	-
Commelinaceae					
Commelina erecta L.	N		HC	Cr, LO	-
Convolvulaceae					
Dichondra sericea Sw.	N		HC	Cr, LO	A. Mailhos et al. 289 (MVFA)
Evolvulus sericeus Sw.	N		CH	Cr, LO, Sh	A. Mailhos et al. 137 (MVFA)
Ipomoea procumbens Mart. ex Choisy	N	Pr	HC	Cr, LO	A. Mailhos et al. 124 (MVFA)
Cucurbitaceae					
Ceratosanthes multiloba Cogn.	N	Pr	CH	LO	A. Mailhos et al. 122 (MVFA)
Cyperaceae					
Abildgaardia ovata (Burm. f.) Kral	N		CR	Cr	A. Mailhos et al. 277 (MVFA)
Bulbostylis consanguinea (Kunth) C.B. Clarke	N		CR	Cr	A. Mailhos et al. 191 (MVFA)
Bulbostylis juncoides (Vahl) Kük. ex Osten	N		CR	Cr, LO, Sh	A. Mailhos et al. 275 (MVFA)
Carex phalaroides Kunth	N		CR	Cr, LO	-
Carex sororia Kunth	N		CR	LO	A. Mailhos et al. 296 (MVFA)
Cyperus aggregatus (Willd.) Endl.	N		CR	Cr, LO	A. Mailhos et al. 187 (MVFA)
Cyperus reflexus Vahl	N		CR	Cr, LO	A. Mailhos et al. 253 (MVFA)
Fimbristylis dichotoma (L.) Vahl	Co	LC	HC	Sh	-
Rhynchospora barrosiana Guagl.	N		CR	Cr	A. Mailhos et al. 280 (MVFA)
Rhynchospora setigera Griseb.	N		CR	Cr	A. Mailhos et al. 172 (MVFA)
Scleria sellowiana Kunth	N		CR	Cr	A. Mailhos et al. 273 (MVFA)
Dioscoreaceae					
Dioscorea microbotrya Griseb.	N		CR	LO	A. Mailhos et al. 216 (MVFA)
Dryopteridaceae					
Rumohra adiantiformis (G. Forst.) Ching	N	LC	CR	Cr, LO	A. Mailhos et al. 254 (MVFA)
Ericaceae					
Agarista eucalyptoides (Cham. & Schltdl.) G. Don	N	Pr	PH	Cr, Sh	A. Mailhos et al. 205 (MVFA)
Erythroxylaceae					
Erythroxylum microphyllum A. St.-Hil.	N	Pr	NP	LO	A. Mailhos et al. 256 (MVFA)
Euphorbiaceae					
Acalypha communis Müll. Arg.	N		CH	Cr, LO	A. Mailhos et al. 118 (MVFA)
Bernardia sellowii Müll. Arg.	N	Pr	CH	Cr, LO, Sh	A. Mailhos et al. 315 (MVFA)

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Chiropetalum foliosum (Müll. Arg.) Pax & K. Hoffm.	En-RPG		CH	Cr, LO	A. Mailhos et al. 310 (MVFA)
Chiropetalum intermedium Pax & K. Hoffm.	N	Pr	CH	Cr, LO	A. Mailhos et al. 255 (MVFA)
Euphorbia burkartii Bacigalupo	En-RPG		CR	Cr	A. Mailhos et al. 264 (MVFA)
Euphorbia papillosa A. St.-Hil.	N		HC	Cr	A. Mailhos et al. 303 (MVFA)
Tragia melochioides Griseb.	N	Pr	HC	LO	A. Mailhos et al. 128 (MVFA)
Tragia uberabana Müll. Arg.	N		HC	Cr, LO	A. Mailhos et al. 291 (MVFA)
Fabaceae					
Ancistrotropis clitorioides (Mart. ex Benth.) A. Delgado	N		CH	Cr, LO, Sh	P. Izaguirre et al. (MVFA 18624)
Betencourtia australis (Malme) L.P. Queiroz	En-RPG		CH	Cr, Sh	-
Betencourtia gracillima (Benth.) L.P. Queiroz	N		HC	Cr, LO, Sh	-
Desmanthus tatuhyensis Hoehne	N		CH	Cr, LO	A. Mailhos et al. 284 (MVFA)
Desmodium arechavaletae Burkart	N		CH	Cr	-
Desmodium incanum (Sw.) DC.	N		CH	Cr, LO	A. Mailhos et al. 119 (MVFA)
Eriosema tacuaremboense Arechav.	N		HC	Sh	A. Mailhos et al. 260 (MVFA)
Lathyrus subulatus Lam.	N		CR	Cr	A. Mailhos et al. 222 (MVFA)
Lupinus bracteolaris Desr.	N		HC	LO	-
Lupinus multiflorus Desr.	N		HC	Cr	A. Mailhos et al. 305 (MVFA)
Macroptilium prostratum (Benth.) Urb.	N		HC	Cr, LO	A. Mailhos et al. 152 (MVFA)
Mimosa dolens Vell.	N	LC/Pr	CH	Cr	B. Rosengurtt B7014 (MVFA)
Mimosa flagellaris Benth.	N		HC	Cr, LO, Sh	B. Rosengurtt B7027 (MVFA)
Mimosa rupestris Benth.	N	Pr	CH	Cr, LO	A. Mailhos et al. 309 (MVFA)
Nanogalactia heterophylla (Gillies ex Hook.) L.P. Queiroz	N		HC	Cr, LO	A. Mailhos et al. 116 (MVFA)
Nanogalactia pretiosa (Burkart) L.P. Queiroz	N		HC	Sh	-
Poiretia tetraphylla (Poir.) Burkart	N		HC	LO	-
Pomaria pilosa (Vogel) B.B. Simpson & G.P. Lewis	N		CH	Cr	-
Rhynchosia corylifolia Mart. ex Benth.	N		CH	Cr, LO, Sh	A. Mailhos et al. 123 (MVFA)
Rhynchosia lineata Benth.	N		CH	LO	A. Mailhos et al. 125 (MVFA)
Rhynchosia sp.	N		CH	Cr	-
Stylosanthes leiocarpa Vogel	N		HC	LO	A. Mailhos et al. 115 (MVFA)
Stylosanthes montevidensis Vogel	N		HC	Cr, LO, Sh	A. Mailhos et al. 184 (MVFA)
Gentianaceae					
Zygostigma australe (Cham. & Schltdl.) Griseb.	N		HC	Sh	-
Gesneriaceae					
Sinningia lutea Buzatto & R.B. Singer	En-RPG		HC	Cr, LO, Sh	A. Mailhos et al. 231 (MVFA)
Hypericaceae					
Hypericum connatum Lam.	N		HC	Cr, LO	A. Mailhos et al. 148 (MVFA)
Hypoxidaceae					
Hypoxis decumbens L.	N		CR	Cr	-
Iridaceae					
Cypella fucata Ravenna	N		CR	Cr, Sh	A. Mailhos et al. 171 (MVFA)
Gelasine elongata (Graham) Ravenna	N		HC	Cr, LO	-
Sisyrinchium micranthum Cav.	N		TH	Cr, LO	A. Mailhos et al. 250 (MVFA)

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Sisyrinchium palmifolium L.	N		HC	Cr, LO	-
Sisyrinchium scariosum I.M. Johnst.	N		HC	Cr, LO, Sh	-
Sisyrinchium vaginatum Spreng.	N		TH	Cr, LO, Sh	A. Mailhos et al. 308 (MVFA)
Lamiaceae					
Cantinoa mutabilis (Rich.) Harley & J.F.B. Pastore	N		CH	LO	A. Mailhos et al. 144 (MVFA)
Linaceae					
Cliococca selaginoides (Lam.) C.M. Rogers & Mildner	N		CH	Cr, LO	-
Linum burkartii Mildner	N	Pr	CH	Cr	A. Mailhos et al. 282 (MVFA)
Loganiaceae					
Spigelia stenophylla Progel	N		CH	Cr, Sh	P. Izaguirre et al. (MVFA 18678)
Lythraceae					
Cuphea glutinosa Cham. & Schltdl.	N		CH	Cr	A. Mailhos et al. 178 (MVFA)
Malpighiaceae					
Janusia guaranitica (A. St.-Hil.) A. Juss.	N		CH	LO	A. Mailhos et al. 299 (MVFA)
Malvaceae					
Krapovickasia flavescens (Cav.) Fryxell	N		CH	LO	A. Mailhos et al. 142 (MVFA)
Krapovickasia urticifolia (A. St.-Hil.) Fryxell	N		CH	LO	A. Mailhos et al. 127 (MVFA)
Pavonia aurigloba Krapov. & Cristóbal	N		CH	Cr, LO	A. Mailhos et al. 293 (MVFA)
Pavonia glechomoides A. St.-Hil.	N		CH	Cr, LO	A. Mailhos et al. 252 (MVFA)
Sida spinosa L.	N		CH	LO	-
Melastomataceae					
Chaetogastra gracilis (Bonpl.) DC.	N		CH	Cr, Sh	-
Moraceae					
Dorstenia brasiliensis Lam.	N		HC	Cr	-
Myrtaceae					
Psidium salutare (Kunth) O. Berg	N		CR	Cr, Sh	E. Marchesi & I. Grela (MVFA 27084)
Orchidaceae					
Brachystele arechavaletae (Kraenzl.) Schltr.	N		CR	Cr	-
Cyrtopodium brandonianum Barb. Rodr.	N	Pr	CR	Sh	-
Habenaria parviflora Lindl.	N	LC	CR	Cr	-
Pelexia sp.	N		CR	Cr	-
Orobanchaceae					
Buchnera longifolia Kunth	N		CH	Cr, Sh	I. Grela et al. (MVFA 26707)
Oxalidaceae					
Oxalis brasiliensis G. Lodd. ex Drapiez	N		HC	Cr	-
Oxalis conorrhiza Jacq.	N		CR	Cr, LO	A. Mailhos et al. 278 (MVFA)
Oxalis lasiopetala Zucc.	N		CR	Cr, LO	A. Mailhos et al. 138 (MVFA)
Oxalis sp.	N		CR	Cr	-
Passifloraceae					
Passiflora caerulea L.	N		CH	LO	A. Mailhos et al. 129 (MVFA)
Piriqueta taubatensis (Urb.) Arbo	N	Pr	HC	Cr, LO, Sh	A. Mailhos et al. 93 (MVFA)
Pinaceae					
Pinus taeda L.	Ex-IAS	LC	PH	Cr	-

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Plantaginaceae					
Angelonia integerrima Spreng.	N		CR	Cr	-
Mecardonia tenella (Cham. & Schltdl.) Pennell	N		CH	Cr	-
Plantago brasiliensis Sims	N		HC	Sh	-
Plantago myosuros Lam.	N		TH	Cr	-
Plantago tomentosa Lam.	N		HC	Cr, LO	A. Mailhos et al. 279 (MVFA)
Poaceae					
Agenium villosum (Nees) Pilg.	N		HC	Cr, LO, Sh	-
Agrostis montevidensis Spreng. ex Nees	N		HC	Cr, Sh	A. Mailhos et al. 200 (MVFA)
Andropogon lateralis Nees	N		HC	Cr, Sh	A. Mailhos et al. 242 (MVFA)
Andropogon macrothrix Trin.	N		HC	LO	-
Andropogon ternatus (Spreng.) Nees	N		CR	LO, Sh	A. Mailhos et al. 207 (MVFA)
Anthenantia lanata (Kunth) Benth.	N		HC	Cr	-
Aristida circinalis Lindm.	N		HC	Cr, LO	-
Aristida jubata (Arechav.) Herter	N		HC	LO	-
Aristida laevis (Nees) Kunth	N		HC	Cr, LO	B. Rosengurtt B7009 (MVFA)
Aristida megapotamica Spreng.	N	Pr	HC	Sh	-
Aristida pallens Cav.	N		HC	Cr, LO	A. Mailhos et al. 249 (MVFA)
Aristida venustula Arechav.	N		HC	Cr, LO	-
Axonopus affinis Chase	N		CR	Cr	-
Axonopus argentinus Parodi	N		CR	Cr, LO	A. Mailhos et al. 269 (MVFA)
Axonopus siccus (Nees) Kuhlm.	N		HC	Cr, LO, Sh	A. Mailhos et al. 181 (MVFA)
Axonopus suffultus (J. C. Mikan ex Trin.) Parodi	N		CR	Cr, LO, Sh	-
Bothriochloa laguroides (DC.) Herter	N		HC	Cr, LO	A. Mailhos et al. 176 (MVFA)
Bromidium tandilense (Kuntze) Rúgolo	N		TH	Sh	-
Bromus auleticus Trin. ex Nees	N		HC	Cr, LO	-
Chascolytrum lamarckianum (Nees) Matthei	N		HC	Cr, LO, Sh	-
Chascolytrum subaristatum (Lam.) Desv.	N		HC	Cr, LO	-
Cinnagrostis alba ssp. *tricholema* (Roseng., B.R. Arrill. & Izag.) P.M. Peterson, Soreng, Romasch. & Barberá	N		HC	Cr, LO, Sh	A. Mailhos et al. 268 (MVFA)
Cynodon dactylon (L.) Pers.	Ex-IAS		HC	Cr	-
Danthonia cirrata Hack. & Arechav.	N		HC	Cr, LO, Sh	-
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	N		HC	Cr, Sh	P. Izaguirre et al. (MVFA 18672)
Digitaria californica (Benth.) Henrard	N	Pr	CR	LO	P. Izaguirre et al. (MVFA 18672)
Digitaria sp.	N			Cr	-
Digitaria swalleniana Henrard	N		CR	LO	A. Mailhos et al. 214 (MVFA)
Eleusine tristachya (Lam.) Lam.	N		HC	LO	A. Mailhos et al. 113 (MVFA)
Elionurus muticus (Spreng.) Kuntze	N		HC	Cr, LO, Sh	-
Eragrostis airoides Nees	N		HC	Cr	A. Mailhos et al. 170 (MVFA)
Eragrostis bahiensis Schrad. ex Schult.	N		HC	Cr	A. Mailhos et al. 174 (MVFA)
Eragrostis lugens Nees	N		HC	Cr, LO	A. Mailhos et al. 175 (MVFA)
Eragrostis neesii Trin.	N		HC	Cr, LO	A. Mailhos et al. 203 (MVFA)
Eragrostis perennis Döll	N	Pr	HC	Cr, LO	A. Mailhos et al. 212 (MVFA)
Eragrostis polytricha Nees	N		HC	Cr, LO	A. Mailhos et al. 204 (MVFA)

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Eustachys retusa (Lag.) Kunth	N		HC	LO	A. Mailhos et al. 143 (MVFA)
Festuca australis Nees	N		TH	LO	-
Gymnopogon burchellii (Munro ex Döll) Ekman	N	Pr	HC	Cr	A. Mailhos et al. 220 (MVFA)
Jarava filifolia (Nees) Ciald.	N		HC	Cr, LO	A. Mailhos et al. 99 (MVFA)
Melica brasiliana Ard.	N		HC	Cr, LO	A. Mailhos et al. 314 (MVFA)
Melica rigida Cav.	N		HC	LO	A. Mailhos et al. 287 (MVFA)
Microbriza poimorpha (J. Presl) Parodi ex Nicora & Rúgolo	N		HC	Cr	-
Nassella filiculmis (Delile) Barkworth	N		HC	LO	A. Mailhos et al. 247 (MVFA)
Nassella megapotamia (Spreng. ex Trin.) Barkworth	N		HC	LO	A. Mailhos et al. 288 (MVFA)
Nassella melanosperma (J. Presl) Barkworth	N		HC	Cr	-
Nassella pauciciliata (Roseng. & Izag.) Barkworth	Re-Uy	Pr	HC	Cr	A. Mailhos et al. 241 (MVFA)
Panicum olyroides Kunth	N	Pr	HC	Cr, LO	A. Mailhos et al. 317 (MVFA)
Panicum peladoense Henrard	N	Pr	HC	Cr, LO	A. Mailhos et al. 139 (MVFA)
Paspalum guenoarum var. *guenoarum* Arechav.	N		HC	Cr, LO, Sh	A. Mailhos et al. 135 (MVFA)
Paspalum notatum Flüggé	N		HC	LO	A. Mailhos et al. 112 (MVFA)
Paspalum plicatulum Michx.	N	LC	HC	Cr, LO	B. Rosengurtt B7035 (MVFA)
Paspalum polyphyllum Nees ex Trin.	N		HC	Cr, LO, Sh	A. Mailhos et al. 197 (MVFA)
Paspalum quarinii Morrone & Zuloaga	N		HC	LO	A. Mailhos et al. 149 (MVFA)
Paspalum urvillei Steud.	N		HC	Cr	A. Mailhos et al. 225 (MVFA)
Piptochaetium lasianthum Griseb.	N		HC	LO	-
Piptochaetium montevidense (Spreng.) Parodi	N		HC	Cr, LO, Sh	-
Piptochaetium ruprechtianum E. Desv.	N		HC	LO	A. Mailhos et al. 285 (MVFA)
Piptochaetium stipoides (Trin. & Rupr.) Hack. ex Arechav.	N		HC	Cr	A. Mailhos et al. 226 (MVFA)
Poa lanigera Nees	N	LC	HC	Cr, LO	-
Poidium uniolae (Nees) Matthei	N		HC	Cr, Sh	A. Mailhos et al. 265 (MVFA)
Saccharum angustifolium (Nees) Trin.	N		HC	Cr	-
Schizachyrium glaziovii Peichoto	N		HC	LO, Sh	A. Mailhos et al. 136 (MVFA)
Schizachyrium microstachyum (Desv. ex Ham.) Roseng., B.R. Arrill. & Izag.	N		HC	Cr, LO, Sh	-
Schizachyrium salzmannii (Trin. ex Steud.) Nash var. *aristatum* (Hack.) Peichoto	N		HC	Cr, Sh	-
Schizachyrium spicatum (Spreng.) Herter	N		HC	Cr, LO, Sh	A. Mailhos et al. 248 (MVFA)
Schizachyrium tenerum Nees	N		HC	Cr, LO, Sh	A. Mailhos et al. 154 (MVFA)
Setaria parviflora (Poir.) Kerguélen	N		HC	Cr, LO	A. Mailhos et al. 177 (MVFA)
Setaria vaginata Spreng.	N		HC	LO	A. Mailhos et al. 290 (MVFA)
Sorghastrum pellitum (Hack.) Parodi	N		HC	Cr, LO	-
Sporobolus aeneus var. *angustifolia* (Döll) S. Denham & Aliscioni	N		HC	Sh	A. Mailhos et al. 261 (MVFA)
Sporobolus indicus (L.) R. Br.	N	LC	HC	LO	A. Mailhos et al. 147 (MVFA)
Steinchisma hians (Elliott) Nash	N		HC	Cr, LO	A. Mailhos et al. 179 (MVFA)
Trachypogon spicatus (L. f.) Kuntze	N		HC	LO, Sh	B. Rosengurtt B7016 (MVFA)
Tridens brasiliensis (Nees) Parodi	N		HC	Cr	A. Mailhos et al. 168 (MVFA)
Tripogonella spicata (Nees) P.M. Peterson & Romasch.	N		HC	LO	A. Mailhos et al. 213 (MVFA)

Appendix. (Continuation).

Family/Species	Origin	Conservation status	Lifeform	Formation	Voucher
Polygalaceae					
Monnina cuneata A. St.-Hil.	N		CH	Sh	E. Marchesi & I. Grela (MVFA 27090)
Polygala adenophylla A. St.-Hil. & Moq.	N		HC	Cr	A. Mailhos et al. 272 (MVFA)
Polygala brasiliensis L.	N		HC	Cr	A. Mailhos et al. 276 (MVFA)
Polygala linoides Poir.	N		HC	Cr	-
Polygala sp.	N			Cr	-
Polypodiaceae					
Pleopeltis lepidopteris (Langsd. & Fisch.) de la Sota	N		CR	LO	A. Mailhos et al. 126 (MVFA)
Primulaceae					
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult.	N		PH	Cr	M. Bayce et al. (MVFA 17238)
Pteridaceae					
Adiantopsis chlorophylla (Sw.) Fée	N		CR	Cr, LO	-
Doryopteris triphylla (Lam.) Christ	N		CR	LO	-
Rhamnaceae					
Colletia paradoxa (Spreng.) Escal.	N		NP	LO	-
Rubiaceae					
Borreria brachystemonoides Cham. & Schltdl.	N	Pr	CH	Cr, LO	A. Mailhos et al. 313 (MVFA)
Galianthe centranthoides (Cham. & Schltdl.) E.L. Cabral	N		HC	Cr, LO, Sh	A. Mailhos et al. 173 (MVFA)
Galianthe fastigiata Griseb.	N		HC	Cr, Sh	A. Mailhos et al. 169 (MVFA)
Galium atherodes Spreng.	N	Pr	CH	Cr, LO, Sh	A. Mailhos et al. 292 (MVFA)
Richardia humistrata (Cham. & Schltdl.) Steud.	N		CH	Cr, LO	-
Salicaceae					
Xylosma tweediana (Clos) Eichler	N		PH	LO	A. Mailhos et al. 131 (MVFA)
Selaginellaceae					
Selaginella sellowii Hieron.	N		HC	LO	A. Mailhos et al. 150 (MVFA)
Smilacaceae					
Smilax campestris Griseb.	N		CH	Cr, LO	A. Mailhos et al. 130 (MVFA)
Solanaceae					
Calibrachoa ovalifolia (Miers) Stehmann & Semir	N		CH	Cr, LO, Sh	A. Mailhos et al. 243 (MVFA)
Petunia integrifolia (Hook.) Schinz & Thell.	N		CH	Cr	-
Solanum commersonii Dunal	N		CR	Cr	-
Solanum pseudocapsicum L.	N		CH	LO	A. Mailhos et al. 140 (MVFA)
Thymelaeaceae					
Daphnopsis racemosa Griseb.	N		NP	LO	-
Urticaceae					
Parietaria debilis G. Forst.	N		TH	LO	-
Verbenaceae					
Glandularia thymoides (Cham.) N. O'Leary	N		CH	Cr	A. Mailhos et al. 302 (MVFA)
Lantana montevidensis (Spreng.) Briq.	N		CH	Cr, LO, Sh	A. Mailhos et al. 120 (MVFA)
Lippia coarctata Tronc.	En-RPG		HC	Cr	A. Mailhos et al. 185 (MVFA)
Lippia hieracifolia Cham.	N	Pr	CH	Cr, Sh	A. Mailhos et al. 164 (MVFA)
Verbena intermedia Gillies & Hook. ex Hook.	N		HC	Cr	A. Mailhos et al. 270 (MVFA)
Violaceae					
Pombalia parviflora (L. f.) Paula-Souza	N		TH	LO	-