BIOGEOGRAPHICAL STUDIES OF VENEZUELAN SPECIES OF *STYLOSANTHES* (LEGUMINOSAE)

Estudios biogeográficos de las especies venezolanas de *Stylosanthes* (Leguminosae)

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ABSTRACT

Stylosanthes is a mainly Neotropical genus comprising *ca.* 25 species with Venezuela hosting high species richness. Despite of the economic importance of some species as forage legumes, the biogeography of *Stylosanthes* in Venezuela has hitherto been poorly studied. Information of herbarium specimens and germplasm accessions was collated in order to assess distribution, range size, geographic species richness and rarity in the country. *Stylosanthes guianensis* has the widest geographical distribution and the largest range size. The highest species richness occurs in the eastern plains ("Llanos") (7-10° N, 62-65° W). The endemic *S. sericeiceps* and *S. venezuelensis* fall within the rarest category. This study contributes to better understand the pattern of biogeographical variation of Venezuelan *Stylosanthes* species, and can help to design conservation strategies.

Key words: distribution, Fabaceae, range size, rarity, species richness

RESUMEN

Stylosanthes es un género principalmente neotropical, encontrándose en Venezuela una considerable riqueza específica. A pesar de la importancia econó-

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mica de algunas especies como leguminosas forrajeras, la biogeografía de *Stylosanthes* en Venezuela ha sido poco estudiada. Información de herbarios y bancos de germoplasma fue recopilada para evaluar distribución, tamaño del área biogeográfica, riqueza específica y rareza. *Stylosanthes guianensis* tiene la distribución geográfica más amplia y ocupa la mayor área biogeográfica. La mayor riqueza específica se encuentra en los Llanos (7-10° N, 62-65° O). Dos especies endémicas, *S. sericeiceps* y *S. venezuelensis*, pertenecen a la categoría más rara. Este estudio contribuye a comprender los patrones de variación biogeográfica de las especies venezolanas de *Stylosanthes* y podrá asistir en diseñar estrategias de conservación.

Palabras clave: distribución, Fabaceae, rareza, riqueza específica, tamaño del área biogeográfica

INTRODUCTION

The legume *Stylosanthes* Sw. is a mainly Neotropical genus comprising *ca.* 25 species although estimates of up to 50 species exist in the literature (Klitgaard & Lavin 2005). Only *S. fruticosa* (Retz.) Alston (Africa, Asia), *S. erecta* P. Beauv. (Africa) and *S. sundaica* Taub. (Asia) have been reported outside the American continent (Nooteboom 1961; Mannetje 1984).

Stylosanthes species grow in different ecological environments (Stace & Edye 1984) and since some species have potential for improving low-input agricultural production systems, the genus has been the target of a number of germplasm collection missions oriented to the development of cultivars (Schultze-Kraft *et al.* 1984). Currently some species are used as forage and/or cover crop, and for land rehabilitation in sub-Saharan Africa, tropical Asia, tropical America and Australia (Chakraborty 2004).

South America is considered as the main center of diversity of *Stylosanthes* species (Stace & Edye 1984), Brazil and Venezuela being the countries with the highest *Stylosanthes* species richness. While 25 species have been reported for Brazil, mainly in the Central-West region (Costa & Ferreira 1984), there are 11 species in Venezuela, three of them being endemic to the country (Calles & Schultze-Kraft 2010).

Despite of the great diversity and the economic importance of the genus, the biogeography of *Stylosanthes* species in Venezuela has so far been poorly studied. Such information, however, is important for the design and implementation of conservation strategies. At present and as far as Venezuelan species are concerned, only a taxonomic revision of the genus is available (Calles & Schultze-Kraft 2010), but in that work the geographical distribution of species is restricted to the mention of the states where each species is reported to occur. During a recent endeavor to collect wild legumes in Venezuela (Guenni *et al.* 2006), the lack of geographical information about the genus was considered to be an important shortcoming.

Since natural ecosystems are increasingly affected by human activities, biologists contend that many plant species are pushed to the brink of extinction (*e.g*., McIntyre 1992). Particularly, species considered as rare are the main focus of conservationists, because of their preciousness and/or fragility of their populations (Rabinowitz *et al.* 1986), and the danger of extinction is, in general, esteemed higher for rare species than for others (Terborgh & Winter 1980; McIntyre 1992). However, developing a well-defined and meaningful concept of rarity is complex. For the present research, the classification proposed by Rabinowitz (1981) was chosen. It comprises attributes (*i.e.*, geographic range, habitat specificity, local population size) that are closely related to rarity itself.

For the sound management of biological diversity, including its conservation, a good understanding of the species' geographical distribution is needed. Consequently, the objectives of the research presented here were to: (1) document the natural geographical distribution and range size of Venezuelan *Stylosanthes*, (2) assess *Stylosanthes* species richness for Venezuela, and (3) determine their degree of rarity in the country.

METHODS

Geographical distribution and range size

Since insular Venezuela has been poorly surveyed, as far as *Stylosanthes* species are concerned, this study focuses on the Venezuelan mainland. Label information of a total of 910 herbarium specimens (for the

exsiccatae list the reader is referred to the electronic edition of Calles & Schultze-Kraft 2010) was collated in order to assess and document the distribution and range size of the genus in Venezuela. These herbarium specimens are held by 30 herbaria (abbreviations after Thiers 2008+) of which four are non-indexed (their abbreviations, in italics, are taken from Calles & Schultze-Kraft 2010): BM, CAR, *COJ*, CORO, G, GUYN, HERZU, *HMBLUZ*, HOH, IRBR, K, M, MER, MERC, MERF, MO, MY, MYF, NCSC, NY, P, PH, PORT, TFAV, UCOB, *UNET*, UOJ, US, *USB*, VEN. When georeferenced locations were not provided on herbarium specimen labels, they were identified using maps of the Venezuelan Servicio Autónomo de Geografía y Cartografía Nacional, whenever possible. However, 41.5% of the studied specimens were duplicates or their location could not be georeferenced based on the information on the herbarium labels. Consequently, only 532 specimens were used to plot the distribution and to calculate the range size.

Additional site information on Venezuelan *Stylosanthes* collections was obtained from the International Center for Tropical Agriculture (CIAT)'s forage germplasm (*i.e.*, seed) database and used to complement the information about geographical distribution and range size. The database was directly provided, as Excel format, by CIAT staff. In total, information from 416 germplasm accessions was used in this research. The respective species identifications were done by *Stylosanthes* experts during the germplasm collecting expeditions and/or later in plant introduction nurseries.

Information about collection sites (geographic coordinates) was plotted onto the Venezuelan map for biodiversity studies (Ferrer-Paris & Rodríguez 2010). In this map, the Venezuelan mainland is divided into 1345 grid cells of 15 × 15' latitude and longitude. Species range sizes were calculated, as proposed by Hunter (2005), by the number of grid cells occupied by each species, which in turn were expressed as percentages of the total number of grids covering the Venezuelan mainland. Maps presented in this study are only intended to show the geographical distribution of *Stylosanthes* species in Venezuela and there is no intention, so ever, to express an opinion about Venezuelan boundaries nor to interfere in any boundary dispute. For reference, a political map of the country, showing also the boundaries of the individual states, is provided (Fig. 1).

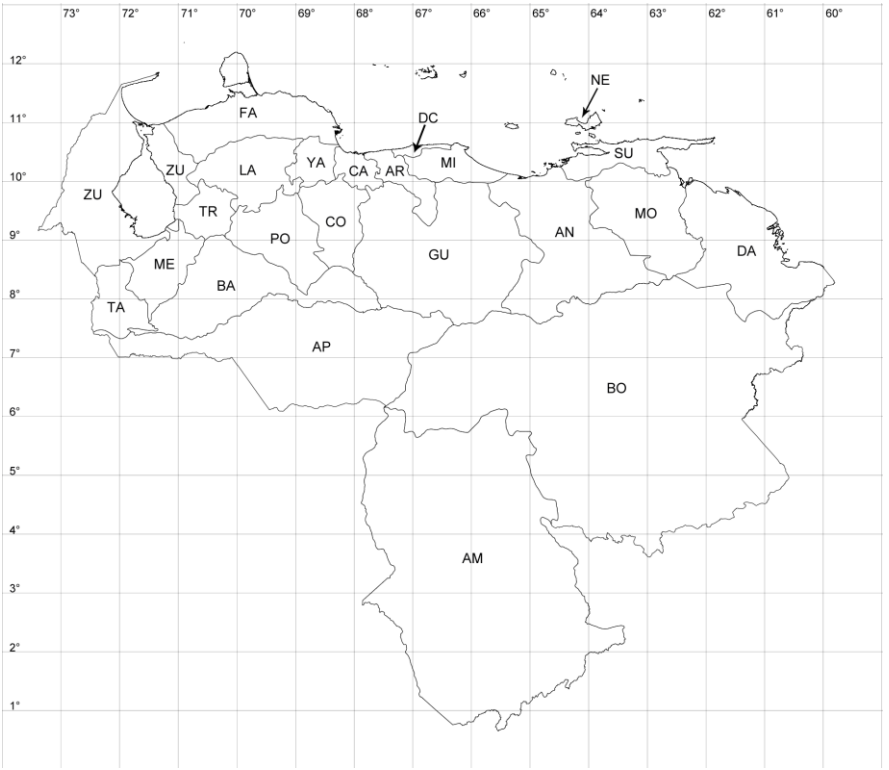

Fig. 1. Political map of Venezuela presenting the boundaries of the following states: Amazonas (AM), Anzoátegui (AN), Apure (AP), Aragua (AR), Barinas (BA), Bolívar (BO), Carabobo (CA), Cojedes (CO), Delta Amacuro (DA), Falcón (FA), Guárico (GU), Lara (LA), Mérida (ME), Miranda (MI), Monagas (MO), Nueva Esparta (NE), Portuguesa (PO), Sucre (SU), Táchira (TA), Trujillo (TR), Yaracuy (YA), Zulia (ZU) and the Distrito Capital (DC, including the state of Vargas which was created in 1998).

Geographical species richness

Richness of Venezuelan *Stylosanthes* species was obtained by overlaying maps of species distribution using the software ArcGIS Desktop 10 (education edition). The number of species within 1° latitudinal and longitudinal bands was obtained in order to correlate richness and geographic occurrence, using a non-linear regression (polynomial of degree three) (adapted from Hunter 2005).

Rarity classification

Rabinowitz (1981) developed a system to classify species rarity, based on three attributes: geographic range, habitat specificity and local population size. Different combinations of these attributes allow species to be classified into eight categories, *i.e.*, common species (non-rare) and seven forms of rarity. In the study presented here, this approach was used to classify the rarity of the 11 *Stylosanthes* species in the country. The geographic range was considered to be small if less than 1% of the grid cells were occupied by a species. Habitat was classified on the basis of herbarium label information and germplasm passport data and considered as restricted if the species was collected only in one vegetation type. Population sizes were designated as small or large based on observations during field trips.

RESULTS

Geographical distribution and range size

Geographical distributions of the *Stylosanthes* species in Venezuela are presented in Fig. 2-10. *Stylosanthes* species have a broad distribution and can be found in different vegetation types (*e.g.*, savannas, deciduous forests, xeric shrub-land; vegetation classification according to Huber & Alarcón 1988). Regarding annual total precipitation (ATP), the species occur at sites with an average ATP ranging from 935 to 1290 mm, with the exception of *S. falconensis* (570 mm only). In general, the length of the dry period (DP; here defined as number of months with less than 60 mm rainfall) is between 4.1 and 6.7 months; except for *S. falconensis* with a very long DP (8.0 months) and *S. sericeiceps* with a very short DP (2.6 months).

Stylosanthes guianensis has the widest geographical distribution (Fig. 2) and the largest range size, occupying 7.14% of all 15' grid cells (Fig. 11). The species occurs throughout the country, with high-density areas in eastern and western Venezuela. It is the only *Stylosanthes* species that has also been collected south of latitude 4° N. It is found on acid to neutral soils at a wide range of both elevations (10-1900 m asl) and vegetation types such as treeless and wooded savanna, and in clearings of deciduous, semi-deciduous and evergreen forests.

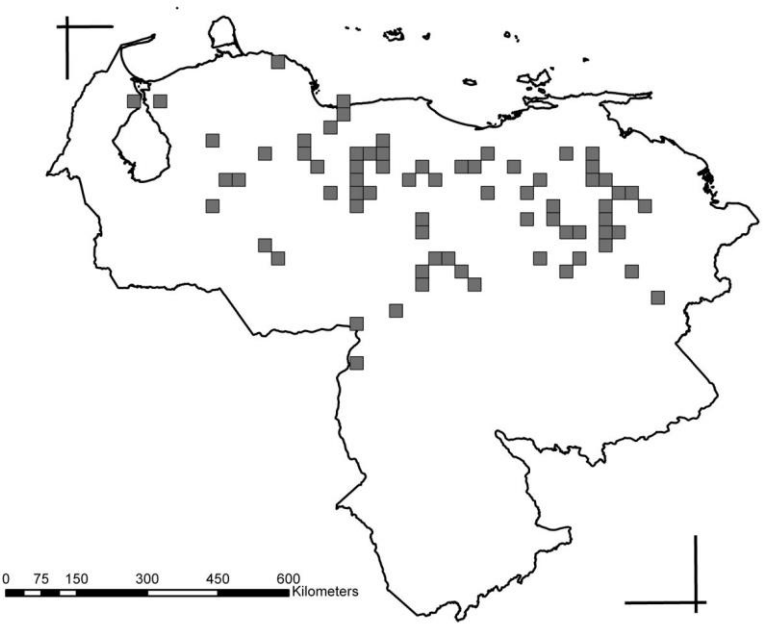

Fig. 2. Geographical distribution of *Stylosanthes guianensis* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

Stylosanthes gracilis is mainly distributed in eastern Venezuela (Fig. 3) with only a few collection sites in the western part of the country. The species has the second largest range size, occupying 6.47% of all 15' grid cells (Fig. 11). It is found at elevations of 15-1200 m asl and occurs mainly in treeless and wooded savanna. *Stylosanthes gracilis* has been collected in soils with pH between 4.2 and 6.

Stylosanthes humilis is mainly distributed throughout central Venezuela (Fig. 4), specifically in the plains ("Llanos"). It has also been collected in the foothills of the Andes and in coastal areas of north-western Venezuela. It occupies 4.83% of the grid cells (Fig. 11). The species occurs on acidic soils (pH 4.4-5.1) at elevations of 10-700 m asl, mainly in treeless and wooded savanna, but also in xerophytic forests and in clearings of deciduous and evergreen forests.

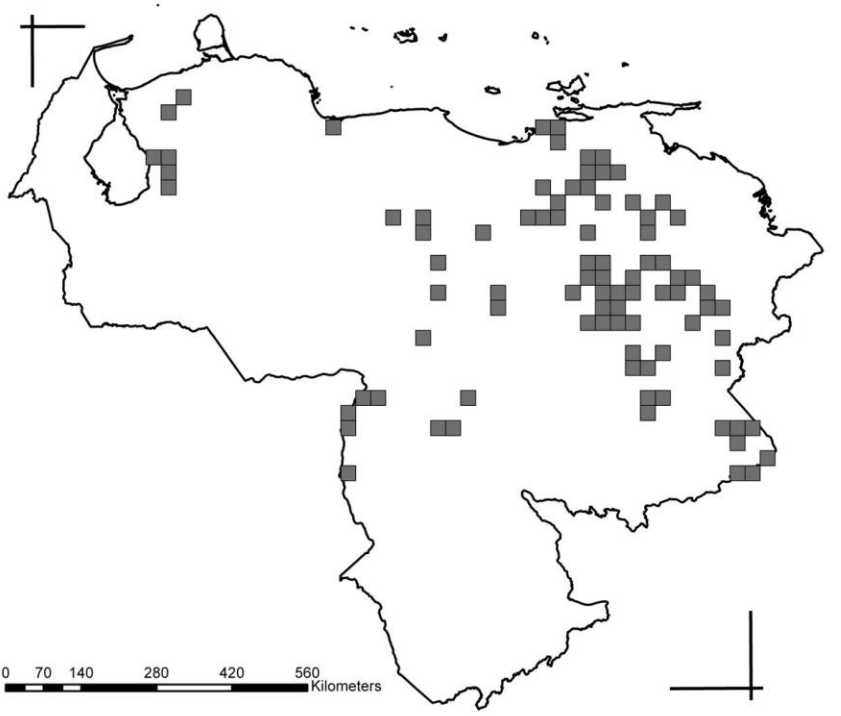

Fig. 3. Geographical distribution of *Stylosanthes gracilis* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

Stylosanthes viscosa is distributed in two areas that are isolated from each other (Fig. 5), with a major proportion of sites in eastern Venezuela and a minor proportion in western Venezuela. The species has a range size of 4.54% (Fig. 11). It is found at elevations of 0-725 m asl in treeless and wooded savanna, clearings of deciduous and evergreen forests and xeric shrub-land. *Stylosanthes viscosa* has been collected in soils with pH 4.5-6.2.

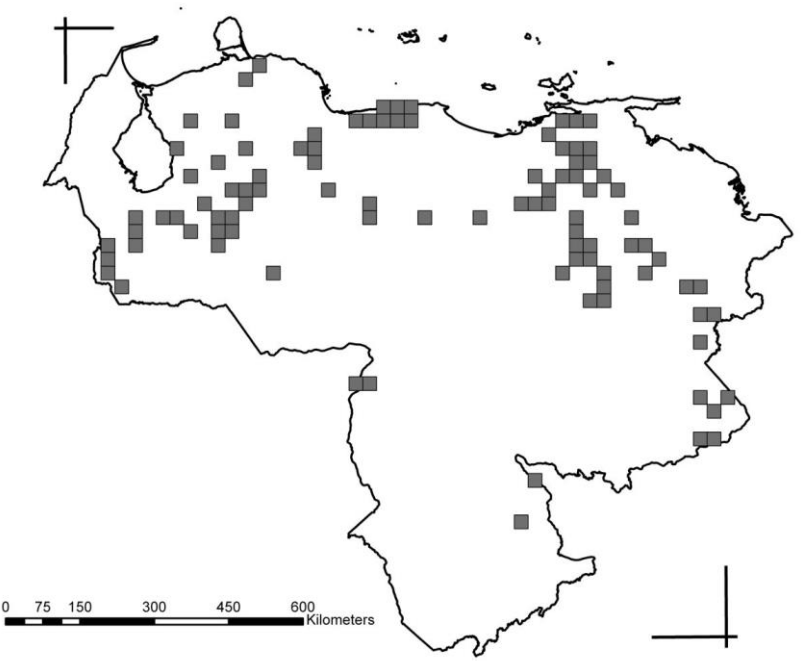

Fig. 4. Geographical distribution of *Stylosanthes humilis* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

Stylosanthes hamata is distributed throughout the coastal areas from north-western to north-central Venezuela, the Andes, the Eastern, Central and Western Llanos, and some coastal areas in north-eastern Venezuela (Fig. 6). It occupies 4.01% (Fig. 11) of the grid cells. The species found at elevations of 0-900 m asl in savanna, clearings of deciduous forests and coastal xeric and thorny shrub-land. It has been collected on soils with pH 5-7.5.

Stylosanthes scabra is distributed from the Andes to the Venezuelan Coastal Range (including both its eastern and western sections), with some collections originating also from the northern part of the Eastern, Central and Western Llanos (Fig. 7). The species has a range size of 3.49% (Fig. 11). It is found at elevations of 630-1200 m asl and occurs in savanna, xeric shrub-land and clearings of deciduous and evergreen forests, on soils with pH 4.3-7.3.

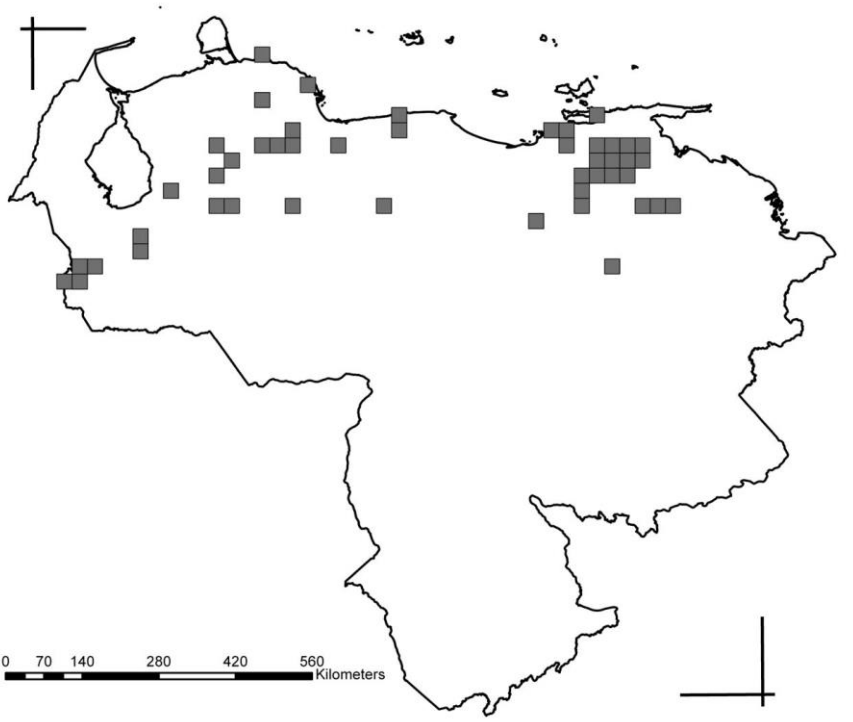

Fig. 5. Geographical distribution of *Stylosanthes viscosa* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

Stylosanthes capitata is mainly distributed in the Eastern Llanos (Fig. 8); a few collections were made in the Central Llanos. It occupies 1.78% of the grid cells (Fig. 11). This species is mainly found at low elevations (10-300 m asl) in savanna environments on very sandy, acid soils where it occurs in mostly small populations.

Stylosanthes angustifolia is mainly distributed in central Venezuela, *i.e.*, the Central Llanos (Fig. 9); a few collections are from the Eastern Llanos. The species has a range size of 1.34% (Fig. 11). It is found at elevations of 30-290 m asl and occurs in treeless and wooded savanna and in the ecotone of savanna-deciduous forest. *Stylosanthes angustifolia* has been collected on acid soils (pH 4.2-5.6).

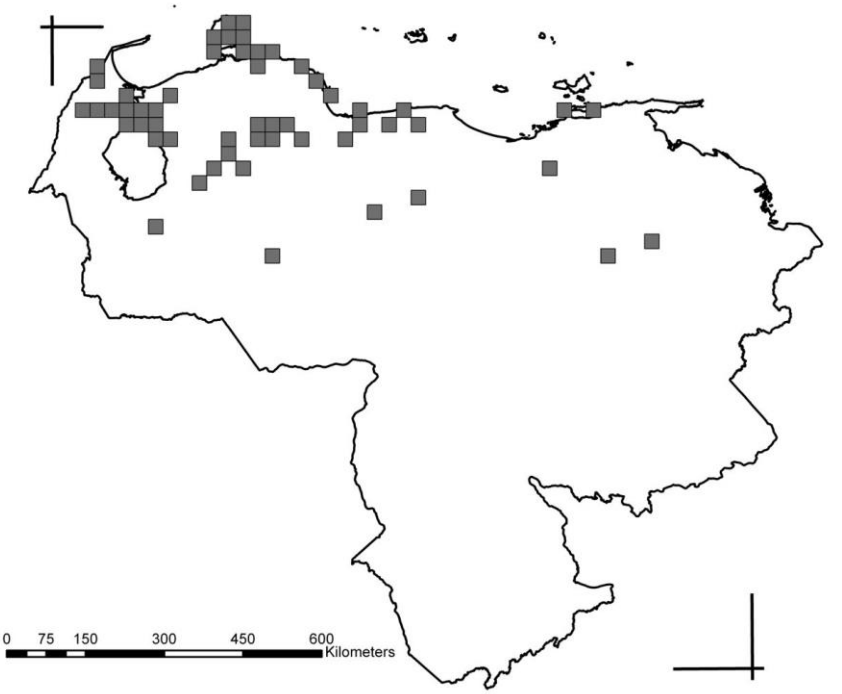

Fig. 6. Geographical distribution of *Stylosanthes hamata* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

The endemic species, *Stylosanthes falconensis*, *S. sericeiceps* and *S. venezuelensis*, have very restricted geographical distributions (Fig. 10), confined to mountain areas. They occupy less than 0.2% of the grid cells (Fig. 11). *Stylosanthes falconensis* occurs only in the San Luis Mountain Range (State of Falcón) at elevations of 900-1200 m asl and has been reported from open areas of low-montane deciduous dry tropical forest. It has been collected on neutral to slightly alkaline soils (pH 7.1-7.7). *Stylosanthes sericeiceps* occurs only in the Andes (some spots in the state of Mérida) at elevations of 500-2500 m asl and has been reported from xeric shrub-land. It has been collected on soils with pH 5.5-7.5. *Stylosanthes venezuelensis* occurs only in the Coastal Range, in the vicinity of Caracas, at elevations of 900-1000 m asl in clearings of semi-deciduous forest. It has been collected on soils with pH 7.3.

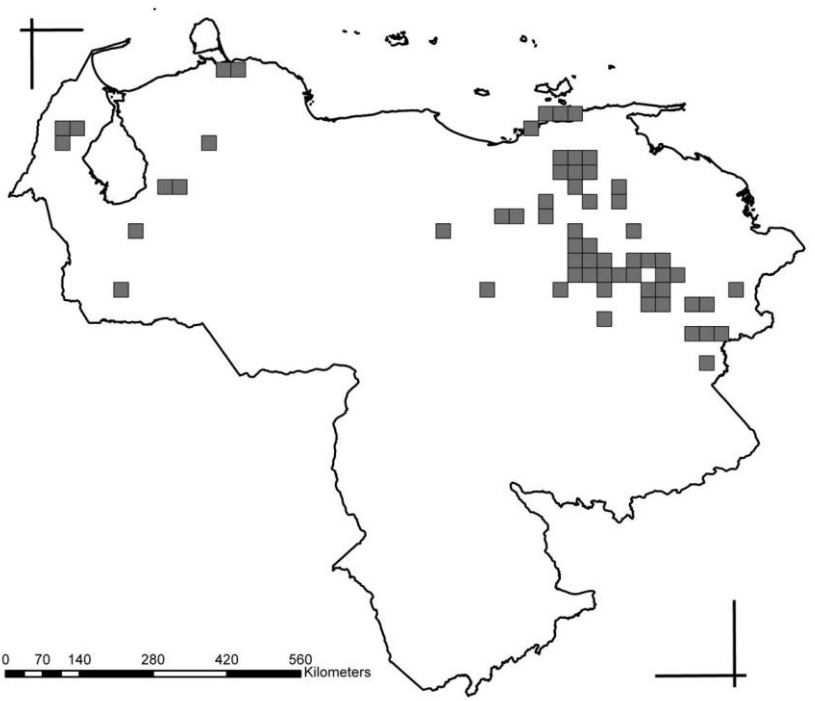

Fig. 7. Geographical distribution of *Stylosanthes scabra* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

Geographical species richness

Based on the information compiled from herbarium specimens and germplasm accessions, the distribution of *Stylosanthes* species extends essentially over the whole country (Fig. 12). However, in southern Venezuela, this genus occurs only sparsely. Furthermore, the absence of *Stylosanthes* species in the extreme east of Venezuela, including Paria Peninsula and the easternmost coastland, is noteworthy. Nevertheless, it is the eastern part of Venezuela (comprising most of the sandy savanna environments) where the highest species richness is found (up to seven species per grid cell).

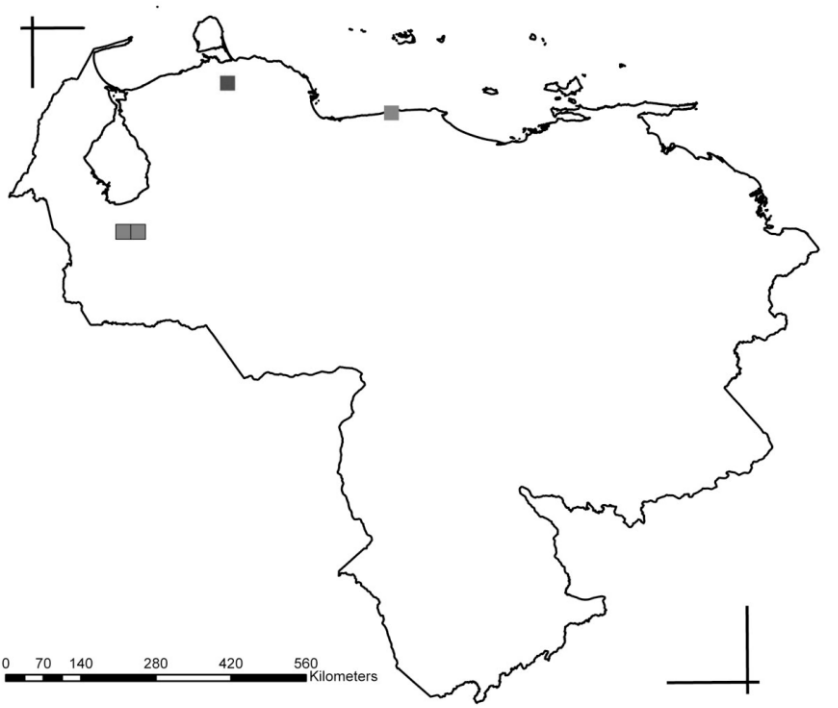

Fig. 8. Geographical distribution of *Stylosanthes capitata* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

Regarding the relationship between richness and both latitude and longitude, the highest richness is found between 7 and 10° latitude North (R2 = 0.981), and between 62 and 65° longitude West (R2 = 0.454).

Rarity classification

Stylosanthes guianensis, *S. hamata*, and *S. humilis* have a wide geographical distribution and are found in different environments and in large populations. Consequently, they are to be considered as non-rare species according to Rabinowitz (1981) (Table 1). The remaining Venezuelan *Stylosanthes* species classify as rare. Only two species fall within the rarest category, namely, *S. sericeiceps* and *S. venezuelensis* (Table 1).

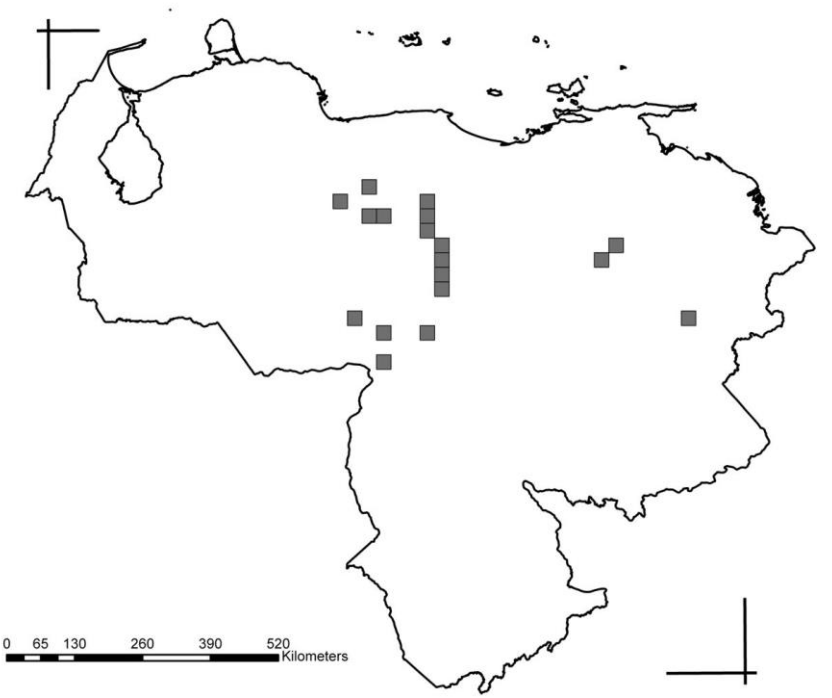

Fig. 9. Geographical distribution of *Stylosanthes angustifolia* depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

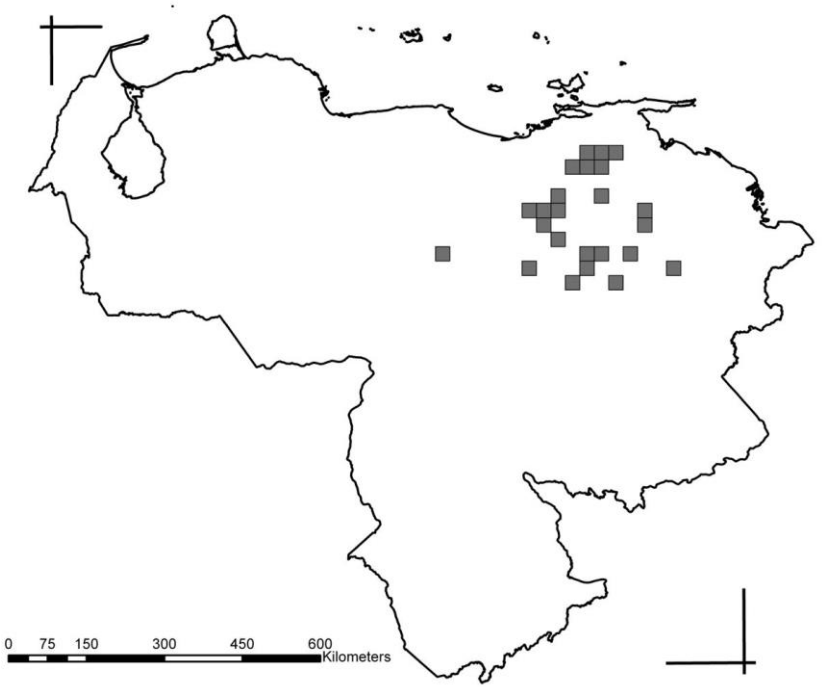

Fig. 10. Geographical distribution of *Stylosanthes falconensis* (red), *S. sericeiceps* (grey) and *S. venezuelensis* (green) depicted by means of 15 × 15' latitude and longitude grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

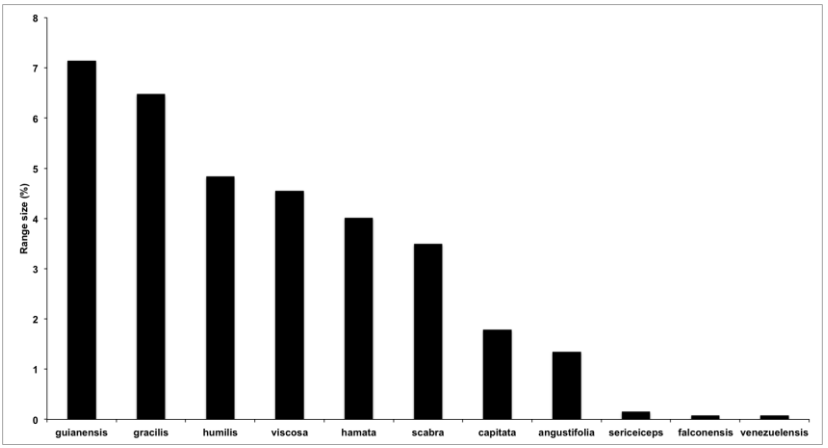

Fig. 11. Range size of Venezuelan *Stylosanthes* species. Bars indicate the percentage of 15 × 15' grid cells occupied by each species. The whole of mainland Venezuela is covered by 1345 grids.

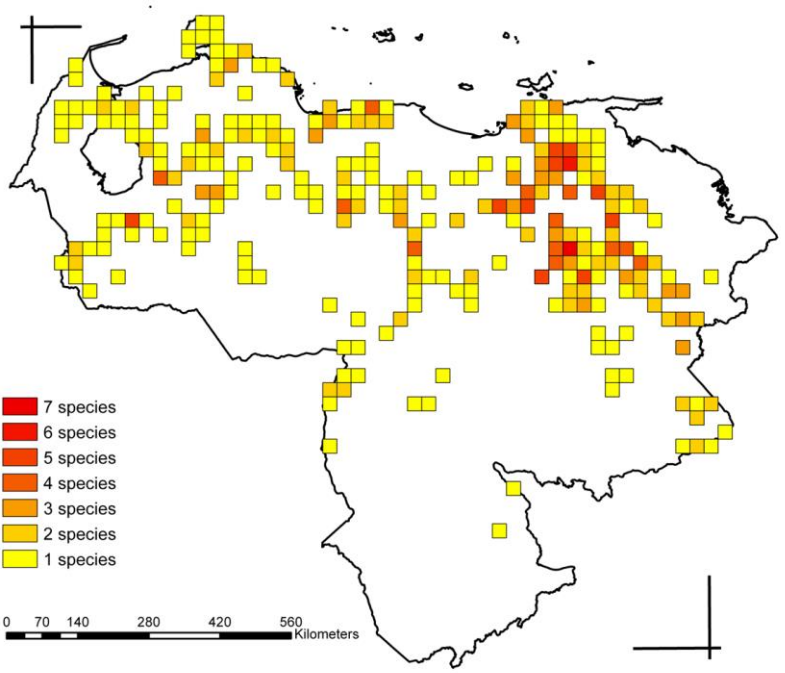

Fig. 12. Richness of *Stylosanthes* species in Venezuela, depicted by 15 × 15' grid cells. Perpendicular lines indicate longitude 73° W and latitude 12° N (left top corner) and longitude 61° W and latitude 1° N (right bottom corner).

Table 1. Rarity classification of Venezuelan *Stylosanthes* species after Rabinowitz (1981).

Geographical distribution	Large		Small	
Habitat specificity	Broad	Restricted	Broad	Restricted
Local population size				
Large	*S. guianensis* *S. hamata* *S. humilis*	*S. gracilis*		*S. falconensis*
Small	*S. scabra* *S. viscosa*	*S. angustifolia* *S. capitata*		*S. sericeiceps* *S. venezuelensis*

*Grey intensity indicates increases in rarity level, with white referring to non-rare species (*S. guianensis*, *S. hamata*, *S. humilis*) and the darkest grey to the rarest species (*S. sericeiceps*, *S. venezuelensis*).

DISCUSSION

Geographical distribution and range size

Venezuela covers an area of almost one million km^2 where more than 600 vegetation types have been described in an existing variety of topographic conditions (Huber & Alarcón 1988; MARN 2000). However, since the largest distance within one grid cell is 28 km, our results are based on the assumption that there is no major vegetation and topography variation within a given grid cell.

In general, *Stylosanthes* species are distributed throughout the whole country, with *S. gracilis*, *S. guianensis* and *S. humilis* having the widest distribution and the largest range sizes. In contrast, *S. sericeiceps*, *S. falconensis* and *S. venezuelensis* have very restricted distributions and small range sizes. Only few *Stylosanthes* herbarium specimens and germplasm accessions are known from the states of Amazonas, Apure and Delta Amacuro. Since Amazonas and Delta Amacuro had been systematically surveyed by botanists (Steyermark *et al.* 1995–2005), the natural distribution of the genus probably does not extend to these states, Amazonas being characterized mainly by forest cover and Delta Amacuro mainly by flooded areas. In the case of Apure, the lack of records could be due to both the absence of the species (the state is characterized by extended areas under seasonal flooding and severe drought due to local soil conditions) and/or few botanical surveys and germplasm collecting activities in the past. As far as the endemic species, *S. falconensis*, *S. sericeiceps* and *S. venezuelensis*, are concerned, only a small number of herbarium specimens have been collected as yet; therefore, information about their natural distribution may be improved by further plant explorations.

Biogeography studies are largely based upon herbarium specimens. However, the inclusion of data from germplasm collection missions, in which herbarium specimens are only rarely collected, may considerably increase the information about a species' geographical distribution. This was shown by Guenni *et al*. (2006) and discussed for *Stylosanthes* in Venezuela by Calles *et al.* (2016). In this context, it is important to take into account that germplasm collecting missions are often conducted along roads that may favor those species that have a particular colonizing potential.

Geographical species richness

The relationship between richness and both latitude and longitude shows that richness of *Stylosanthes* species in Venezuela is centered between 7 and 10° latitude North and 62 and 65° longitude West. This area is characterized by low elevations, sandy and very acid soils, specifically in the eastern savannas (states of Anzoátegui, Monagas and north-eastern Bolívar), suggesting that *Stylosanthes* species might have diversified in such environmental conditions and therefore a large number of species are adapted to it. This also supports the hypothesis of Stace & Cameron (1984) that *Stylosanthes* species originate in open lowland areas. In the case of Venezuela, these natural environments are represented by habitats such as well-drained seasonal savannas with isolated trees, savanna-forest ecotones and open deciduous forests. Additionally, the particular richness in this area may also indicate that the region is a center of diversification of the genus.

Raising of the Andes may have fragmented ecosystems leading to the development of new niches and disruption of gene flows by creating new topographic barriers (Cox & Moore 2000). Thus, isolated *Stylosanthes* populations might have been driven into further diversification. This is supported by the fact that all endemic species occur at elevations above 950 m asl.

IMPLICATIONS FOR CONSERVATION

In view of the use potential of a number of Venezuelan *Stylosanthes* species (Calles *et al.* 2016), conservation of *Stylosanthes* species should be considered because in many cases their natural habitats are being rapidly converted into agricultural land (Guenni *et al.* 2006). Though loss of habitat does not necessarily imply the eventual extinction of a species, it is definitely the cause of reduction of genetic diversity.

None of the Venezuelan *Stylosanthes* species has yet been included in the Red List of the Venezuelan Flora (Llamozas *et al.* 2003). However, the endemic *Stylosanthes* species are classified as very rare according to the criteria of Rabinowitz (1981): for *S. falconensis* and *S. sericeiceps* it is estimated that, based on field observations, the area of occupancy is less than 500 km2 with less than five populations per species.

Furthermore, habitat quality is prone to decline due to urban expansion (*S. sericeiceps*) and intensification of agricultural activities (*S.*

falconensis). Consequently, according to the IUCN (2001) criteria, both taxa are to be considered as endangered [category B2a + B2b(iii)]. Regarding the third endemic species, *S. venezuelensis*, its area of occupancy is less than an estimated 100 km2 and a continuous decline of the number of mature individuals has been observed in the last years. Therefore, and according to the IUCN (2001) criteria, this taxon is to be considered as critically endangered [category B1a + B1b(v)].

This biogeographical study may contribute to better understand the pattern of variation of Venezuelan *Stylosanthes* species. The new knowledge should be used as a basis for designing conservation strategies for the genus. Furthermore, by providing evidence about the three endemic species being endangered, it contributes to drawing the attention to the need of concrete measures to conserve diversity within an important genus.

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