Eriocaulaceae in the Brazilian Amazon and the use of Species Distribution Modelling in its conservation

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Abstract

Following a survey in herbaria in Brazil and abroad, complemented by a survey of the literature and searches of biodiversity data, 66 taxa of Eriocaulaceae have been identified in the Brazilian Amazon, as defined by the states of Acre, Amapá, Amazonas, Pará, Rondônia and Roraima. Six genera of Eriocaulaceae were found in the Amazon with the following taxon numbers: *Comanthera* (3 taxa), *Eriocaulon* (10), *Paepalanthus* (15), *Rondonanthus* (2), *Syngonanthus* (35) and *Tonina* (1). Of this total, 25 taxa present distributions in the states of the Amazon and other Brazilian states (considered as widely distributed) and the remaining 41 taxa are restricted to the Amazon Rainforest biome. The distribution data for 31 species were used for Species Distribution Modelling, due to the low number of occurrence points reported for the other taxa, 17 of those are known from a single location. The overlap of these models indicates areas from Amapá, Amazonas, Pará and Roraima where modelled species are most likely to occur. These data can further contribute to the location of new populations of species of Eriocaulaceae. New detection of Eriocaulaceae species can assist in filling the gaps on their geographic distribution and ecology, contributing to the protection or restoration of priority areas set aside for their conservation.

Key words: geographical distribution, species conservation, potential geographic distribution modeling.

Resumo

Com base em espécimes de herbários do Brasil e exterior, complementado pela literatura pertinente e buscas em sites de biodiversidade, foram identificados 66 táxons de Eriocaulaceae para a Amazônia brasileira, definida pelos estados do Acre, Amapá, Amazonas, Pará, Rondônia e Roraima. Seis gêneros de Eriocaulaceae foram encontrados na Amazônia com os seguintes números de táxons: *Comanthera* (3 táxons), *Eriocaulon* (10), *Paepalanthus* (15), *Rondonanthus* (2), *Syngonanthus* (35) e *Tonina* (1). Desse total, 25 táxons foram considerados como de distribuição ampla e os restantes 41 táxons são restritos ao bioma Floresta Amazônica. Os dados de distribuição para apenas 31 táxons foram utilizados para Modelagem de Distribuição de Espécies, devido ao baixo número de pontos de ocorrência reportados para os outros táxons, 17 dos quais conhecidos de uma só localidade. A sobreposição desses modelos mostrou áreas do Amapá, Amazonas, Pará e Roraima como tendo maior probabilidade de ocorrência para as espécies modeladas. Os dados obtidos permitirão a localização de novas populações das espécies de Eriocaulaceae. Novas detecções das espécies de Eriocaulaceae podem ajudar a preencher as lacunas sobre sua distribuição geográfica e ecologia, contribuindo para a proteção ou restauração de áreas prioritárias para sua conservação.

Palavras-chave: distribuição geográfica, conservação de espécies, modelagem de distribuição geográfica potencial.

Introduction

The Eriocaulaceae is a pantropical family of around 1,400 species placed in 10 genera (Giulietti *et al.* 2012a). Molecular studies corroborated by morphological data show two well-supported lineages: Eriocaulaceae subf. Eriocauloideae, which includes the genera *Eriocaulon*, with about 500 species and a pantropical and subtropical distribution, and *Mesanthemum*, with about 15 species restricted to Africa. Eriocaulaceae subf. Paepalanthoideae includes the remaining eight genera, which, apart from the North American *Lachnocaulon*, occur

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mainly in South America (Andrade *et al.* 2010; Giulietti *et al.* 2012a). Giulietti & Hensold (1990) have commented that the Paepalanthoideae have two centers of diversity, the main being in the mountains of Central Brazil, especially in the Espinhaço range in Minas Gerais and Bahia, and the other in the mountains of Northern South America, especially in Venezuela, where eighty eight species in six genera occur (Hensold 1999). In Paepalanthoideae the main genera are *Paepalanthus* with 500 species (Trovó *et al.* 2013) and *Syngonanthus* with 150 species (Echternacht *et al.* 2014), which occur predominantly in South America, but with some species in North and Central America, the Caribbean and also in Africa. The monotypic genus *Tonina* has a Neotropical distribution, and the remainder: *Actinocephalus*, *Comanthera*, *Leiothrix*, and *Rondonanthus* are restrict to South America, this last being restricted to the very North of the continent (Ruhland 1903; Giulietti & Hensold 1990; Hensold 1999; Parra *et al.* 2010; Andrade *et al.* 2010; Giulietti *et al.* 2012a; Trovó *et al.* 2013; Echternacht *et al.* 2014).

In Brazil, there are 625 species in eight genera, occurring in all regions and biomes of the country (BFG 2015). The main center of diversity of the family in the country is situated in the upper parts of the mountains that compose the Espinhaço range in the states of Minas Gerais and Bahia, associated with "campo rupestre" vegetation. The other species occur in lakes and fresh water lagoons, especially species of *Eriocaulon*, in other mountains not associated with the Espinhaço range, in "cerrado" vegetation and in coastal dunes ("restingas") (Giulietti & Pirani 1988; Giulietti & Hensold 1990; Giulietti *et al.* 1997; Echternacht *et al.* 2011; Hensold *et al.* 2012; Trovó *et al.* 2015).

The Eriocaulaceae possess very small unisexual flowers with white scarious sepals and petals, which are grouped in compact monoecious capitula at the end of a scape. The scapes, with the capitula and flowers, when detached from the rest of the plant, continue to appear living, from which the popular names of "everlasting plants", or in Brazil "sempre-vivas", originate. Because of their beauty, the scapes and capitula are collected and sold as decoration in the house, and has resulted in an intensive extractive industry (Giulietti *et al.* 1988, 1996; Oliveira *et al.* 2015).

Also, a large proportion of the species of Eriocaulaceae are considered to be rare or endemic to a small area. Giulietti *et al.* (2009) lists 109 species of the family as rare, nine of which are restricted to

the Amazon Rainforest biome. The high level of endemism in the Eriocaulaceae is often mentioned, especially for the Espinhaço range, where most studies have been concentrated (Giulietti & Hensold 1990; Giulietti *et al.* 1997). Echternacht *et al.* (2011) lists 77 species of the genera *Actinocephalus*, *Comanthera* e *Paepalanthus* for the Espinhaço range of Minas Gerais. This high level of endemism of Eriocaulaceae in the Campo Rupestre, certainly contributes to the position that this vegetation type supports the highest level of endemism in the country: There are 1,951 endemic species, 39.6% of the 4,928 listed (BFG 2015). In the "Livro Vermelho da Flora do Brasil" 12 species of Eriocaulaceae are listed as threatened, and are defined particularly by the high level of endemism, and for two species on account of their commercial importance in the trade of Everlasting Flowers (Martinelli & Moraes 2013). These same species were listed in Decree no. 443 of the Ministry of the Environment of Brazil, which included no Eriocaulaceae from Amazonia (MMA 2014). Regarding projects involving the conservation of Eriocaulaceae, an Action Plan for the Conservation of "Sempre Vivas" is currently being developed, initially focusing on 20 species from the Espinhaço range, of which five are of concern, due to the high level of commercial extraction, and 15 due to their very local endemism (MMA 2015).

BFG (2015) notes that, of the five other Brazilian biomes, the Amazon Rainforest biome showed the least increase in the number of new species since the original "Catálogo das Espécies do Brasil" (Forzza *et al.* 2010) was published, and which showed a decrease in the number of endemic species in the biome. The authors consider that this situation is due to the relatively very small number of scientific plant collections made in the Northern Region of Brazil, in relation to its size.

Our knowledge of the Eriocaulaceae of Amazônia is extremely fragmented and based on very few published works, of which could be mentioned: Koernicke (1863), who mentions 17 species for the Brazilian Amazon, based primarily on collections made by Spruce and Schomburgk. Ruhland (1903) who increased this number to 20, mostly including species of *Paepalanthus* ser. *Leptocephali* Ruhland and of *Syngonanthus*. The most important work published on the Eriocaulaceae of Amazonia was by Hensold (1999), who accounts for 88 species for the Flora of the Venezuelan Guayana. Also, various species were described by Moldenke and Herzog from the region (see Results and Appendix 1).

More recently, studies of Amazonian species involving both phylogenetic and taxonomic research are now under way, and these continue lines of research already published: Hensold & Giulietti (1991) for *Rondonanthus*, Parra *et al.* (2010) for *Comanthera*, Giulietti *et al.* (2012b) for *Philodice*, Echternacht *et al.* (2014, 2015) and Watanabe (2015) for *Comanthera* and *Syngonanthus*.

At the start of 2005, the first author received a request from Dr. Ricardo Secco, then the Curator of the Herbarium at the Museu Paraense Emilio Goeldi (MG), to determine the large number of still unidentified specimens of Eriocaulaceae collected in Amazonia, which were held there. This material was sent directly to the Royal Botanic Gardens of Kew (K), where the first author was carrying out her post-doctoral studies, engaged in a study of type material of Eriocaulaceae held in European herbaria. The process of identifying the specimens from MG herbarium was the start of a study of Amazonian material with a view to producing a list of Eriocaulaceae of the region. In spite of the relatively large number of species, which were recorded from the Amazon Rainforest biome of Brazil, a large proportion of these was poorly known and restricted to the type material or very few other collections.

The objectives of the present work are to present a preliminary list of Eriocaulaceae species occurring in the Brazilian Amazon and to determine potential occurrence areas using known distributional data of Amazonian Eriocaulaceae using Species Distribution Modelling. The results obtained and the discussion presented in this paper should make possible the discovery and collection of new populations of rare or little-known species. This will contribute to the filling of gaps in our understanding of the family in the Amazon biome and provide data to aid their conservation.

Material and Methods

Elaboration of the list of Eriocaulaceae species

As referred in the Introduction, the curator of the herbarium MG sent a loan of the material to K for studies of Giulietti, A.M. in 2005. The initial examination of these specimens, followed by subsequent visits to herbaria in Rio de Janeiro (RB) and Manaus (INPA), demonstrated the rich taxonomic diversity of the Eriocaulaceae in the Amazon region, with a species number much greater than the 20 species originally proposed by Ruhland (1903). From there arose an interest to develop a list of species from the Brazilian Amazon, as a first step towards a better understanding of their diversity (Appendix 1).

The six core Amazonian states: Acre, Amapá, Amazonas, Pará, Roraima, and Rondônia, were selected to provide data for the elaboration of the list of taxa (Appendix 1). The North of Mato Grosso state and the North-western of Tocantins, in spite of now being form of the Amazon Rainforest biome, were not included in this study, because of our very sparse understanding of the Eriocaulaceae of these areas. Visits were also made to study the collections of a number of Brazilian and foreign herbaria, especially for type material: B, BM, E, F, HBG, K, INPA, M, MG, NY e RB (acronyms according Thiers [continuously updated]). These data were complemented with those from the taxonomic bibliography of Koernicke (1863), Ruhland (1903) e Hensold (1999), as well as those of *Rondonanthus* (Hensold & Giulietti 1991), *Philodice* (Giulietti *et al.* 2012b), *Comanthera* subg. *Comanthera* (Parra & Giulietti 2010) and *Comanthera* subg. *Thysanocephalus* (Echternacht *et al.* 2015). Special attention was paid to the protologues of the species, principally those described by Herzog and Moldenke, referred in the Appendix 1.

Development of the Species Distribution Modelling

We used Species Distribution Modeling (SDM) (Franklin 2009) to detect potential occurrence areas of Eriocaulaceae. We selected the eight least correlated environmental variables from an original dataset of 20 variables (following Aguirre-Gutierrez 2013; Giannini *et al.* 2015) provided by Worldclim website (Hijmans *et al.* 2005), which were based on temperature and precipitation averages obtained from meteorological stations around the world for the last 50 years. The eight variables (with a resolution of 5 arc-minute) were Annual Mean Temperature; Isothermality; Max Temperature of Warmest Month; Min Temperature of Coldest Month; Mean Temperature of Driest Quarter; Precipitation of Wettest Month; Precipitation of Wettest Quarter; and Precipitation of Coldest Quarter. Altitude was excluded from the remained eight variables due to its high correlation. We did not include any other variable besides climate (such as soil, for example) due to the lack of such information with high resolution covering all the studied area.

The Maximum Entropy algorithm (Maxent - Philipps *et al*. 2006) was used to perform SDM because it is especially useful for species that contain low known number of occurrence points and also, because it requires only presence points (and not absence points, as the case of other algorithms) (Wisz *et al*. 2008). We used 20% of occurrence points (randomly sampled by the Maxent program) to perform an internal test aiming to estimate the Area Under Receiver-Operating Curve (AUC). AUC varies from 0–1 and values near to 1 indicate good accuracy (Stockwell *et al*. 2002).

Aiming to define the complete known species geographical distribution, especially of those occurring outside the Amazon Rainforest biome, we used the data included in the Appendix 1 and complemented it with species occurrence data from speciesLink biodiversity data provider (<http://splink.cria.org.br>). From the 66 selected species of Eriocaulaceae, only 31 presented more than 10 occurrence points and were modelled. Draft maps of each species were firstly plotted on the speciesLink website and visually checked, aiming to detect erroneous data (such as points occurring on water bodies) and, after that, the data were corrected using ArcGIS (Esri Inc.).

At the end of SDM procedure, all the obtained models for each species (31 models) were normalized, that is, we standardized the scale of probability of each model to vary from 0–1. After that, all the obtained models (31 models) were united in one final model. We did this aiming to show the areas with the highest probability of occurrence of the studied species. This final model was normalized again, but we rescaled it to vary from 0–100% of occurrence probability. For all these procedures, we used the 'raster' package (Hijmans 2014) for R (R Development Core Team. 2011). Finally, we plotted this final model as a map using ArcGIS (Esri Inc.).

Results

For Eriocaulaceae 66 taxa were identified from the Brazilian Amazon Rainforest biome, including the following genera, with their respective number of species and varieties: *Comanthera* (3 species), *Eriocaulon* (10 species), *Paepalanthus* (13 species and 2 varieties), *Rondonanthus* (2 species), *Syngonanthus* (30 species and 5 varieties) and *Tonina* (1 species) (Tab. 1, Appendix 1). Of the six taxa at varietal level, five were described from the Brazilian Amazon: *Paepalanthus piresi*

var. *piresi*, *P. piresi* var. *villosus*, *Syngonanthus bracteosus* var. *scrupulosus*, *S. egleri* var. *egleri* and *S. egleri* var. *pomboensis*. Of special interest is the presence of *Rondonanthus* only in this region of Brazil, and the proportionally high representation of species of *Eriocaulon* with 17.5% of the 57 reported from all Brazil and *Syngonanthus* with 37% of the 94 species reported (BFG 2015).

From the total of taxa surveyed, 24 species and two varieties were found to have a wide geographical distribution within the six Amazonian states in Brazil, elsewhere in other Brazilian biomes, and also outside the country. All the 42 remaining taxa have distributions restricted to the Amazon Rainforest biome, with 21 species and one variety presenting a wider distribution within the biome, extending to other areas outside Brazil. The remaining 14 species and four varieties are each restricted to a single locality within the biome (Tab. 1; Appendix 1).

It was possible to generate potential distribution models for only 30 species and one variety, of which 19 species and one variety are of wide distribution, and 12 species are restricted to the Amazon Rainforest biome (Appendix 2). All models presented an AUC of over 0.8, suggesting results of a good quality.

We draw attention to the following models as examples which display a pattern of wide distribution, represented by *Comanthera xeranthemoides*, *Syngonanthus gracilis*, and *S. nitens* (Fig. 1) and those models with a distribution pattern restricted to the Amazonian Forest, represented by *Eriocaulon tenuifolium*, *Paepalanthus fasciculatus* and *Syngonanthus fenestratus* (Fig. 2).

Bringing together all the models obtained, two distinct groups were encountered for the geographical distribution of species of Eriocaulaceae of the Brazilian Amazon: 1 - including species of wide distribution, some with a northern limit in Central America and reach along the coastal dunes ("restingas") via Maranhão and North-east Brazil as far as the southern limits of the tropics. 2 - Including the species whose occurrence is more concentrated in Amazonia, extending westwards as far as Mato Grosso state, or to the South-east via Tocantins and Goiás states. The modelling pattern of all species confirms that the major probability of species occurrence is within the Amazonian Rainforest and Cerrado biomes (Fig. 3). In Amazonia, the state of Pará (principally eastern and south-eastern areas) and the eastern region of Amapá, Amazonas

Table 1 – List of Eriocaulaceae species recorded for the Brazilian Amazon Rainforest Biome (states of Acre, Amazonas, Amapá, Pará, Roraima and Rondônia).
Tabela 1 – Lista de espécies de Eriocaulaceae registradas para o Bioma Floresta Amazônica Brasileira (estados do Acre, Amazonas, Amapá, Pará, Roraima e Rondônia).

Genus	Species	Variety	Scientific Name Authorship	Distribution Widespread	Distribution concentrated in the Amazon Rainforest Biome	Recorded from only one locality	Used for SDM
Comanthera	*kegeliana*		(Koern.) L.R. Parra & Giul.		X		X
Comanthera	*reflexa*		(Gleason) L.R. Parra & Giul		X		X
Comanthera	*xeranthemoides*		(Bong.) L.R. Parra & Giul.	X			X
Eriocaulon	*carajasense*		Moldenke		X	X	
Eriocaulon	*cinereum*		R. Brown	X			X
Eriocaulon	*gibbosum*		Koernicke	X			X
Eriocaulon	*guyanense*		Koernicke		X		
Eriocaulon	*herzogii*		Moldenke		X	X	
Eriocaulon	*humboldtii*		Kunth		X		X
Eriocaulon	*milhoense*		Herzog		X	X	
Eriocaulon	*setaceum*		Linnaeus	X			X
Eriocaulon	*spruceanum*		Koernicke	X			
Eriocaulon	*tenuifolium*		Klotzsch ex Koernicke		X		X
Paepalanthus	*bifidus*		(Schrad.) Kunth	X			X
Paepalanthus	*chiquitensis*		Herzog	X			X
Paepalanthus	*fasciculatus*		(Rottb.) Kunth		X		X
Paepalanthus	*fasciculoides*		Hensold		X	X	
Paepalanthus	*gleasonii*		Moldenke		X	X	
Paepalanthus	*lamarckii*		Kunth	X			X
Paepalanthus	*major*		(Moldenke) Hensold		X	X	
Paepalanthus	*perpusillus*		Kunth		X		
Paepalanthus	*piresii*	*piresii*	Moldenke		X	X	
Paepalanthus	*piresii*	*villosus*	Moldenke		X	X	
Paepalanthus	*polytrichoides*		Kunth		X		X
Paepalanthus	*singularis*		Moldenke		X		
Paepalanthus	*subtilis*		Miq.	X			X
Paepalanthus	*sulcatus*		Hensold		X	X	
Paepalanthus	*tortilis*		(Bong.) Koernicke	X			X
Rondonanthus	*capillaceus*		(Klotzsch ex Koernicke) Hensold & Giul.		X		
Rondonanthus	*roraimae*		(Oliv.) Herzog		X	X	
Syngonanthus	*allenii*		Moldenke		X		

Genus	Species	Variety	Scientific Name Authorship	Distribution Widespread	Distribution concentrated in the Amazon Rainforest Biome	Recorded from only one locality	Used for SDM
Syngonanthus	*amapensis*		Moldenke		X		
Syngonanthus	*amazonicus*		Moldenke		X	X	
Syngonanthus	*anomalus*		(Koernicke) Ruhland	X			X
Syngonanthus	*bellus*		Moldenke	X			
Syngonanthus	*biformis*		(N.E.Br) Gleason	X			X
Syngonanthus	*bisumbellatus*		(Steudel) Ruhland		X		X
Syngonanthus	*blackii*		Moldenke		X	X	
Syngonanthus	*bracteosus*	*scrupulosus*	Moldenke		X	X	
Syngonanthus	*cachimbonsis*		Moldenke		X	X	
Syngonanthus	*caulescens*		(Poir.) Ruhland	X			X
Syngonanthus	*cuyabensis*		(Bong.) Giul., Hensold & L.R. Parra	X			
Syngonanthus	*davidsei*		Huft	X			X
Syngonanthus	*densiflorus*		(Koernicke) Ruhland	X			X
Syngonanthus	*densus*		(Koernicke) Ruhland	X			
Syngonanthus	*dichroanthus*		Hensold	X			
Syngonanthus	*diversifolius*		(Moldenke) M. Watanabe		X	X	
Syngonanthus	*egleri*	*egleri*	Moldenke		X		
Syngonanthus	*egleri*	*pomboensis*	Moldenke		X	X	
Syngonanthus	*fenestratus*		Hensold		X		X
Syngonanthus	*gracilis*		(Bong.) Ruhland	X			X
Syngonanthus	*heteropeploides*		Herzog Repert		X	X	
Syngonanthus	*humboldtii*	*humboldtii*	(Kunth) Ruhland	X			
Syngonanthus	*lanatus*		Moldenke		X		
Syngonanthus	*longipes*		Gleason		X		X
Syngonanthus	*nitens*		(Bong.) Ruhland	X			X
Syngonanthus	*oblongus*		(Koernicke) Ruhland	X			
Syngonanthus	*setifolius*		Hensold		X		X
Syngonanthus	*sickii*		Moldenke		X	X	
Syngonanthus	*simplex*		(Miq.) Ruhland		X		
Syngonanthus	*spongiosus*		Hensold		X		
Syngonanthus	*tenuis*	*bulbifer*	(Huber) Hensold	X			X
Syngonanthus	*trichophyllus*		Moldenke		X		X
Syngonanthus	*umbellatus*		(Lam.) Ruhland	X			X
Syngonanthus	*williamsii*		(Moldenke) Hensold		X		X
Tonina	*fluviatilis*		Aubl.	X			X
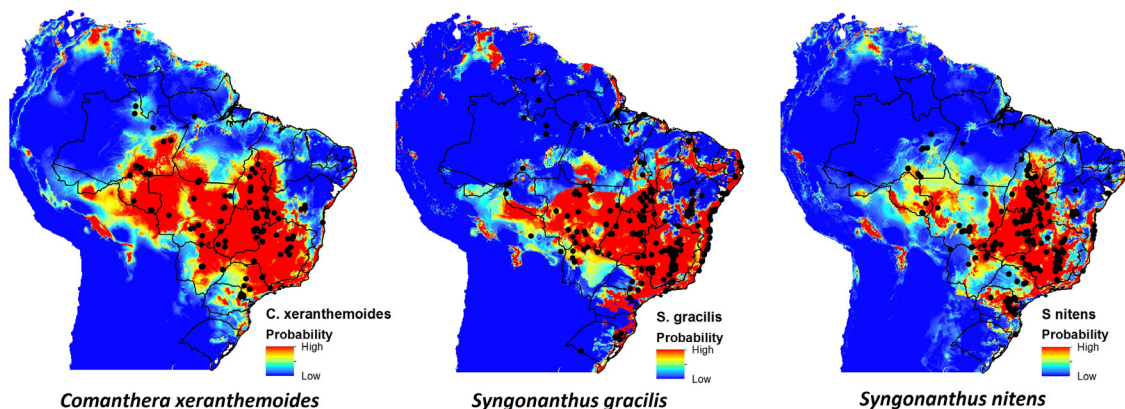
Figure 1 – Three examples of Eriocaulaceae species whose occurrence points and Species Distribution Modelling show wide distribution in Brazil. Warmer colors (near red) indicates high occurrence probability.
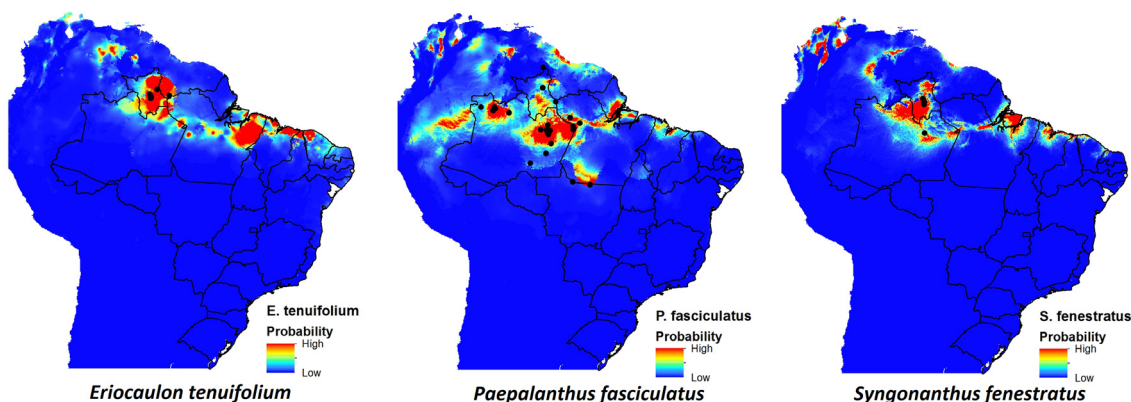**Figura 1** – Três exemplos de espécies de Eriocaulaceae cujos pontos de ocorrência e Modelagem de Distribuição de Espécies mostram uma ampla distribuição geográfica no Brasil. Cores mais quentes (perto do vermelho) indicam alta probabilidade de ocorrência.

and Roraima states are pinpointed. In the Cerrado, the South of Pará, northern of Mato Grosso and Rondônia, Tocantins, Goiás and some areas in Maranhão state are highlighted.

When superimposing the potential areas obtained with the 31 species used by SDM, it can be seen there is a high level of agreement (Fig. 3). Areas with the largest number of species occurring in the same localities or areas very close, and arranged by state, are:

a) Amapá. Rio Oiapoque region, 12 species, all widely distributed.

b) Amazonas. Barcelos: Serra do Aracá with 11 species, including *Paepalanthus gleasonii* only known from this locality. Novo Ariapuanã: Rio Aripuanã with 10 species, including *Syngonanthus bracteosus* var. *scrupulosus* only known from this locality. Manaus and surroundings: with nine species including *Syngonanthus heteropeploides* only known from this locality. São Gabriel da Cachoeira: Rio Issana with four species, including *Syngonanthus amazonicus* only known from this locality. Santa Isabel do Rio Negro: Pico da Neblina with three species, including *Paepalanthus major*

Figure 2 – Three examples of Eriocaulaceae species whose occurrence points and Species Distribution Modelling show distribution restricted to the Amazon Rainforest biome. Warmer colors (near red) indicates high occurrence probability.
Figura 2 – Três exemplos de espécies de Eriocaulaceae cujos pontos de ocorrência e Modelagem de Distribuição de Espécies mostram uma distribuição geográfica restrita ao bioma Floresta Amazônica. Cores mais quentes (perto do vermelho) indicam alta probabilidade de ocorrência.

and *P. sulcatus* only known from this locality. Other areas which should be mentioned are: Manicorá: Rio Cururu with 10 species, on the borders of Rondônia; Humaitá with seven species, and Borba with five species.

c) Pará. Novo Progresso: Serra do Cachimbo with 11 species, with three taxa, *Paepalanthus piresii* var. *piresii*, *Syngonanthus cachimboensis* and *S. sickii*, only known from this locality. Parauapebas: Serra dos Carajás with eight species, including *Eriocaulon carajasense*, *Paepalanthus fasciculoides* and *Syngonanthus diversifolius*, only known from this locality. Oriximiná: Rio Mapuera with six species, including *Paepalanthus singularis*, only known from this locality. There

Figure 3 – Occurrence probability based on the potential distribution of 31 species of Eriocaulaceae, using Species Distribution Modelling and Geographic Information Systems – A. Oiapoque; B. Barcelos; C. Novo Ariapuanã; D. Manaus; E. São Gabriel da Cachoeira; F. Santa Isabel do Rio Negro; G. Manicorá; H. Humaitá; I. Borba; J. Novo Progresso; K. Parauapebas; L. Oriximiná; M. Santarém; N. Vigia; O. Monte Roraima. Warmer colors (near red) indicates high occurrence probability.

Figura 3 – Probabilidade de ocorrência baseada na distribuição potencial de 31 espécies de Eriocaulaceae, utilizando-se Modelagem de Distribuição Geográfica e Sistemas de Informação Geográfica – A. Oiapoque; B. Barcelos; C. Novo Ariapuanã; D. Manaus; E. São Gabriel da Cachoeira; F. Santa Isabel do Rio Negro; G. Manicorá; H. Humaitá; I. Borba; J. Novo Progresso; K. Parauapebas; L. Oriximiná; M. Santarém; N. Vigia; O. Monte Roraima. Cores mais quentes (perto do vermelho) indicam alta probabilidade de ocorrência.

are also important localities for the collection of Eriocaulaceae in the Santarém area, Alto Tapajós with 11 species, and Vigia with five species.

d) Roraima. The most important site here is the Parima Mountains with Mount Roraima presenting two species, including the only locality known for a record of *Rondonanthus roraimensis*.
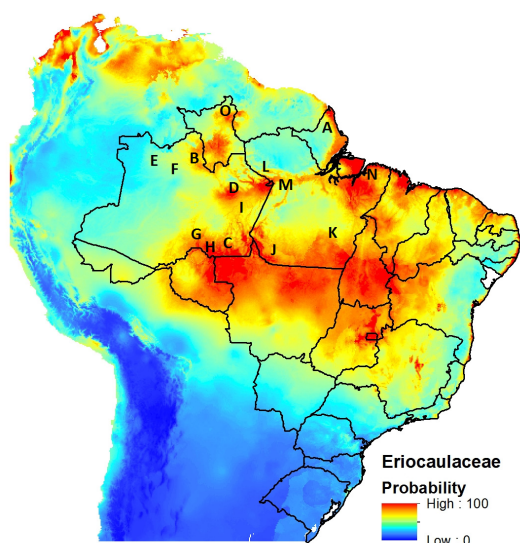
e) Rondônia. All the species recorded from this state have wide distribution and are associated with cerrado areas, which extend into the neighboring areas of Mato Grosso, Tocantins, Goiás, some areas in Maranhão and also outside Brazil in Bolívia.

Discussion

The supposedly low occurrence of Eriocaulaceae species in Northern Brazil is primarily a reflection of the small number of species mentioned from the area in the classic works, such as the *Flora Brasiliensis* (Koernicke 1863) and in *Das Pflanzenreich* (Ruhland 1903). Only 20 taxa are mentioned for the area in these works, and some of the names mentioned therein are now in the synonymy of other accepted names. Additionally, with the exception of the few taxa described from the 19th and early 20th century collections of Spruce and Ule, the remainder were described from collections made outside Brazil, especially Guiana, Jamaica, and Surinam.

In the early 1900s, there was an increase in collections from the Amazon, notably by Luetzelburg, which were deposited in the Munich Herbarium, and described particularly by Herzog. In the 1960–1990s, Prance and collaborators collected many Eriocaulaceae especially from the state of Amazonas, and Paulo Cavalcanti and Murça Pires in the state of Pará, which provided material for the description of many new taxa by H. Moldenke. In the same period, there was an active development of floristic studies in the Guayana Highlands of Venezuela, which provided many new taxa of Eriocaulaceae, and species of other families from the region.

Steyermark (1982) considered the Venezuelan Highland as a refugee area, and the geological formations as well the present-day physiography as the main factors responsible for the region's plant distribution and endemism. Hensold (1999) recorded seven genera and 88 species of Eriocaulaceae from the Venezuelan mountains. The author included *Philodice* but it was placed in synonymy of *Syngonanthus* (Giulietti *et al.* 2012b). Also four species referred as *Syngonanthus*,

actually are included in *Comanthera*. Comparing the species lists from the Venezuelan Highland and the Brazilian Amazon Rainforest biome, all the genera and 42 species have been recorded from both areas. It is now known that 100% of the species of *Comanthera, Rondonanthus* and *Tonina* are common to the two areas, while in *Paepalanthus* the percentage is 84.6%, for *Syngonanthus* 57.1% and for *Eriocaulon* it is 50% of species. Most of these species, common to the two areas, have wide distributions, while a few other merit mention: *Paepalanthus fasciculoides* occurs in Venezuela only on the "Cerro Cotorra" in Bolivar state, at an altitude of 600 m, and in Brazil only on the Serra dos Carajás, in Pará state, Brazil, at about 800 m altitude. In this latter locality, from where the type material originated (Hensold 1991, 1999), populations with numerous individuals occur, varying from caulescent to acaulous plants. *Paepalanthus major* was described from material collected on the Serra da Neblina, in Amazonas state, Brazil, and also occurs on Auyán-tepui in Venezuela (Hensold 1991).

An analysis of the general distribution of Eriocaulaceae taxa show that a relatively small number of species are widely distributed (ca. 39,4%) while the majority (60.6%) show a restricted distribution within the Amazon Rainforest biome. Of these, 22.3% are known only from a single locality. This arrangement of species as differentiated distribution patterns appears to be common in different areas, as much in the Tropics as in temperate regions (Henrys *et al*. 2015; Smart *et al*. 2015).

In Amazonia, three species show a wider and disjunct pantropical distribution pattern in the tropics. These are *Eriocaulon cinereum* and *E. setaceum*, which are aquatic plants occurring in Asia, Africa and tropical America. The third species, *Paepalanthus lamarckii,* occurs in West Africa and in the Americas from Central America to South-east Brazil (Ruhland 1903; Giulietti & Hensold 1990).

Species with a neotropical distribution can be cited: *Paepalanthus bifidus*, *P. tortilis*, *P. subtilis*, *Syngonanthus caulescens*, *S. davidsei*, *S. gracilis*, *S. nitens* and *Tonina fluviatilis*. All these species are composed of populations of annual plants, occurring in damp, sandy soils. *P. bifidus* e *T. fluviatilis* occur in low-lying areas, associated especially with the forests in eastern Amazonia or in the coastal restingas, where they extend both northwards and south, as far as South-east Brazil.

The remaining species are particularly associated with mountain ranges, reaching southwards to Minas Gerais or São Paulo, and in the case of *S. caulescens* as far as Argentina.

The species *Comanthera xeranthemoides*, *Eriocaulon gibbosum*, *E. humboldtii*, *Paepalanthus chiquitensis*, *Syngonanthus densiflorus* and *S. longipes* occur mainly in savanna areas (Cerrado Biome), extending mostly towards the Central-Western of Brazil and also parts of Bolivia and Colombia.

Populations of Eriocaulaceae can be found in diverse areas of the Amazon Rainforest biome and in Cerrado Biome, although some areas are characterized by the higher number of species, as was noted in the Results. These areas can be tentatively classified into four groups, based on the Brazilian relief classification (Ross 1990) and their structures and forms (Ross 2013).

Areas included in the "Sedimentary Plateau" of the eastern (Oriental) Amazon River. This plateau results from Tertiary and Mesozoic sediments and reaches altitudes up to 300 to 400 m. The main areas include Manaus (AM), Santarém and Vigia (PA). The annual Eriocaulaceae species from those areas occur especially along river margins and littoral restingas.

Areas included in the "Sedimentary Plateau" of the western (Occidental) Amazon River. This plateau reaches a maximum altitude of 200 m, being formed from Tertiary and Quaternary sediments of the Solimões Formation. The main areas include São Gabriel da Cachoeira, Borba and Oriximiná (AM). The annual Eriocaulaceae species from those areas occur especially along river margins.

Areas included in the "Crystalline Plateau" named "Residuais Norte-Amazônico" (Northern Amazonian Residuals). They are a series of disjunct mountains of the Pre-cambrian origin, which form part of the Guiana Shield. They extend from Amapá state up to the northern part of Amazonas state, with altitudes in general between 600–1000 m, and include the highest Brazilian plateaus, such as Pico da Neblina (Serra do Imeri, Amazonas) with 2,995 m and Monte Roraima (Serra do Pacaraima, Roraima) with 2,734 m. The substrates are of sandstone, quartzite, granite or volcanic inclusions and the main vegetation is "Campo Rupestre". The main areas include Oiapoque, Barcelos, Santa Isabel do Rio Negro, Monte Roraima, and other mountain areas nearby, where the perennial Eriocaulaceae species usually occur.

Areas included in the "Crystalline Plateau" named "Residuais Sul-Amazônico" (Southern Amazonian Residuals). This covers a large area from southern Pará to Rondônia state. In the West, in areas such as Nova Aripoanã, Manicorá, Humaitá and Novo Progresso, there are formations with an ancient sedimentary cap, characterized by flat tops with altitudes up to 1000 m, covered with a cerrado vegetation. In the East, also occur residual reliefs up to 900 m altitude, originating from ancient volcanism, associated with intrusions and folding, as can be found in the Serra dos Carajás in Parauapebas. In these mountains, there are an intermingling of different types of forest formation, and the upper parts is normally occupied with "Campo Rupestre" overlying ironstone, locally recognized as the "vegetation of canga". The flora on the canga on this area is rich and diversified with about 600 species of plants and there are annual and perennial Eriocaulaceae species.

The study presented here will aid the collection of new species and new populations of Eriocaulaceae. It should also prove useful in the search for species of other families of Angiosperms, which display a similar distribution and share areas in Amazonia with the same edaphic and climatic features. The species thus collected will provide the bases for further taxonomic, phylogenetic and biogeographical studies, which will help our understanding of the vegetation history of the Amazon basin. This is a region of immense changes in the past, which suffered the impact of the rise of the Andes, the change in the direction of the waters of the Amazon River eastward, as well as major climatic changes during and since the Quaternary, as referred by Fiaschi & Pirani (2009). The results of species modelling will also be a key contribution towards the future selection of priority areas of conservation/ restoration within the region.

Acknowledgment

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