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Delimiting floristic biogeographic districts in the Cerrado and assessing their conservation status

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Corresponding Author:	Renata Françoso Universidade de Brasilia Instituto de Ciencias Biologicas Brasília, DF BRAZIL
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universidade de Brasilia Instituto de Ciencias Biologicas
Corresponding Author's Secondary Institution:	
First Author:	Renata Françoso
First Author Secondary Information:	
Order of Authors:	Renata Françoso
	Kyle G. Dexter
	Ricardo B. Machado
	R. Toby Pennington
	José Roberto R. Pinto
	Reuber A. Brandão
	James A. Ratter
Order of Authors Secondary Information:	
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	Conselho Nacional de Desenvolvimento Científico e Tecnológico (303838/2016-8) — Mr. Ricardo B. Machado
	Natural Environment Research Council (NE/I028122/1) — Mr. Kyle G. Dexter Mr. R. Toby Pennington
	Conselho Nacional de Desenvolvimento Científico e Tecnológico (307701/2014-0) — Mr. José Roberto R. Pinto
Abstract:	The Cerrado is a biodiversity hotspot in central Brazil that represents the largest expanse of savanna in the Neotropics. Here, we aim to identify and delimit biogeographic districts within the Cerrado, to provide a geographic framework for conservation planning and scientific research prioritisation. We used data from 588 sites with tree species inventories distributed across the entire Cerrado. To identify districts, we clustered sites based on their similarity in tree species composition. To investigate why districts differ in composition, we 1) determined the proportion of tree species in different districts that derive from other biomes, to assess the influence of neighbouring biomes upon geographically marginal districts and 2) assayed key climatic differences between districts, to test the effect of environmental factors upon compositional differences. We found seven biogeographic districts within the Cerrado.

	Marginal districts have a large proportion of tree species characteristic of Amazonia and Atlantic Forest, but the Cerrado endemic species are also important. Further, districts differed significantly for multiple climatic variables. Finally, to provide a preliminary conservation assessment of the different districts, we assessed their rate of land conversion and current coverage by protected areas. We found that districts in the south and southwest of the Cerrado have experienced the greatest land conversion and are the least protected, while those in the north and northeast are less impacted and better protected. Overall, our results show how biogeographic analyses can contribute to conservation planning by giving clear guidelines on which districts merit greater conservation and management attention.
Response to Reviewers:	Dr. David L. Hawksworth Editor-in-Chief Biodiversity and Conservation I am pleased to inform you that all the corrections were made. We were requested to exclude the author citations after scientific names in Table 2. We exclude both, in table 2 and in the online resource. Thank you for your attention. Please do not hesitate to contact us if you have any question. kind regards, Renata Françoso

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Renata D. Françoso, Kyle G. Dexter, Ricardo B. Machado, R. Toby Pennington, José R.R. Pinto, Reuber A. Brandão, James A. Ratter.

Françoso, R.D. (Corresponding author, arenatafrancoso@gmail.com; +55 61 3107-5645; ORCID ID 0000-0002-6369-8317)[1]

Dexter, K.G. (kyle.dexter@ed.ac.uk; ORCID ID 0000-0001-9232-5221) [2,3]

Machado, R.B. (rbmac@unb.br; ORCID ID 0000.0002.6508.9005)[4]

Pennington, R.T. (t.pennington@exeter.ac.uk; ORCID ID 0000-0002-8196-288X)[2,5]

Pinto, J.R.R. (jrrpinto@unb.br; ORCID ID 0000-0003-2028-6176)[6]

Brandão, R.A. (reuberbrandao@gmail.com; ORCID ID 0000-0003-3940-2544)[6]

Ratter, J.A. (j.ratter@rbge.ac.uk)[2]

[1] Graduate Program in Ecology, University of Brasília. Address: Campus Universitário Darcy Ribeiro, Brasília, DF, Brasil.

[2] Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh EH3 5LR, U.K.

[3] School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, U.K.

[4] Zoology Department, Biological Science Institute, University of Brasília. Address: Campus Universitário Darcy Ribeiro, Brasília, DF, Brasil

[5] Geography, University of Exeter, Exeter EX4 4RJ, U.K.

[6] Department of Forest Engineer, Faculty of Technology, University of Brasília. Address: Campus Universitário Darcy Ribeiro, Brasília, DF, Brasil.

ABSTRACT

The Cerrado is a biodiversity hotspot in central Brazil that represents the largest expanse of savanna in the Neotropics. Here, we aim to identify and delimit biogeographic districts within the Cerrado, to provide a geographic framework for conservation planning and scientific research prioritisation. We used data from 588 sites with tree species inventories distributed across the entire Cerrado. To identify districts, we clustered sites based on their similarity in tree species composition. To investigate why districts differ in composition, we 1) determined the proportion of tree species in different districts that derive from other biomes, to assess the influence of neighbouring biomes upon geographically marginal districts and 2) assayed key climatic differences between districts, to test the effect of environmental factors upon compositional differences. We found seven biogeographic districts within the Cerrado. Marginal districts have a large proportion of tree species characteristic of Amazonia and Atlantic Forest, but the Cerrado endemic species are also important. Further, districts differed significantly for multiple climatic variables. Finally, to provide a preliminary conservation assessment of the different districts, we assessed their rate of land conversion and current coverage by protected areas. We found that districts in the south and southwest of the Cerrado have experienced the greatest land conversion and are the least protected, while those in the north and northeast are less impacted and better protected. Overall, our results show how biogeographic analyses can contribute to conservation planning by giving clear guidelines on which districts merit greater conservation and management attention.

Key words: Neotropical Savanna; Phytogeography, Indicator Species, Brazilian Savanna, Biogeographic Regionalization.

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INTRODUCTION

Human activity has affected natural resources to such a high level that it has generated a global biodiversity crisis (Jenkins 2003; Maxwell et al. 2016). Biodiversity threats are distributed unevenly across the globe (Brooks et al. 2006), with developing countries in the tropics currently representing the most vulnerable regions (FAO 2015). Land conversion will persist into the next decades due to agricultural expansion and intensification, especially in South America and sub-Saharan African (Jenkins 2003), affecting mainly tropical savannas (Grace et al. 2006). Brazil is one of the top four countries in South America in terms of predicted habitat loss (FAO 2015), which is concentrated in the Brazilian Cerrado (MMA/IBAMA 2011), a global biodiversity hotspot (Myers et al. 2000). Several thousand hectares of natural vegetation are converted every year in the Cerrado, at rates higher than observed in the Amazon (MMA 2017).

Despite the biological importance of the Cerrado, which originally covered more than 2 million km^2, nearly 50% of its natural vegetation has been cleared, chiefly due to agricultural expansion (MMA 2015). This continuous and intensive conversion is not randomly distributed, but prevalent in some geographic regions and vegetation types (Bianchi and Haig 2012). For example, land conversion has tended to follow the implementation of roads and other infrastructure, which took place first in the south of the Cerrado. Further, additional large declines of the Cerrado vegetation have been predicted over the next 50 years (Ferreira et al. 2012), especially in tableland areas with open vegetation formations, which are more suitable for the establishment of mechanized agriculture. By 2030, we may expect natural vegetation to be found mostly in protected areas (Klink and Machado 2005). Currently, only 3% of the remaining natural vegetation in the Cerrado is maintained in areas of strict protection equivalent to the IUCN categories I to III (Françoso et al. 2015). Regional variation in species composition and the non-uniform human occupation of the Cerrado implies the need for specifically tailored conservation policies, based on regional planning. However, conservation efforts in the Cerrado have not followed any clear plan, with protected areas being established opportunistically on a case-by-case basis (Françoso et al. 2015). Among nine described global approaches to conservation prioritization (Brooks et al. 2006), the Cerrado represents a reactive conservation scenario, with decisions based on threat, contrasting with Amazonia where decisions are often based on opportunity.

Ideally, conservation efforts and resources should be focused on areas that harbor the greatest proportion of regional biodiversity, including a diversity of ecological communities, the majority of regionally endemic species, and characteristic environmental conditions. By conserving representative examples of different biological communities and ecosystems that occur within a region, the majority of species in that region will also be conserved (Groves et al. 2002).

Biogeographic regionalization aims to represent distinct biological natural areas on a map (Morrone 2018), which can support conservation policies and scientific investigations. The identification of homogeneous natural areas, based on animal and plant communities, at regional, continental or global scales, is a common approach in ecology and biogeography (e.g. Wallace 1876; Clements and Shelford 1939; Dice 1943; Udvardy 1975). To unify the nomenclature used for floral and faunal biogeographic regions, Udvardy (1975) proposed a hierarchical division with realms, biotic provinces and districts. Realms occur at continental scales and follow the large faunal regions of Wallace (1876). Provinces are subdivisions of realms, comprising large subcontinental regions, characterized by the major biome that occupies the area. The third biogeographical level, the district, encompasses smaller differences within provinces.

Districts are essential to drive conservation efforts, since they represent unique features of the provinces (Udvardy 1975). Higher or lower levels, such as regions or dominions, may also be used (Morrone 2014).

The identification of biogeographic units in a large and threatened ecosystem, such as the Cerrado, is necessary for recognizing distinct biological communities with different conservation needs, and to subsequently adjust conservation actions for different parts of the biome. Several studies have been conducted to identify conservation priority areas in the Cerrado. These have used different approaches, such as the distribution of endemic species (Simon and Proença 2000; Silva and Bates 2002; Diniz-Filho et al. 2008; Nogueira et al. 2011; Carmignotto et al. 2012; Azevedo et al. 2016), the identification of vicariant processes (de Mello et al. 2015), macroecology (Diniz-Filho et al. 2008, 2009) or species community composition (Ratter and Dargie 1992; Ratter et al. 1996, 2003; Aguiar et al. 2015; Amaral et al. 2017). The Cerrado biome harbours three to five main areas of endemism, depending on the studied group. These areas (the Central Plateau, Veadeiros Mountain Range, Guimarães Mountain Range, Espinhaço Mountain Range, and Araguaia Valley) have been recorded in studies based on distribution patterns of vertebrates (Diniz-Filho et al. 2008), birds (Silva and Bates 2002), herpetofauna (Nogueira et al. 2011; de Mello et al. 2015; Azevedo et al. 2016) and species of *Mimosa* (Simon and Proença 2000).

Here we focus on the ecological approach of clustering localities based on similarity in tree species composition because it is relevant for guiding conservation planning and the design of protected areas networks (Whittaker et al. 2005; de Mello et al. 2015; DRYFLOR 2016). Ecological biogeography often relies on cluster methods for identifying patterns in the distribution of organisms across landscapes, and group localities based on their similarities in species composition (Kreft and Jetz 2010). An alternative approach of historical biogeography is to delimit areas of endemism, where the distribution of two or more endemic taxa overlap (Morrone and Url 1994; Szumik and Goloboff 2004). In this case, overlapping species distributions are assumed to result from vicariant processes, such as tectonic-isolating events (Sanmartín 2012). We consider these assumptions to be unreasonable in the Brazilian Cerrado due to its young geological age (<10 MY; Simon et al. 2009) and because of evidence that neotropical tree communities are assembled by dispersal (Pennington and Dick 2004; Dexter et al. 2017). In contrast with the historical biogeography approach, ecological biogeography searches for patterns in the current distribution of organisms that are determined by recent dispersal processes and environmental filters (Morrone et al. 1995).

Biogeographic studies based on community composition in the Cerrado show large areas that are relatively homogeneous in species composition (Ratter and Dargie 1992; Ratter et al. 1996, 2003; Aguiar et al. 2015; Mews et al. 2016; Amaral et al. 2017). In a series of studies published from 1996 to 2003, Ratter and colleagues proposed six Floristic Provinces within the core area of Cerrado, and another two disjunct areas in the Amazon (Ratter and Dargie 1992; Ratter et al. 1996, 2003, 2011). These studies were based on an extensive sampling effort for woody plants of the Cerrado, including more than 900 species of trees and large shrubs, and representing the most extensive botanical biogeographic study of the Cerrado to date.

Here, we aim to identify biogeographic districts within the Cerrado biome, based on a large dataset for woody plants, primarily trees, and propose specific regions as the first level of biodiversity surrogates for conservation planning in the Cerrado. Therefore, we are not interested in areas of endemism *per se*, because we do not want to neglect any part of the Cerrado, even if there are no regionally endemic species present. We expand the woody plant floristic database of Ratter et al. (2003) from 376 to 588 sites and delimit biogeographic districts using up-to-date analytical methods, accounting for biases that may have been present in previous analyses. We also determine which species are characteristic for each district using indicator species analysis (Dufrêne and Legendre 1997; De Cáceres et al. 2010). We verify climatic differences amongst the biogeographic districts and, finally, present a conservation assessment of each district in terms of land conversion and protected area coverage, to guide future conservation efforts in the Cerrado.

METHODS

Study area and database

We used floristic data from 588 inventories and floristic surveys distributed across the Cerrado, which is a geographic region delimited by IBGE (2004) and which is largely covered by savanna vegetation, but also includes other major vegetation types such as grasslands and deciduous and evergreen riparian forests. We focused on cerrado *sensu lato*, which includes savanna vegetation and woodland or tall savanna (*cerradão*), since they are floristically similar (Ribeiro and Walter 2008). We did not include deciduous, semi-deciduous, or gallery forests, because of sample gaps for these vegetation types, differences in sample methods and effort, and because savannas cover almost 70% of the biome (Coutinho 2006). We also included some samples of savanna sites in the transition zones with adjacent biomes. The detailed database is in preparation for publication in an open access data journal linked to a repository.

We restricted our analyses to trees and large shrubs (plants with a woody stem that reaches 2 m tall or more), because few studies in our data compilation included other vascular plants such as herbs. We checked the scientific names, habits and distributions of the species in the Flora do Brasil website (Flora do Brasil 2016), which follows the APG IV taxonomy updates (APG IV 2016). We used the *flora* package (Carvalho 2017) in R to extract species information. The final database includes 814 species, belonging to 77 plant families, with 202 species restricted to one site. Most of these unique samples are species more associated with other biomes or vegetation types, occurring only occasionally in savanna habitats. Thus, few single-site occurrences actually represent Cerrado endemics.

Analyses

Since different tools have been developed for different biogeographic approaches, there is a great variety of methods that can be used to identify biogeographic entities (see Morrone 2018). Considering various cluster methods, there are several options that can give divergent results (Leger et al. 2015). Among the most used methods, the k-means clustering has shown good performance in biogeographic studies (Tichý et al. 2011; Vavrek 2016). For delimiting Cerrado biogeographic districts, we performed a k-means cluster analysis excluding singletons, since they provide no information in similarity analysis (Magurran 1988).

We calculated a fuzzy version of the Jaccard similarity index using the *fuzzySim* (Barbosa 2016) and the *vegan* (Oksanen et al. 2014) packages in R (R Core Team 2016). This involved two steps: (1) the calculation of a fuzzy version of the species occurrence matrix and (2) the calculation of the Jaccard similarity matrix. The fuzzy version of species occurrences is a way to solve gaps and differences in sample methods, since the fuzzy logic searches for a probability of occurrence for each species per site (Barbosa 2015). The *fuzzySim* package provides three solutions for the fuzzy distribution: the prevalence-independent environmental favourability model produces a generalized linear model for each species using environmental variables. We avoided this approach, because many species lacked enough occurrences to run the GLM analysis. The second solution is the Spatial Trend Surface (TSA) model, which provides the spatial structure in species distribution by regressing occurrence data on the spatial coordinates. The third option is the Inverse Squared Distance to Presence (ISDP) for each species, which calculates a spatial interpolation model of the species distributions. We tested the last two methods and compared the results with the original incidence matrix using Mantel correlations. We selected the ISDP matrix, which had greater correlation with the incidence matrix (ISDP $r = 0.67$, $P < 0.001$; TSA $r = 0.56$, $P < 0.001$).

We implemented the k-means method using the *cascadekm* function in the *vegan* package. In the k-means clustering, the observations are associated with the nearest mean point according to the number of groups imposed. The cascade k-means creates several data partitions according to the required number of groups, where a range between the smallest and the largest number of groups is stated *a priori*. Considering our proposal to identify biogeographic districts in the Cerrado, the number of groups could neither be so large as to limit their utility for conservation policies, nor so few that major differences in the spatially extensive and dynamic Cerrado would not be represented. Therefore, we restricted the possible number districts to a range between two and 20 groups. We used the simple structure (SSI) and the Calinski–Harabasz indices to select the optimal number of groups. Both are good predictors when groups are equal in size, but they may not be interpreted literally for differently sized groups (Oksanen et al. 2014). Thus, we considered the best values of each criteria and their congruence to select the best number of groups for our cluster.

To test the robustness of the groups in capturing vicariant patterns, we tested if the composition of Cerrado endemic species, as a subset of the entire data per group, could explain the groups, using the ANOSIM test with 1000 permutation in the *vegan* package (Oksanen et al. 2014). The ANOSIM provides analysis of similarities for matrix data by permutations aiming to identify significant differences between groups. We also selected the endemic species that most explain the differences between the groups, by variable selection with Random Forest (described below).

To document the association between individual species and the biogeographic districts, we conducted an Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) using the *labdsv* package (Roberts 2013), with 100,000 randomizations. The ISA calculates how a species can be associated with one or more groups, and how statistically significant the association is. The index is based on species relative frequencies or relative average abundances in clusters using a null model. Since our dataset consists of species occurrences, only their frequencies were considered. The indicator species value is greatest when all occurrences of the species are restricted to a single group, and when the species occurs in all sites of this group.

In our dataset, only 10% of the species are endemic to the Cerrado, whereas most tree species are widely distributed, being shared with one or more other biomes (Rizzini 1963; Heringer et al. 1977; Oliveira-Filho and Ratter 1995; Françoso et al. 2016). These widely distributed species are important components of Cerrado communities; thus, we cannot ignore their role in defining biogeographic patterns. We classified indicator species according to their distribution across all Brazilian biomes, to understand in which districts the endemic and shared species occur.

We initially examined climatic variation among the biogeographic districts, using 35 bioclimatic variables based on precipitation, temperature, radiation, and moisture (Kriticos et al. 2012). These climatic variables are the mean interpolation of monthly data over a period of 30 to 50 years (reference year 2000) (Hijmans et al.

2004). For data reduction, we excluded some highly correlated variables (correlation greater than 0.70 or lower than -0.70), keeping those that were correlated with the greatest number of other variables. In the end, we retained: mean annual temperature (°C), temperature seasonality (unitless coefficient of variation, or CV), temperature annual range (BIO 5 – BIO 6) (°C), mean annual precipitation (mm), highest weekly radiation (Wm^{-2}), lowest weekly radiation (Wm^{-2}), radiation of coldest quarter (Wm^{-2}) and mean moisture index of coldest quarter.

To determine the best climatic predictors of biogeographic districts, we used variable selection with Random Forest in the *varSelRF* package (Diza-Uriarte 2014), with 50,000 trees. We evaluated the error of the variables by quantifying the number of correct predictions in *randomForest* package (i.e. 'out-of-bag' errror; Liaw and Wiener 2002). Random Forest is a machine learning method that uses several decision trees with different random combinations of the explanatory variables and samples to make a robust variable selection. It is particularly amenable to datasets with many explanatory variables (Liaw and Wiener 2002).

We summarized all species occurrences by generating a matrix where each row was one biogeographic district. We determined the relationships among districts using a consensus tree of 100 resamples, each based on Ward’s hierarchical cluster method and the Jaccard distance, with the *recluster* package (Dapporto et al. 2013).

Biogeographic areas are often limited by natural features (Morrone 2018). Therefore, we used ArcGIS 10.2.1 to produce a map of biogeographic districts, with their boundaries corresponding to known geographic features when this was logical and feasible. To assist in determining district boundaries, we used a digital elevation map (based on images of the Shuttle Radar Topography Mission; NGA and NASA 2000), a map of river catchments, and state boundaries when they coincided with natural features, e.g. the “Serra Geral” mountain chain.

We quantified land conversion and the coverage of protected areas for each biogeographic district. We separated protected areas into strict protection and sustainable use, following the Brazilian legal definitions (Brasil 2000). Strict protection areas correspond to IUCN categories I to III, and sustainable use to categories IV to VI. We also quantified the overlap of districts with Priority Conservation Areas (MMA 2016), to further understand the conservation status of the Cerrado and discuss threats and conservation opportunities. We created the land conversion map for the Cerrado by quantifying the area that was converted during the period from 2010 to 2015, using natural vegetation distribution during 2010 as a baseline. We obtained all geographic data from http://mapas.mma.gov.br/i3geo/datadownload.htm.

RESULTS

The optimal solution for the k-means clustering varied with the selection criteria. The Calinski–Harabasz index was highest for two, four, and eight groups, in that order, while the simple structure index favoured nineteen, eighteen, twenty, and eight groups. Despite the difference between the two criteria, both considered eight groups as a good solution (Figure 1). Seeking a balanced solution, we chose eight as the optimal number of groups. The eight groups showed high spatial aggregation, with little overlap, which was crucial to spatial delimitation of the biogeographic districts (Figure 2).

Most of the spatial boundaries defining the districts followed landscape geomorphological attributes. We named districts based on their geographic position within the Cerrado: South (S), Southeast (SE), Southwest (SW), Central (Ce), West (We), Northwest (NW), and Northeast (NE). One of the groups is composed of sites in transition zones to other biomes in the south, north, and southwest of the Cerrado. Because these sites occurred outside of the Cerrado's boundary, we refer to this group as the "Extralimital" group. To separate this group from the NE district, we used a shapefile of vegetation classes from IBGE (2004b), excluding the non-savanna classes, such as evergreen and deciduous forest, scrub, and other transitional vegetation. There were two major groups of districts in the hierarchical cluster (Figure 3). The first included the northern and western districts (NW, NE, CW, and SW), and the second included the central and southern districts (CE, SE, and S). The Extralimital group does not have a direct connection with either of these overarching groups. Thus, we excluded it from further analyses, since most of its sites are not in the Cerrado biome, and it does not have spatial cohesion.

The ANOSIM results indicated significant differences in endemic species composition among the groups ($r = 0.304$; $P = 0.001$). In the Indicator Species Analysis, 394 species were significantly associated with at least one biogeographic district as presented in the Online Resource 1. The highest numbers of indicator species are in the S (109), NW (89), and CE (73) districts (Table 1). We found 14 species with average frequency higher than 60% considering all the biogeographic districts (*Qualea parviflora*, *Bowdichia virgilioides*, *Connarus suberosus*, *Hymenaea stigonocarpa*, *Dimorphandra mollis*, *Byrsonima coccolobifolia*, *Handroanthus ochraceus*, *Pouteria ramiflora*, *Kielmeyera coriacea*, *Erythroxylum suberosum*, *Roupala montana*, *Tocoyena formosa*, *Diospyros hispida*, *Tabebuia aurea*, *Caryocar brasiliense,* and *Davilla elliptica*). The districts with the greatest number of endemic indicator species are CE and NW, with 19 and 15 endemic indicator species each. In the Random Forest selection, 39 endemic species were selected as the best predictors of the districts (Table

2). The out-of-bag error rate was 22.6% (Online Resource 1). Most of these species are indicators in the CE and NW districts.

The best climatic predictors of the districts, based on the Random Forest analysis, were mean annual temperature, temperature seasonality, mean annual precipitation, highest weekly radiation, lowest weekly radiation, and radiation of the coldest quarter. The out-of-bag error rate was 4.8% (see confusion matrix in the Online Resource 1). Mean annual temperature plays an important role splitting the two main groups of districts found in the dendrogram (CW, NE, NW, and SW versus CE, S, and SE) (Figures 3-4). Each districts is different from the others for at least two climatic parameters (Table 3).

Conservation status varies substantially across the biogeographic districts (Table 4, Figure 5). The conversion rate ranges from 19% in the SW to 90% in the S. The highest protected area coverage is in CE (28.5%), in contrast with 2.7% in SE, highlighting the unbalanced conservation effort across the Cerrado. The protected areas coverage of strict protection and sustainable use varies not only among the districts, but also within districts. The CE district, for example, is covered by 26.6% of sustainable use but only by 1.9% of strict protection areas. Priority Conservation Areas cover more than 23% of all districts, reaching 58% in the CE (Table 4, Figure 6).

Description of Biogeographic districts

The Central (CE) district occupies 24,411 km^2 of the central portion of the Cerrado biome, covering the Distrito Federal (Federal District) and neighbouring areas in Goiás and Minas Gerais states. It mainly occupies the highlands of the Central Plateau, including the headwaters of the Tocantins, Corumbá and Preto rivers. Most of this area is over 900 m a.s.l. This district has low mean annual temperature and low temperature seasonality, despite the high radiation rate of the coldest quarter, which is because of the marked dry season, when clouds are very scarce. CE has 73 indicator species and the greatest number of endemic indicator species (19). Previous studies conducted by the Brazilian Ministry of the Environment suggested that 50.8% of this district overlaps with extremely high Priority Conservation Areas (MMA 2016), and it is the district with the highest proportion of this class within its limits. However, this is one of the most populated areas in the entire Cerrado region, and its coverage by strict protection areas is low, with high land conversion rates.

The Central-west (CW) district covers 417,983 km^2 in the north of Goiás and southern Mato Grosso states. This large district spans the watersheds of the Xingu, Araguaia, and part of the Tocantins rivers, occupying a large area in the central and western portion of the Cerrado. It includes highland areas such as Chapada dos Veadeiros (over 1,500m a.s.l.) and lowland areas along the Araguaia river and along the border with the Pantanal. This district has high temperatures with low seasonal variation. Radiation is also high during the dry season, which corresponds to the coldest quarter in the Cerrado. It has only 21 indicator species, and most of them are widespread, occurring in more than two biomes. In CW the natural vegetation covers 48%, but only 6.2% is protected, of which 1.2% is in the strict category.

The Northeast (NE) district occupies 403,248 km2, covering western Bahia and Piauí, southern Maranhão, and northern Minas Gerais states. The mean annual temperature is high, and the annual precipitation is low. Natural vegetation covered 70% of this BD, and the current protected area coverage is 13.6%. Some important protected areas in the Cerrado are found in the NE district, including the *Veredas-Peruaçu* system of protected areas. However, 23.2% of the NE district is under Extremely High or Very High conservation priority. Furthermore, the Cerrado municipalities that have suffered most degradation over the last years are placed in this district, mainly along the western borders of the state of Bahia (MMA/IBAMA 2011).

The North West (NW) biogeographic district includes mainly the state of Tocantins, covering over 204,646 km^2. The mean annual temperature is high, with low seasonality *i.e.*, the temperature is high year-round, as is the radiation (both highest weekly radiation and radiation of the coldest quarter). It has 89 indicator species, with 15 endemic and 14 shared with the Amazon biome. More than 70% of its area has natural vegetation. The percentage of protected area coverage is the highest among the districts (sustainable use: 8.7%, strict protection: 6.7%), including an important portion of the *Jalapão* mosaic of protected areas.

The South (S) biogeographic district covers nearly all the cerrado in São Paulo state, with 74,902 km^2. The mean annual temperature is the lowest among all districts, and the temperature seasonality is high, due to the proximity to the subtropical zone. The highest weekly radiation and the radiation of the coldest quarter are the lowest among the districts. The number of indicator species is high (109), but most of them also occur in the Atlantic Forest. This unique vegetation is the most threatened among the districts, with only 10% currently consisting of natural vegetation, and the strict protection area represents less than 0.5%. The 23.4% extent of High and Very High conservation priority suggests important opportunities for protected area creation.

The Southeast (SE) biogeographic district has 462,257 km^{2}, comprising most of the Cerrado in Minas Gerais state and the Paraná river basin in Goiás. The Espinhaço mountain range is placed in this district, presenting some of the highest elevation areas in the Cerrado. The mean annual temperature and radiation parameters are average, and seasonality is high, when compared with the other districts. Only 11 species are associated with this district and most of them are endemic. The SE district has been greatly transformed, with only 35% under natural cover. The protected area coverage is less than 3%, and 20% of its area has Very High conservation priority.

The South-West (SW) biogeographic district comprises 321,068 km^2 on the slopes that surround the flooding basin of the Pantanal, and other sites on mountain ranges within it. All localities within the Pantanal flooded basin were classified as SW, suggesting a strong resemblance between the Pantanal and the surrounding Cerrado in tree species composition. Mean annual temperature and temperature seasonality are high, while the highest weekly radiation and the radiation of the coldest quarter are intermediate in relation to the other districts. Amazonia has an important influence on the SW district. Its floristic composition indicates great influence of seasonal forest species and its selected indicator species are commonly found in seasonally dry tropical forests across the Cerrado (Nascimento et al. 2004; Salis et al. 2004; Santos et al. 2007; Kunz et al. 2008; Haidar et al. 2013). Despite the low coverage in protected areas (1.9%), indigenous lands cover 12.3% of this region.

DISCUSSION

We have identified seven biogeographic districts in the Cerrado, which are differentiated based on climatic conditions and species composition. These districts are associated with particular landscapes within the geographic limits of the Cerrado, making them of special interest for conservation policies and management purposes. These areas harbour plant communities divergent in their species composition and have different degrees of habitat loss and coverage by protected areas. The use of large and continuous districts, instead of the discrete endemism centres proposed for the Cerrado in previous studies, allows the formulation and planning of conservation efforts over a much wider region, covering also poorly sampled, but potentially relevant areas.

The patterns recovered in our study were partially observed by Ratter et al. (2003). Nevertheless, we found new biogeographic districts and refined delimitations of existing ones, thus representing an increase in the knowledge of distribution patterns of Cerrado woody species. This includes the Central district, which is placed in the Cerrado core area (Figure 2). Another important finding is the identification of hierarchical patterns in the woody plant communities in the Cerrado. We detected two main groups, distinguished by mean annual temperature values. We also detected differences in the communities of transition zones, especially in the northern region of the Cerrado, in Piauí and Maranhão states. The climatic particularities and the great influence of the Atlantic Forest make the S biogeographic district a consistent natural division of Cerrado (Ratter et al. 2003). On the other hand, the sites inside the Pantanal clustered with the SW district, suggesting a strong relation between the vegetation of the Cerrado and Pantanal.

We found a high influence of neighbouring biomes in all districts, particularly the influence of the Atlantic Forest on the S and of Amazonia on the NW district. Thus, the proximity of neighbouring biomes is important to determining the potential of shared species. Nevertheless, other factors, like climate, may explain varying biome influence on the districts, because their boundaries are dynamic (Werneck et al. 2012). For example, shifts in vegetation distribution as a consequence of climatic fluctuations in savannas (Cole 1960) may have facilitated the exchange of species among the Brazilian biomes (Salgado-Labouriau 2005; Bueno et al. 2017), especially in ecotonal zones. This situation may have driven a bidirectional colonization of species between the Cerrado and adjacent biomes (Oliveira-Filho and Ratter 1995; Colli 2005; Salgado-Labouriau 2005; Scariot and Sevilha 2005; Caetano et al. 2008; Ramos et al. 2009; Simon et al. 2009; Novaes et al. 2010), especially from the forest biomes into the

Cerrado (Simon et al. 2011). This potential floristic exchange may have driven the influence of species characteristic of other biomes on the Cerrado flora (Rizzini 1963; Heringer et al. 1977). Nevertheless, and despite the large shared boundary between the Cerrado and Amazonia, they share few indicator species, which was also reported in previous studies (Rizzini 1963; Heringer et al. 1977). The Amazonia-Cerrado transition represents a complete turnover from savanna to forest communities, even over short distances (Pinto and Oliveira-Filho 1999; Marimon et al. 2006), and this scenario likely affects community composition and the definition of biogeographic districts.

High elevation areas in the Cerrado are known for their high levels of endemism (Silva 1997; Simon and Proença 2000; Alves and Kolbek 2009; Echternacht et al. 2011; Nogueira et al. 2011; Gastauer et al. 2012). These high elevation areas are thought to be refuges for species that were formerly more widespread under past climatic conditions (Antonelli et al. 2010), especially those adapted to lower temperatures. These relictual populations are irreplaceable, bringing great importance to the SE district. Each district houses at least one area of endemism (Table 5), placed in highlands or valleys, which deserves special conservation attention.

The following districts correspond to Ratter’s floristic provinces (Ratter et al., 2003): NE (N & NE floristic province), SE (C & SE floristic province), and S (S floristic province). The Central-west floristic province was subdivided into districts CW, NW, and SW. In Ratter’s classification, the CE and SE district are in the C & SE floristic province. An analysis of the herb–shrub flora of the Cerrado (Amaral et al., 2017) suggested three main phytogeographic regions. Their phytogeographic region number 3 corresponds to the S, SE, and CE districts, and number 6 corresponds to the NE, NW, and partially CW. The SW district is the combination of phytogeographic regions 3 and 7, despite their wide coverage. The small divergences between the regionalization attempts may have arisen from differences in sampling methods and effort, scale, and peculiarities of the different life forms studied. Despite the fact that the limits of their regions are not entirely identical to our biogeographic districts, there is a sufficiently consistent geographic pattern of plant community composition to give confidence to using the districts as the first layer for conservation policies. Comparisons with other taxonomic groups are also needed to confirm the importance and generality of the districts we identified here.

Since several patterns of species distribution, climate characteristics, habitat loss and protected area coverage arise from the identification and delimitation of biogeographic districts, we expect that they will be useful in future studies in the Cerrado focusing on biogeography or conservation. The two groups of districts, cold (CE, S and SE) and hot (CW, NE, NW and SW) districts, have experienced different patterns of land cover change, mainly related to historical processes in Cerrado colonization.

Colonization of the Cerrado has had a main axis from south to north. Consequently, southern regions of the Cerrado have experienced extensive land conversion, and the remaining natural vegetation cover there is poorly protected. New protected areas are urgently needed in these regions to preserve their unique biodiversity, and these should include support for the creation of private reserves. In the northern Cerrado, given the larger amount of natural vegetation remaining, there is greater conservation opportunity, a plan for which can be defined by subsequent, more-detailed studies. Despite this, the creation of new protected areas is still urgent in the region due to high pressure caused by the expansion of agribusiness. The Brazilian Government defined the northern part of the Cerrado, at the conjunction of the states of Maranhão, Tocantins, Piauí and Bahia (“MATOPIBA”) as a priority region for agricultural occupation (Borghetti et al. 2017) and, at present, no conservation strategy has been defined to ensure environmental safeguards there.

The remaining natural vegetation and protected areas are not evenly distributed across the Cerrado. The S district is the least covered by protected areas and is the most impacted by land conversion. The NW district is the least impacted, showing larger natural vegetation remnants and better protected area coverage. This reality imposes two extreme options for Cerrado conservation, which are different, but complementary. In districts with more cover of natural areas (as NE, NW and SW), the proposition of new protected areas in IUCN groups I – III are urgent to preserve irreplaceable areas from the fast pace of the conversion of natural areas. Conversely, in the CE, S, and CW districts, the best strategy is promoting the natural regeneration of degraded Cerrado areas, including direct seeding, (Pellizzaro et al. 2017), along with the creation of private reserves. The Brazilian Protected Areas in the category Private Reserves of the Natural Heritage (RPPNs) are an important tool for biodiversity conservation via the engagement of landowners in the challenge of nature conservation, and for ecotourism promotion (Silva et al. 2015). The management and conservation purposes of RPPNs are similar of those for National Parks (Brasil 2000), making this category very attractive for conservation efforts.

Between 1990-2010, the Cerrado lost 0.6% of its natural vegetation annually (Beuchle et al. 2015), primarily due to livestock and large-scale intensive agriculture (MMA 2015). This rate of habitat loss represents almost 1,700 ha per day, scattered across the Cerrado. At this pace of habitat loss, the creation of protected areas is urgent, involving all social actors and spheres of government. It is important to point out that almost the entire Cerrado biome is found within Brazil. Therefore, despite international concern for Cerrado conservation, the maintenance of this unique global biodiversity hotspot is a Brazilian responsibility (e.g. Strassburg et al. 2017).

More broadly, the total protected area coverage of the Cerrado (8%) (Françoso et al. 2015) is well below the Aichi target of the Convention on Biological Diversity, which is 17%. Even the NW, the less impacted biogeographic district, is not close to reaching this goal. On the other hand, all districts except the S have more than 17% remaining natural vegetation (Table 4), making it possible to achieve much larger protected area coverage. Sadly, there currently seems to be an ongoing process of downsizing, degazettement, downgrading and reclassification of protected areas in Brazil (Bernard et al. 2014).

The biogeographic districts can be combined with other approaches for conservation prioritization in the Cerrado to focus on regional conservation needs, providing more realistic and important information for conservation prioritization, and bringing clearer goals for policy makers and for protected area managers. Several approaches can contribute to conservation in the Cerrado and should take into account the differences in biological communities highlighted herein. Current and future predictions of distribution, based on niche modelling of different taxonomic groups (Siqueira and Peterson 2003; Diniz-Filho 2004; Pinto et al. 2008; Marini et al. 2009; Costa et al. 2010), land conversion prediction modelling (Faleiro et al. 2013), and habitat fragmentation studies (Carvalho et al. 2009; Bianchi and Haig 2012), associated with systematic conservation planning tools (Margules and Pressey 2000), can all contribute to an efficient protected areas system for biodiversity maintenance in the Cerrado. The biogeographic districts harbour different plant communities, that reflect differences in Cerrado biophysical and biological characteristics across its wide distribution, and we expect that these same characteristics can also shape ecological communities and biological interactions.

The characterization of biogeographic districts in other large tracts of natural habitats can be useful for the conservation of the world’s savannas, which are nearly all strongly threatened by human activities (Lima et al. 2018). Since climatic and compositional variation, as we reported here, are also expected to occur in other savannas worldwide (Lehmann et al. 2014), we expect that more detailed biogeographic units can be recovered and used as biodiversity surrogates for conservation planning, with the overarching aim to avoid biodiversity loss worldwide.

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TABLES

Table 1. Number of indicator species significantly associated with the biogeographic districts of the Cerrado (Central – CE, Central-west - CW, North-east - NE, North-west - NW, South - S, South-east - SE, and South-west - SE) and their distribution in the Brazilian biomes. The widely distributed species occur in more than two biomes. Only the significant indicator species were counted (See the Online Resource for the indicator species analysis result).

Distribution	CE	CW	NE	NW	S	SE	SW	Total
Cerrado endemic	19	3	3	15	7	9	2	58
Cerrado and Pantanal	1	0	0	0	0	0	2	3
Cerrado and Amazon	9	6	2	14	6	4	8	49
Cerrado and Caatinga	7	1	4	5	0	0	0	17
Cerrado and Atlantic Forest	12	0	0	3	41	4	6	66
Widely	25	11	9	52	55	11	38	201
Total	73	21	18	89	109	28	56	394

Table 2. Importance of endemic species for the delimitation of the biogeographic districts of the Cerrado (Central – CE, Central-west - CW, North-east - NE, North-west - NW, South - S, South-east - SE, and South-west - SW). MDA = mean decrease accuracy.

Species	**BD**	**MDA**	**CE**	**CW**	**NE**	**NW**	**S**	**SE**	**SW**
Aspidosperma tomentosum	CE	0.015	0.012	0.019	0.021	0.020	0.005	0.007	0.019
Dalbergia miscolobium	CE	0.013	0.005	0.006	0.003	0.013	0.006	0.024	0.034
Eremanthus glomerulatus	CE	0.019	0.076	0.004	0.015	0.017	0.023	0.014	0.011
Eriotheca pubescens	CE	0.015	0.040	-0.001	0.025	0.008	0.024	0.014	0.012
Erythroxylum tortuosum	CE	0.025	0.011	-0.001	0.071	0.009	0.011	0.037	0.047
Guapira noxia	CE	0.030	0.068	0.004	0.086	0.018	0.017	0.020	0.031
Kielmeyera speciosa	CE	0.008	0.026	0.000	0.013	0.005	0.012	0.006	0.005
Ouratea hexasperma	CE	0.037	0.038	0.010	-0.004	0.027	0.171	0.023	0.029
Salacia crassifolia	CE	0.039	0.116	0.012	0.010	0.053	0.065	0.021	0.049
Styrax ferrugineus	CE	0.034	0.189	0.003	0.025	0.027	0.044	0.017	0.014
Tachigali subvelutina	CE	0.038	0.060	0.011	0.035	0.028	0.099	0.017	0.059
Vochysia thyrsoidea	CE	0.030	0.189	0.009	0.022	0.018	0.026	0.008	0.015
Kielmeyera rubriflora	CW	0.036	0.024	0.083	0.050	0.035	0.006	0.012	0.020
Vochysia rufa	CW	0.019	-0.005	0.015	0.016	0.008	0.071	0.007	0.031
Vochysia gardneri	NE	0.015	0.010	0.004	0.051	0.012	0.009	0.013	0.013
Aspidosperma nobile	NW	0.029	0.026	0.019	0.039	0.027	0.040	0.033	0.019
Callisthene hassleri	NW	0.004	0.001	0.000	0.002	0.020	0.001	0.001	0.000
Caryocar coriaceum	NW	0.026	0.011	0.010	0.017	0.101	0.012	0.016	0.015
Davilla elliptica	NW	0.015	0.002	0.015	-0.002	0.024	0.016	0.022	0.021
Diospyros coccolobifolia	NW	0.011	0.007	0.000	0.000	0.053	0.004	0.004	0.005
Diospyros hispida	NW	0.009	0.004	0.002	-0.004	0.023	0.006	0.021	0.006
Heteropterys byrsonimifolia	NW	0.013	0.009	0.004	-0.001	0.039	0.004	0.011	0.026

Mouriri elliptica	NW	0.039	0.070	0.011	0.008	0.037	0.080	0.064	0.020
Pseudobombax longiflorum	NW	0.022	0.001	0.015	0.059	0.033	0.013	0.024	-0.001
Pseudobombax tomentosum	NW	0.021	0.003	0.015	0.025	0.009	0.039	0.011	0.050
Tachigali aurea	NW	0.012	0.001	0.007	-0.010	0.027	0.019	0.023	0.005
Bauhinia rufa	S	0.011	0.003	-0.001	0.017	0.004	0.038	0.012	0.011
Leptolobium elegans	S	0.055	0.031	0.035	0.039	0.038	0.206	0.020	0.051
Miconia paucidens	S	0.003	0.001	0.001	0.001	0.001	0.019	0.001	0.001
Ouratea spectabilis	S	0.043	0.024	0.005	0.030	0.012	0.216	0.014	0.050
Mimosa laticifera	SE	0.004	0.001	0.005	0.005	0.000	0.003	0.008	0.003
Callisthene mollissima	-	0.002	0.002	0.003	0.001	0.004	0.000	0.001	0.000
Lafoensia pacari	-	0.008	-0.004	0.003	0.023	0.016	0.003	0.005	0.007
Pleroma stenocarpa	-	0.003	0.000	0.001	0.001	0.001	0.014	0.001	0.002

Table 3. Number of climatic parameters of Fig. 3 statistically different between the biogeographic district of the Cerrado are the Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE), and South-west (SW).

	CE	CW	NE	NW	S	SE
CW	2					
NE	5	5				
NW	4	5	5			
S	4	6	6	5		
SE	4	5	6	6	5	
SW	5	5	5	6	6	5

Table 4. Biogeographic district total area, remaining natural vegetation, protected area coverage, and Priority Conservation Areas. Conservation effort was measured for protected areas of sustainable use, strict protection, and indigenous territory. All areas are in km^2. The proposed biogeographic districts of the Cerrado are the Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE), and South-west (SW).

BD	**Total area**	**Conv. rate**	**Protected Areas**						**Priority Conservation Areas**					
			Sustainable Use		**Strict Protection**		**Indigenous Territory**		**High**		**Very high**		**Extremely high**	
CE	24,411	63%	6491	26.6%	467.6	1.9%	0	0.0%	0	0.0%	1854	7.6%	12408	50.8%
CW	417,983	52%	20941	5.0%	5064.2	1.2%	17739	4.2%	10471	2.5%	113911	27.3%	36533	8.7%
NE	403,248	30%	24500	6.1%	19110.5	4.7%	11175	2.8%	29868	7.4%	43715	10.8%	50182	12.4%
NW	240,646	29%	20904	8.7%	16140.9	6.7%	22621	9.4%	28399	11.8%	38761	16.1%	27786	11.5%
S	74,902	90%	6366	8.5%	232.4	0.3%	16	0.0%	7601	10.1%	9963	13.3%	101	0.1%
SE	469,257	65%	4758	1.0%	7822.2	1.7%	0	0.0%	38281	8.2%	93860	20.0%	31324	6.7%
SW	321,068	19%	2652	0.8%	3656.7	1.1%	39461	12.3%	15260	4.8%	38352	11.9%	37728	11.8%

Table 5. Previously identified biogeographic units (areas of endemism or biotic elements) within the biogeographic districts of the Cerrado. The districts are Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE), and South-west (SW). The biogeographic units are named according to the original sources.

Reference	**Biological group**	**CE**	**CW**	**NE**	**NW**	**S**	**SE**	**SW**
Azevedo et al., 2016	Anurans and squamates	Central plateau	Veadeiros; Guimarães; Caiapônia	Serra Geral; Chapada das Mesas	Tocantins-Araguaia; Jalapão		Espinhaço Canastra	Parecis; Pantanal-Bodoquena; Paraná plateau
Simon and Proença, 2000	Species in the genus *Mimosa*	Central plateau	Veadeiros; Guimarães				Espinhaço	
Nogueira et al., 2011	Squamate		Guimarães	Serra Geral	Tocantins depression; Upper Tocantins plateaus	Tietê-Rio Grande	Espinhaço	Serra das Araras; Parecis
de Melo et al., 2015	Squamate	Central plateau	Guimarães-Roncador	Serra Geral	Araguaia		Espinhaço	Paraná-Paraguai; Paraguai-Guaporé
Silva and Bates, 2002	Birds		Paranã		Araguaia		Espinhaço	

FIGURE LEGENDS

Figure 1. Values of the Calinski-Harabasz and Simple Structure Indices (SSI) for varying number of groups in k-means clustering based on a fuzzy version of the Jaccard distance. The values of each criterion are standardized as *Z*-values. The Calinski-Harabasz is high for low numbers of groups and the simple structure index selected more groups. A balanced solution favours a classification involving eight groups.

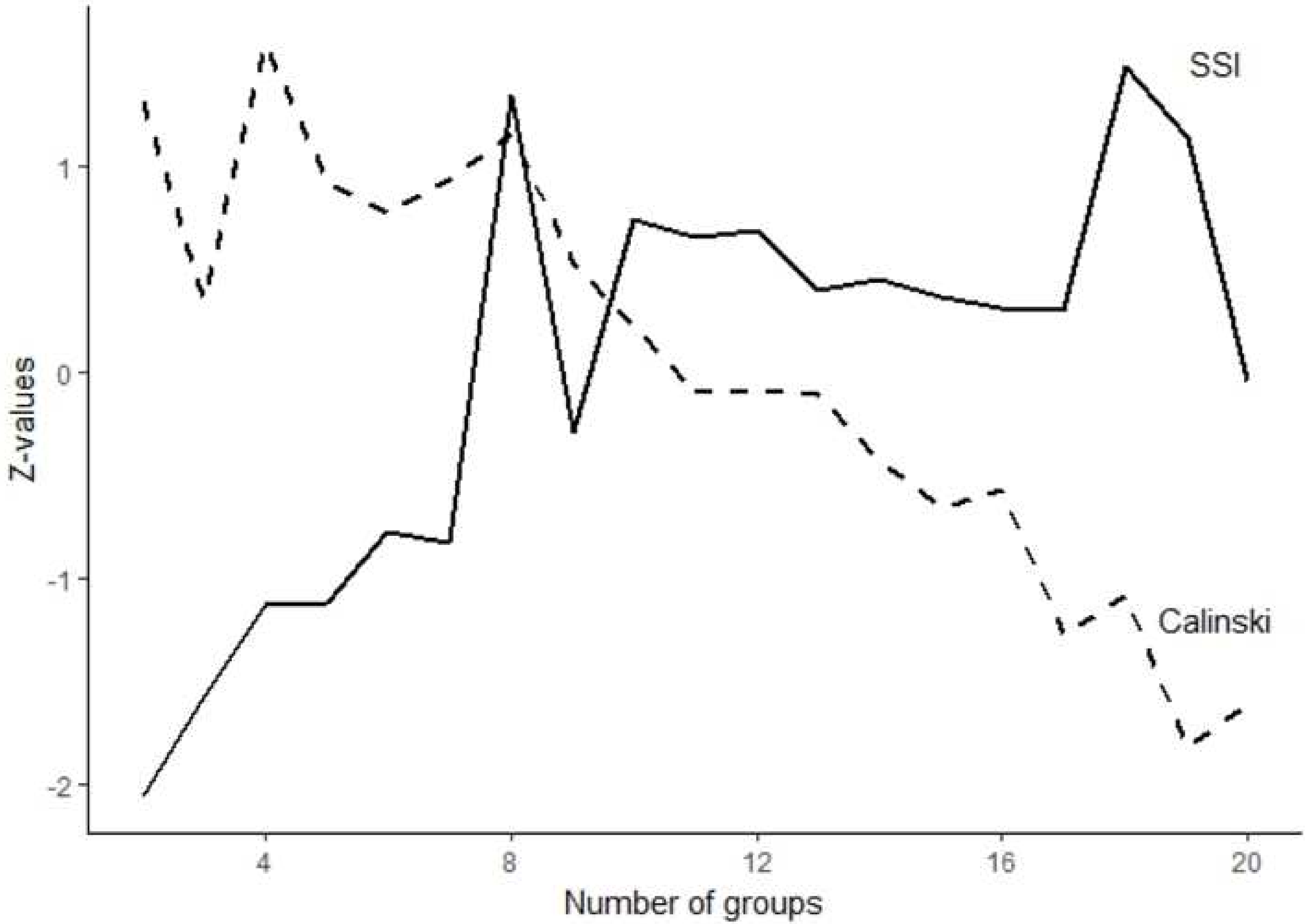
Figure 2. Biogeographic districts of the Cerrado biome in Brazil based on k-means classification and a fuzzy version of the Jaccard distance. The dots represent the surveyed sites used in the cluster analysis and the polygons were based on the distribution of sites in the same group in Fig. 1. The seven districts are Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE), and South-west (SW). The group with the marginal cerrado sites in grey was not considered a district due its predominant occurrence outside of the boundaries of the Cerrado and their disjunct nature.

Figure 3. Consensus tree of the Cerrado biogeographic districts relationships: Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE), South-west (SW), and the Extralimital (Ex) group with the marginal cerrado sites.

Figure 4. Boxplots showing the bioclimatic predictors selected by Random Forest to classify biogeographic districts of the Cerrado biome. Equal letters indicate no significant differences. Otherwise, all groups are significantly different for a given climatic parameter.

Figure 5. Remaining natural vegetation (light green), strict protection (dark green), and sustainable use areas (brown) in the Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE), and South-west (SW) biogeographic districts of the Cerrado. The dashed line delimits the biome and continuous lines mark the districts.

Figure 6. The Brazilian official Priority Conservation Areas (in red) over the remaining natural vegetation (light green), in the Central (CE), Central-west (CW), North-east (NE), North-west (NW), South (S), South-east (SE), and South-west (SW) biogeographic districts of the Cerrado. The shades of red (light to dark) indicate high, very high, and extremely high conservation priority.


SSI
Calinski
Z-values
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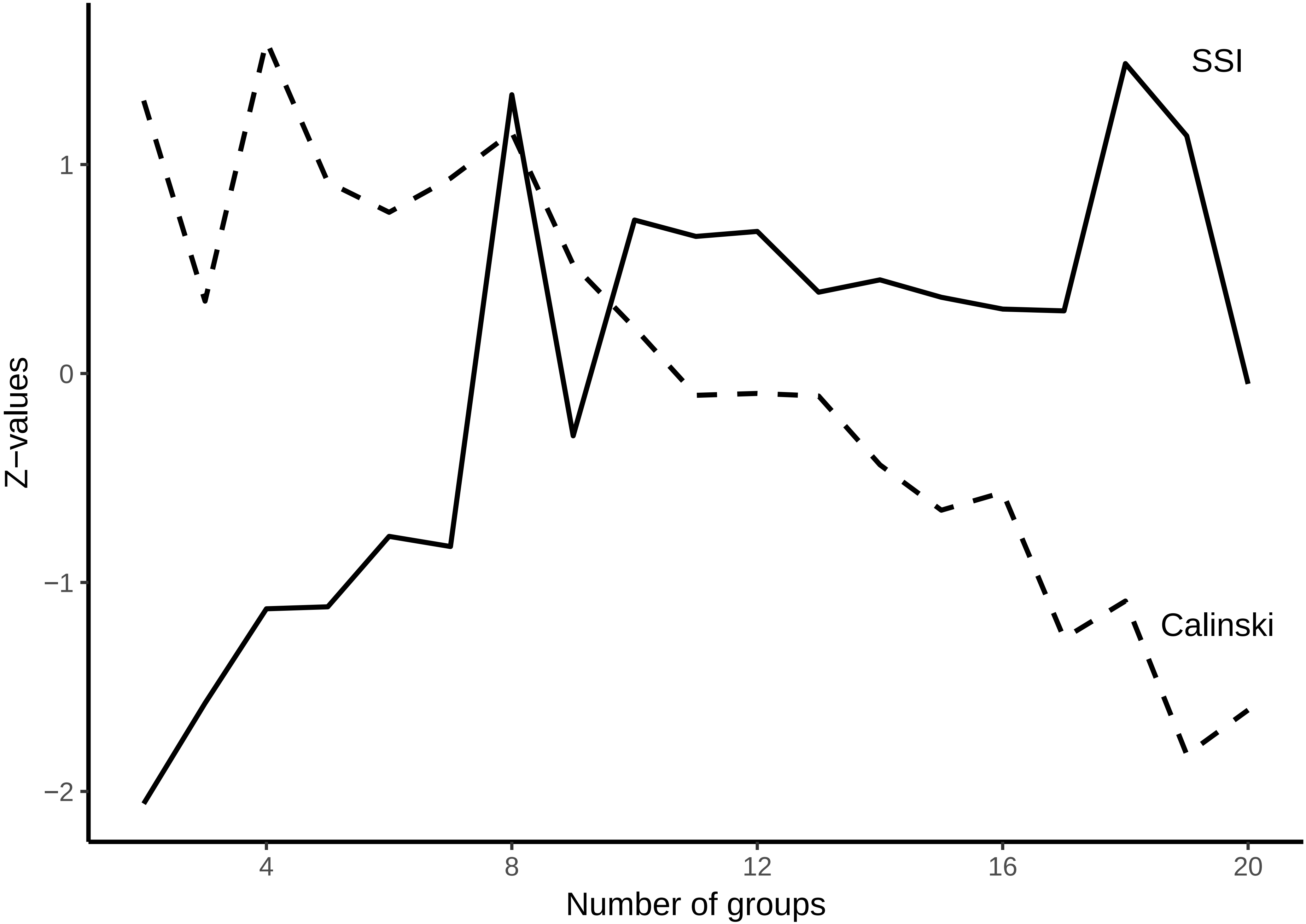
0
-1
-2
4
8
12
16
20
Number of groups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Z−values
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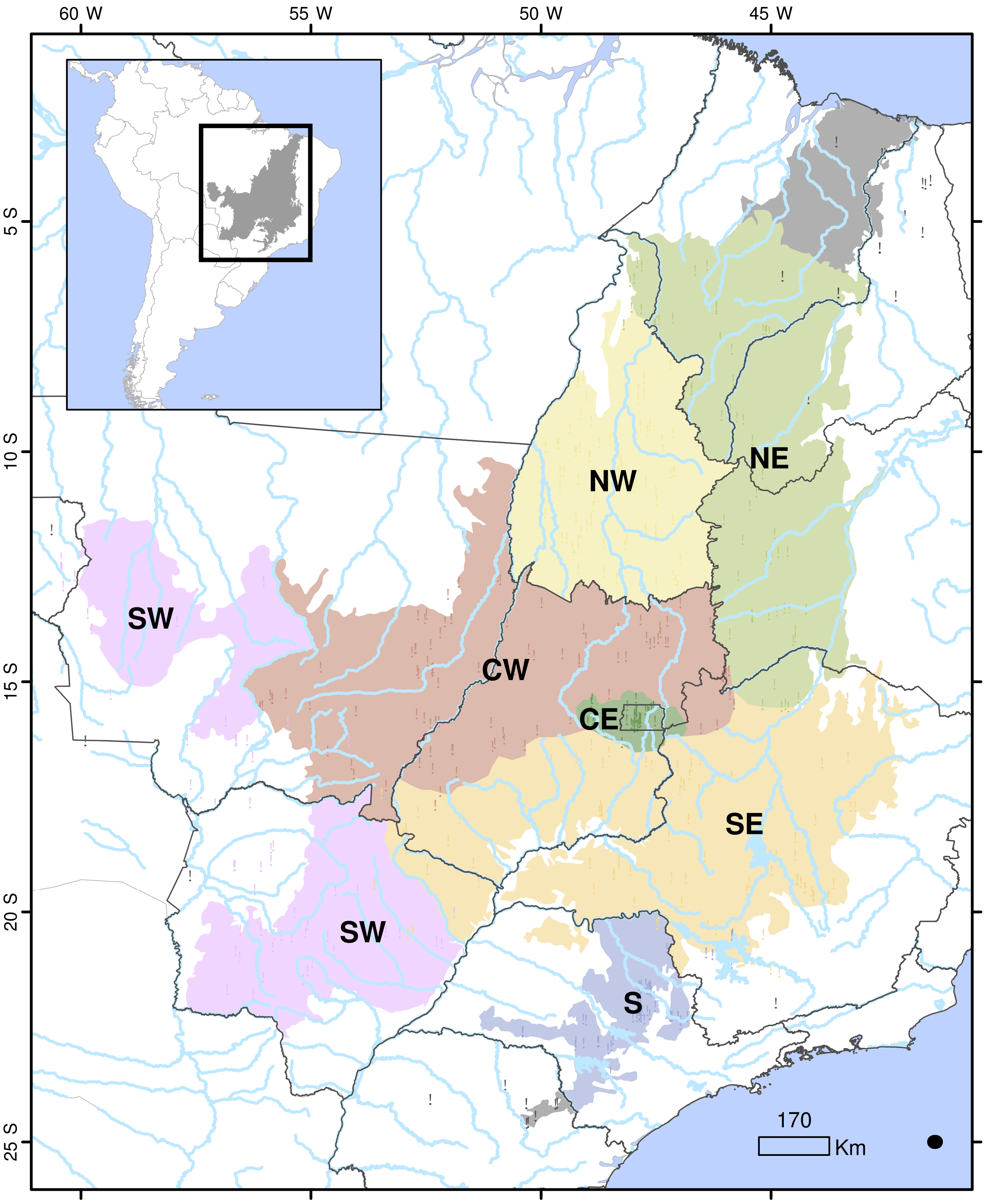
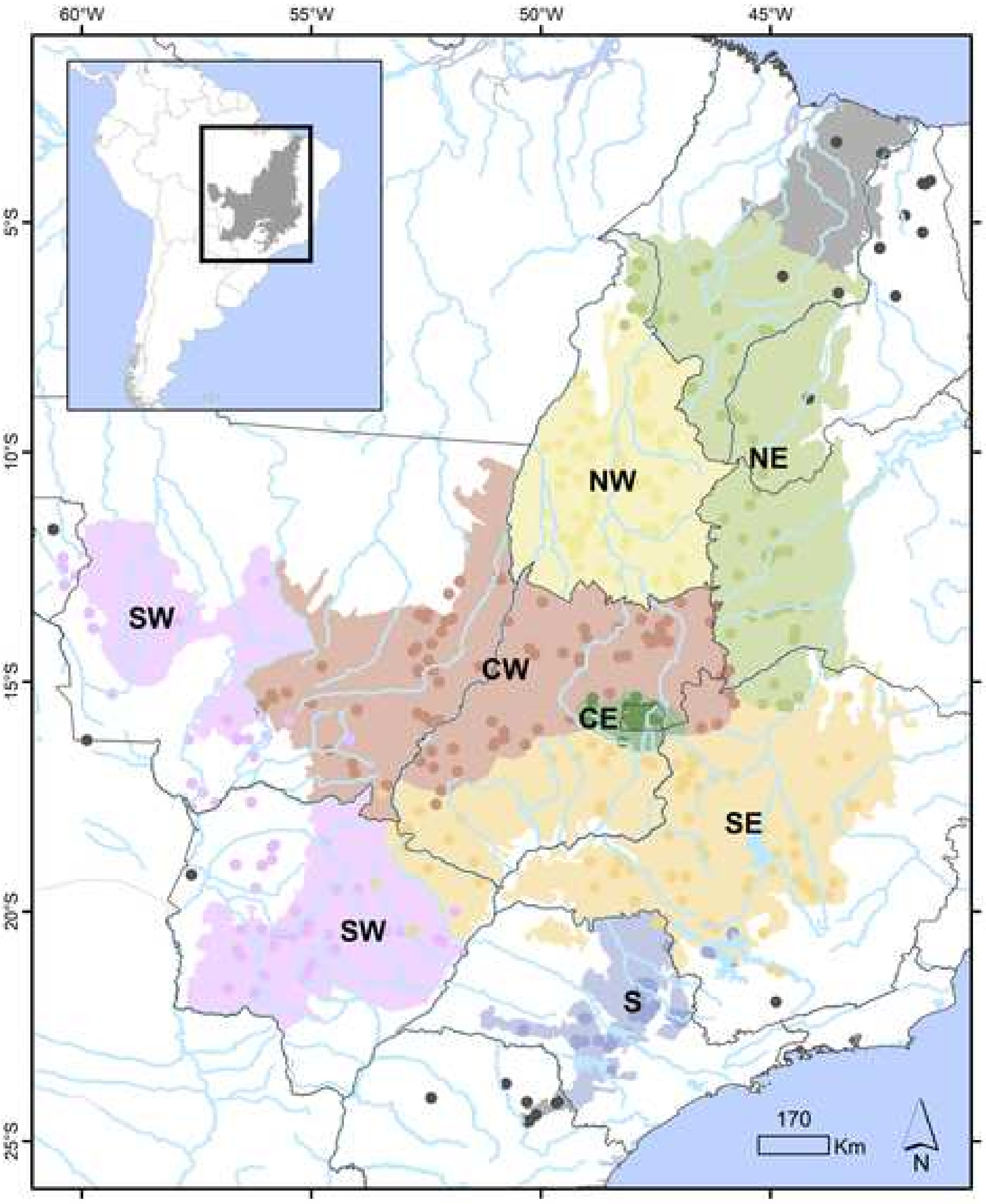
20
Number of groups


60 W
55 W
50 W
45 W
5 S
10 S
15 S
20 S
25 S
NW
NE
SW
CW
CE
SE
SW
S
170
Km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55°W
50°W
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Km
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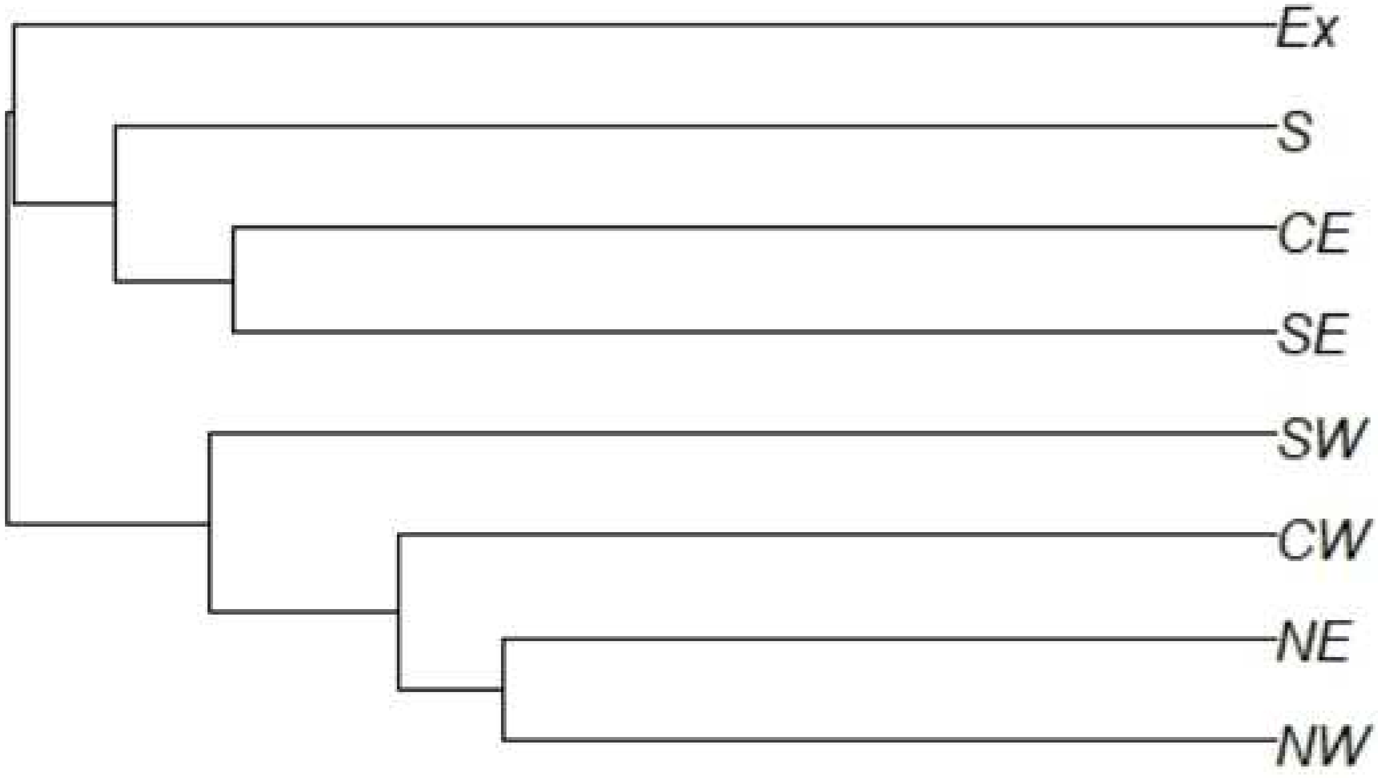
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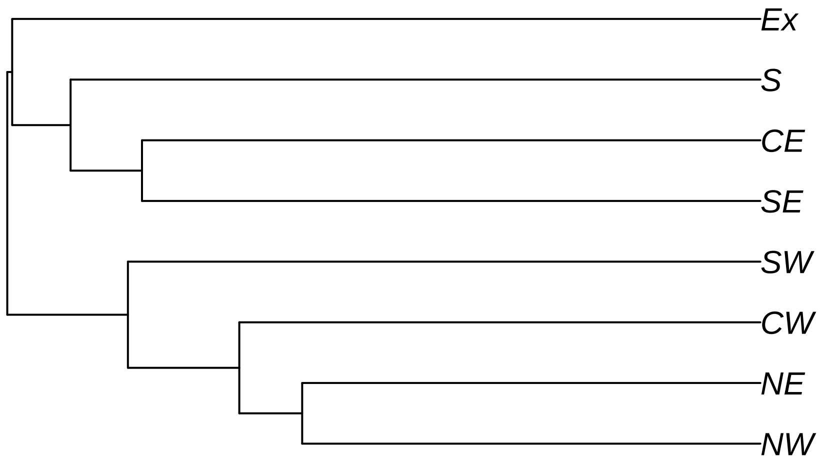
Ex
S
CE
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SW
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NE
NW

Figure 4 eps

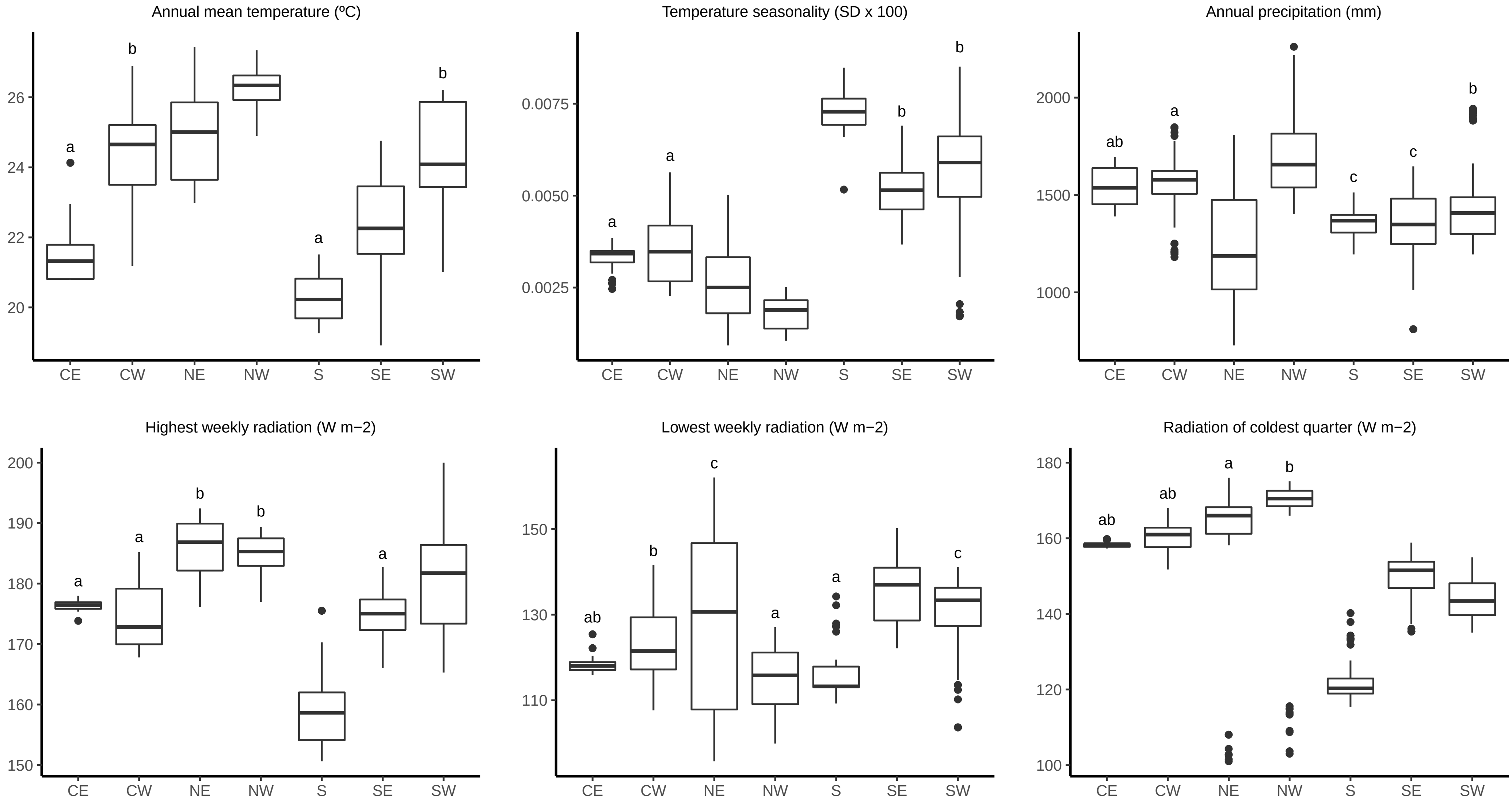
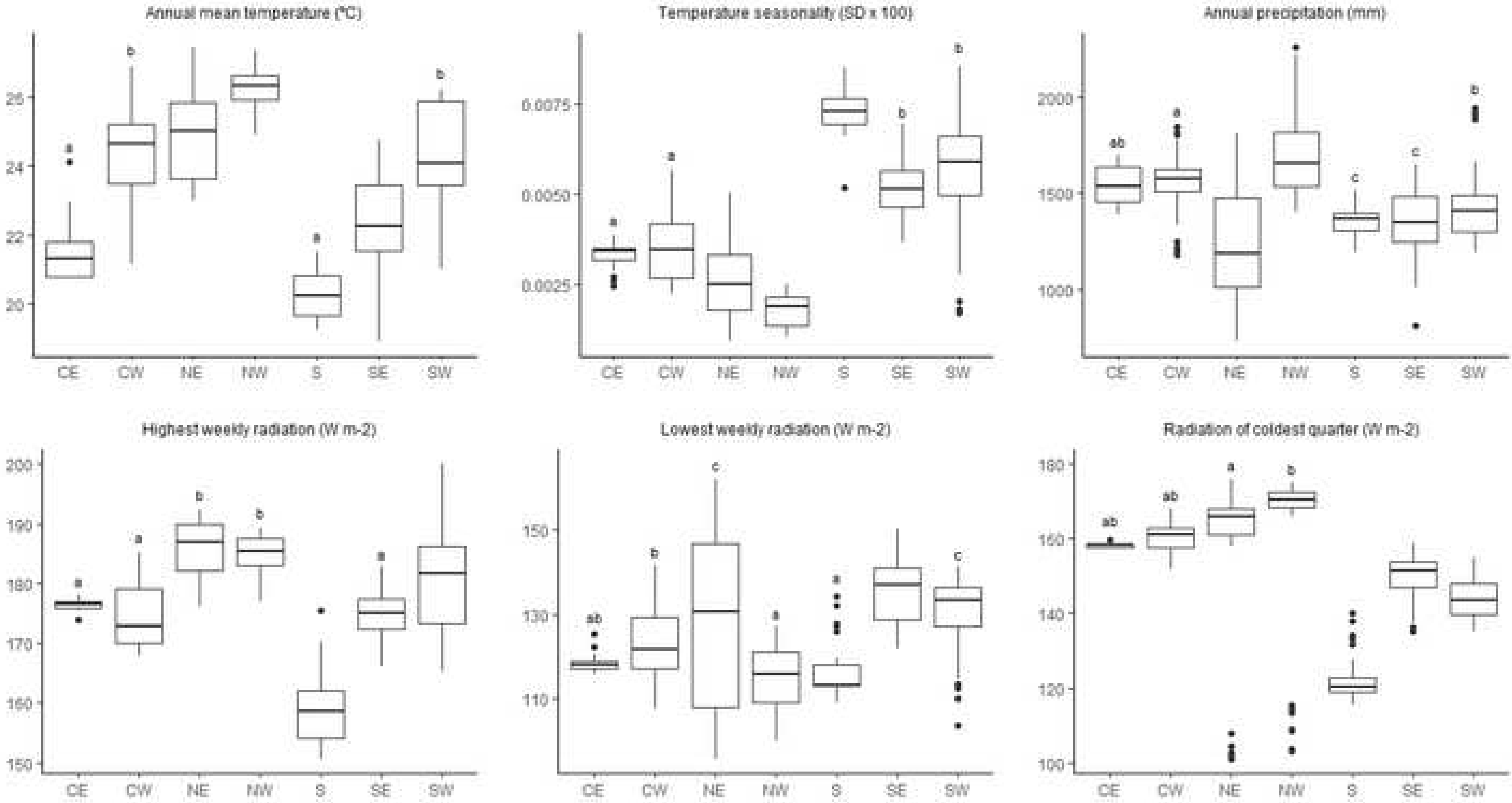
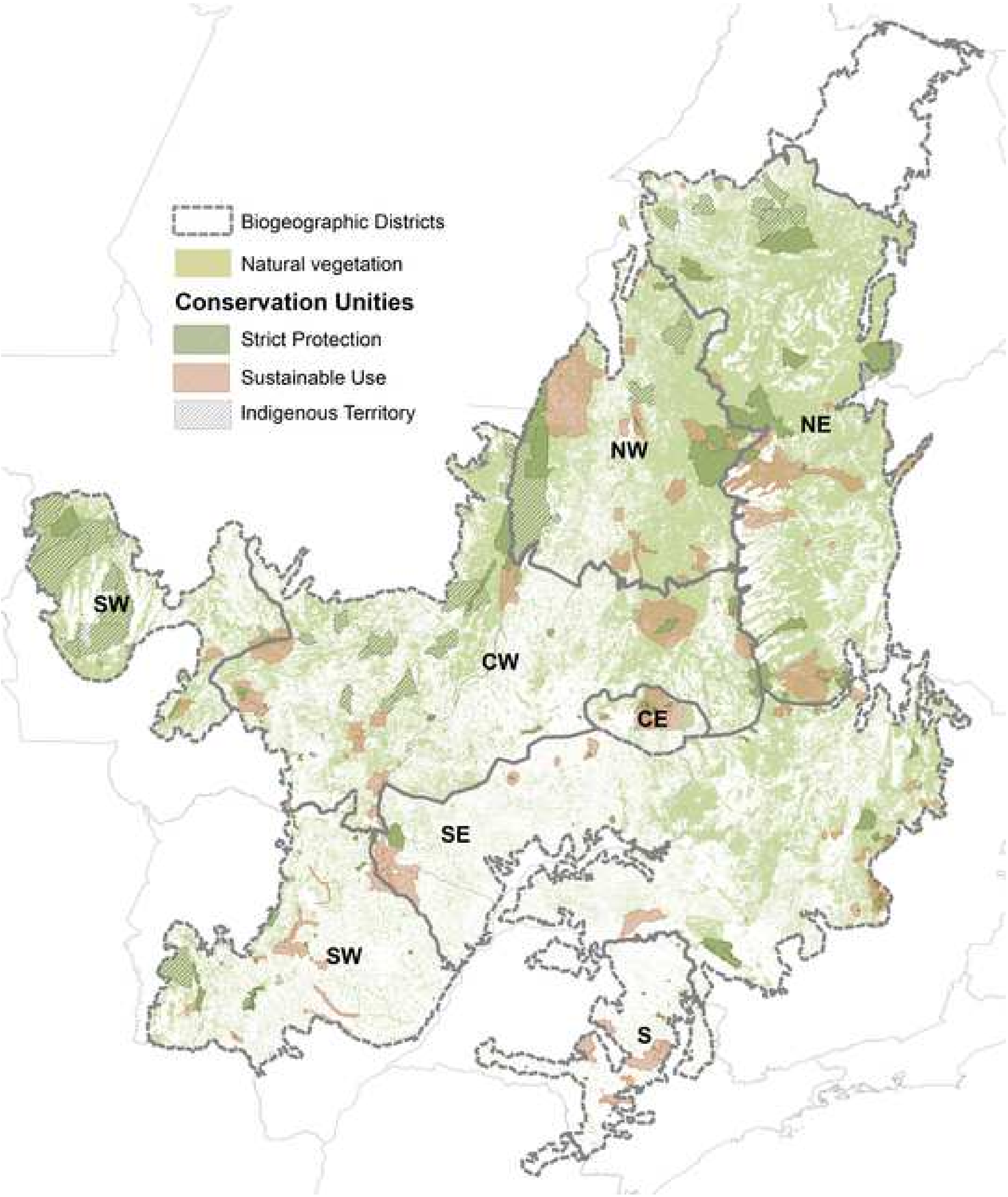
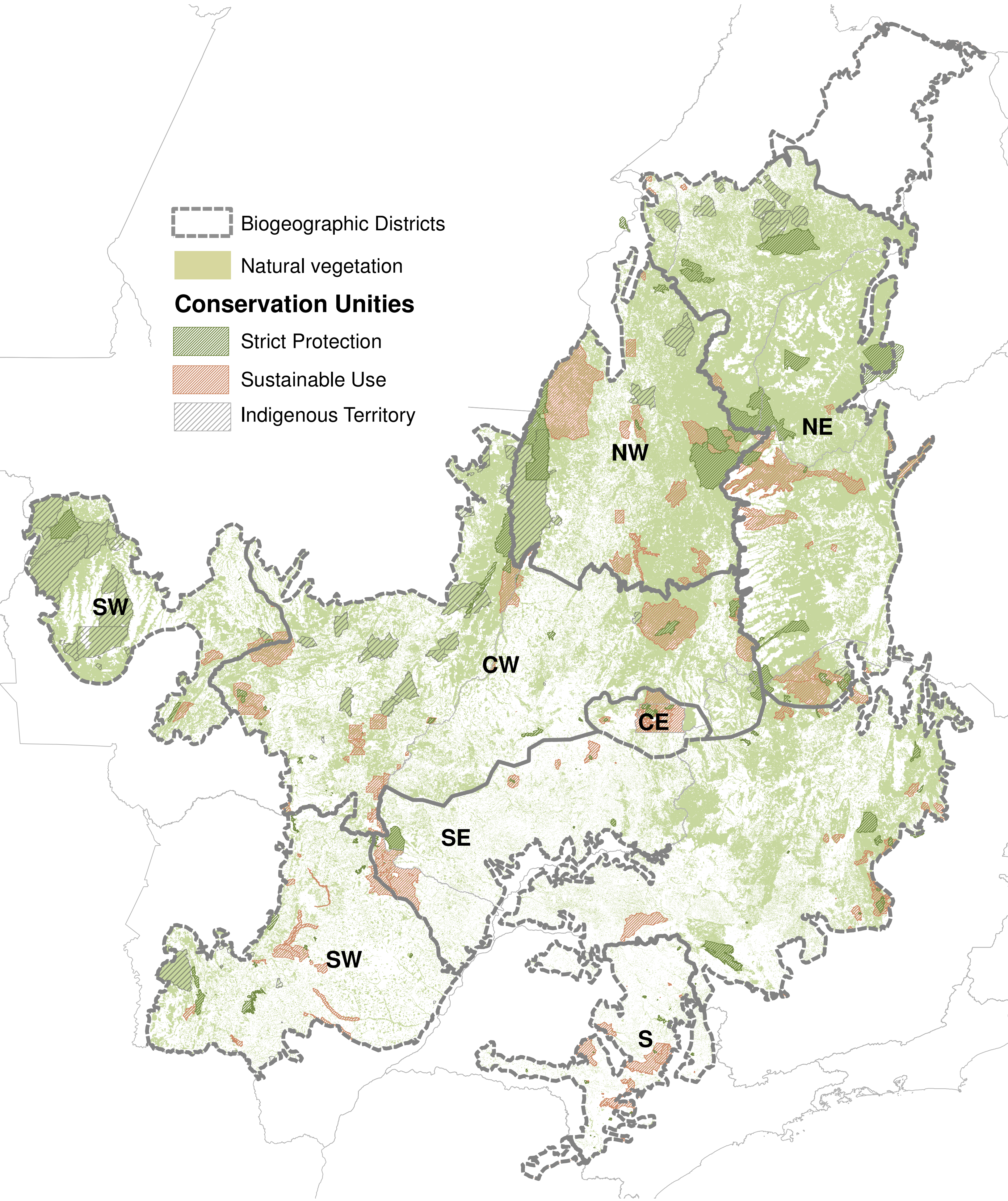

Annual mean temperature (ºC)
26
24
22
20
a
b
a
b
CE
CW
NE
NW
S
SE
SW
Temperature seasonality (SD x 100)
0.0075
0.0050
0.0025
a
a
b
b
CE
CW
NE
NW
S
SE
SW
Annual precipitation (mm)
2000
1500
1000
ab
a
c
c
b
CE
CW
NE
NW
S
SE
SW
Highest weekly radiation (W m−2)
200
190
180
170
160
150
a
a
b
b
a
CE
CW
NE
NW
S
SE
SW
Lowest weekly radiation (W m−2)
150
130
110
ab
b
c
a
a
c
CE
CW
NE
NW
S
SE
SW
Radiation of coldest quarter (W m−2)
180
160
140
120
100
ab
ab
a
b
CE
CW
NE
NW
S
SE
SW

Figure 4 jpg


Annual mean temperature (°C)
20
22
24
26
a
b
a
b
CE
CW
NE
NW
S
SE
SW
Temperature seasonality (SD x 100)
0.0025
0.0050
0.0075
a
a
b
b
CE
CW
NE
NW
S
SE
SW
Annual precipitation (mm)
1000
1500
2000
ab
a
c
c
b
CE
CW
NE
NW
S
SE
SW
Highest weekly radiation (W m-2)
150
160
170
180
190
200
a
a
b
b
a
CE
CW
NE
NW
S
SE
SW
Lowest weekly radiation (W m-2)
110
130
150
ab
b
c
a
a
c
CE
CW
NE
NW
S
SE
SW
Radiation of coldest quarter (W m-2)
100
120
140
160
180
ab
ab
a
b
CE
CW
NE
NW
S
SE
SW


Biogeographic Districts
Natural vegetation
Conservation Unities
Strict Protection
Sustainable Use
Indigenous Territory
SW
NW
NE
CW
CE
SE
SW
S


Biogeographic Districts
Natural vegetation
Conservation Unities
Strict Protection
Sustainable Use
Indigenous Territory
NE
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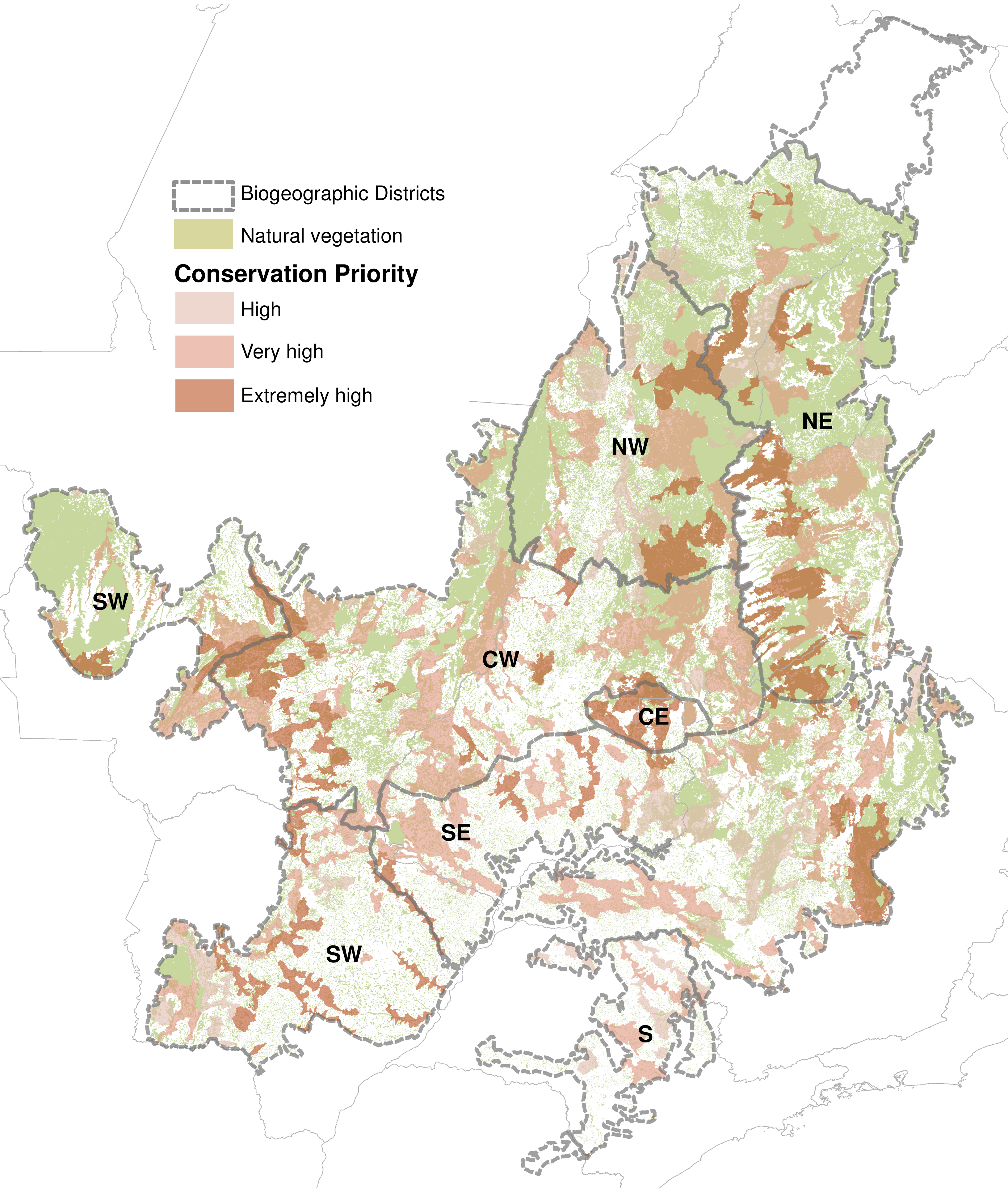
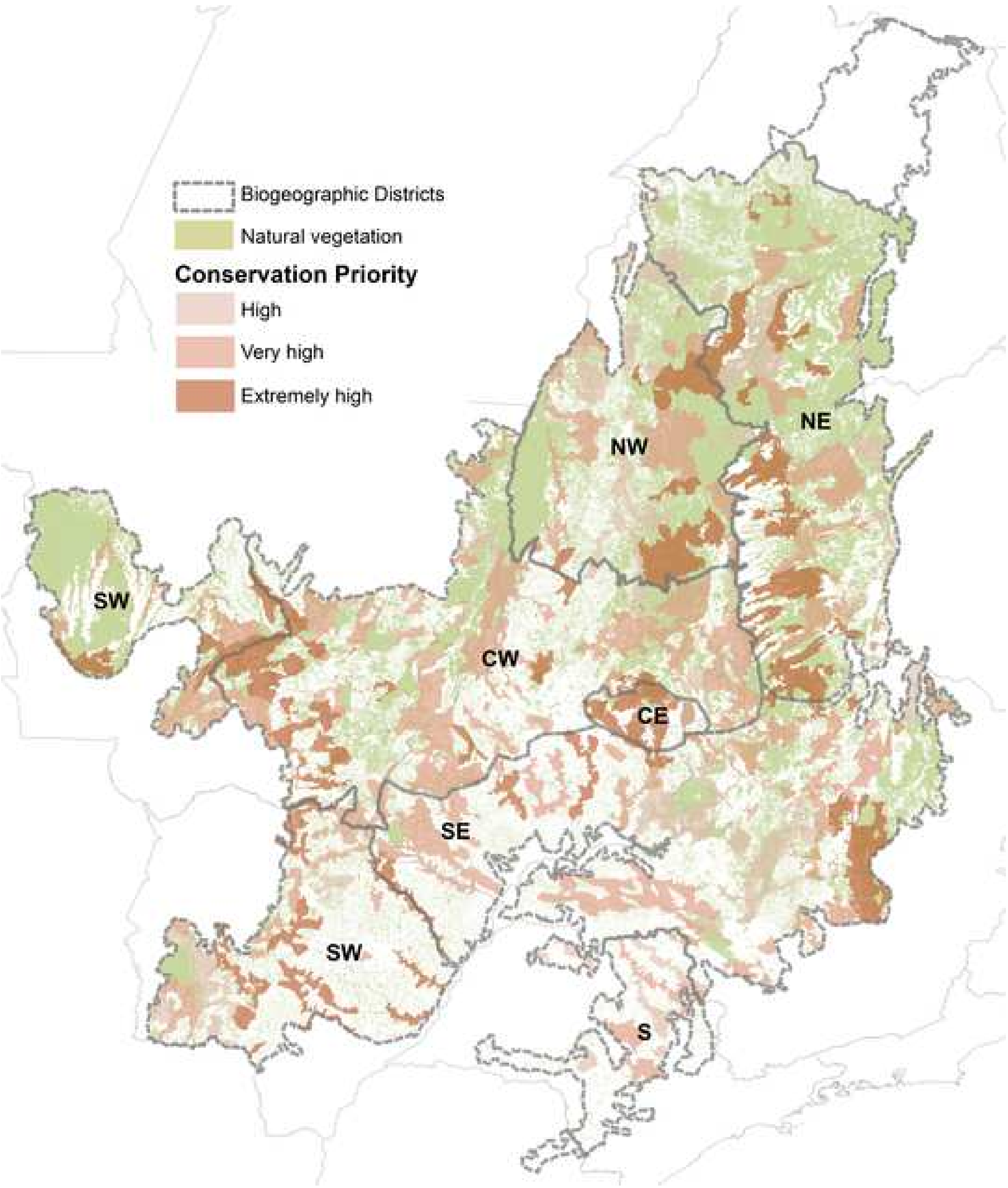

Biogeographic Districts
Natural vegetation
Conservation Priority
High
Very high
Extremely high
NE
NW
SW
CW
CE
SE
SW
S


Biogeographic Districts
Natural vegetation
Conservation Priority
High
Very high
Extremely high
SW
NW
NE
CW
CE
SE
SW
S

Online resource 1