

Can *campo rupestre* vegetation be floristically delimited based on vascular plant genera?

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Abstract A number of floristic and vegetation studies apply the terms *campo rupestre*, *campo de altitude* (or *Brazilian páramo*), and *Tepui* to neotropical azonal outcrop and montane vegetation. All of these are known to harbor considerable numbers of endemic plant species and to share several genera. In order to determine whether currently known combinations of vascular plant genera could help circumscribe and distinguish these vegetation types, we selected 25 floras which did not exclude herbs and compiled them into a single database. We then compared the Sørensen similarities of the genus–assemblages using the numbers of native species in the resulting 1945 genera by multivariate analysis. We found that the circumscription of *campo rupestre* and other Neotropical outcrop vegetation types may not rely exclusively on a combination of genera.

Keywords Vegetation classification · *Campo de altitude* · *Cerrado* · Endemism · Azonal vegetation · Brazil

Introduction

The recognition of community types and their subsequent classification are fundamental tools for scientifically sound landscape and environmental management and biodiversity surveys (for instance Holzner et al. 1986; Humphries et al. 2007; Stanová and Valachovič 2002; Vicensíková and Polák 2003), studies of biogeography (Culek 1996), and ecological conditions (Beskorovainaya and Tarasov 2004; Speisman and Cumming 2007). Classification requires names, but useful names are always too short to be able to convey the variability and richness which they are intended to represent.

The Brazilian word *campo*, when applied to vegetation complexes, means very open vegetation, usually with a negligible tree layer. Various types of *campo* are loosely recognized in Brazilian vegetation, such as *campo de altitude*, *campo limpo* and *campo sujo*, *campo úmido*, and *campo rupestre* (Mendonça et al. 1998; Rizzini 1997). In current botanical literature, *campo rupestre* (from the Lat. *rupestris* meaning “rocky”) is being used to describe Brazilian vegetation with growing frequency (Alves et al. 2007; Alves and Kolbek 1993, 1994; Conceição

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2006; Conceição and Giulietti 2002; Conceição and Pirani 2007; Conceição et al. 2007a, 2007b; Kolbek and Alves 2008; Mourão and Stehmann 2007; Queiroz et al. 1996; Stannard et al. 1995, etc.) which indicates that the name is considered useful.

The *campos rupestres* share several (usually woody) plant species with surrounding savannas and can even be physiognomically similar to *cerrado* (Gottsberger and Silberbauer-Gottsberger 2006). In Brazil, while *cerrado* (zonal savanna) surrounds isolated *campos rupestres* in the state of Goiás and roughly the southern half of the Espinhaço mountain chain, in the northern half of the latter, it is mostly replaced by *caatinga* (Conceição et al. 2007a; Conceição and Giulietti 2002). Several isolated outliers with *campo rupestre* floristic elements occur dislodged from the main Espinhaço chain axis, for instance to the north in the Serra dos Carajás (*canga* on ironstone outcrops protruding from Amazon rainforest) in the State of Pará (Secco and Lobo 1988; Secco and Mesquita 1983; Silva et al. 1996). Within the *Cerrado* domain, detached from the Espinhaço chain, *campo rupestre* on quartzite outcrops occurs south in the Carrancas, Lenheiro, Ouro Grosso and São José ranges (Minas Gerais), west in the Serra Dourada and Serra dos Pirineus (Goiás), and east in the Ibitipoca Range within the domain of the Atlantic rainforest zone of Minas Gerais (Fig. 1).

The terms applied to azonal open outcrop and sand-dwelling vegetation in the Neotropics vary broadly in scale and defining parameters, and is thus difficult to compare. In tropical extra-Andean South America, three main vegetation and floristic complexes associated with outcrops are known: the *Tepuis* on the Guayana shield (usually on sedimentary or metamorphic bedrock) (Steyermark 1979; Anderson 1981; Steyermark et al. 1995), the *campos de altitude* (usually bound to igneous outcrops) (Martinelli 1989; Safford 1999, 2007) and *campos rupestres* (on metamorphic and rarely sedimentary outcrops) on the Brazilian shield (Alves et al. 2007; Stannard et al. 1995). Safford (2007) conducted a genus-level comparison of the *campos de altitude* with several other vegetation types throughout South America. We did not survey the southern *campos* which extend southward of the Brazilian States of Paraná into neighboring countries, because they represent a blocked succession phase tending toward zonal forest vegetation (viz. Behling et al. 2004,



Fig. 1 Localities of *campo rupestre* in Brazil and outcrop vegetation from which floristic data is available. *Solid round dots* *campo rupestre*; *Solid squares* areas with outcrop vegetation and *campo rupestre* floristic elements

2005; Overbeck et al. 2007) and the floristics of their outcrop and mountain components are poorly known. The following assumptions can be made based on available *campo rupestre* surveys:

- 1- *Campo rupestre* is a Brazilian azonal vegetation complex composed by many distinct plant communities (viz. Alves et al. 2007; Conceição et al. 2007a; Conceição and Pirani 2005; Eiten 1978; Giulietti et al. 1987; Harley 1988), and with diversified floristic affinities (Fig. 2).
- 2- The core *campo rupestre* area can be defined as the phytogeographic province of Espinhaço mountains in Bahia and Minas Gerais states and on edaphically comparable outliers in Goiás (viz. Alves et al. 2007; Harley 1988), between latitudes 10°–20°35'S and longitudes 40°10'–44°30'W (Giulietti et al. 2007). It forms a mosaic in altitudes above 600–800 m a.s.l.
- 3- *Campo rupestre* is limited to the presence of rock outcrops (especially quartzite) and the derived shallow, acidic, nutrient-poor, well-drained sandy soils (Alves et al. 2007; de Benites et al. 2003, 2007).
- 4- The main floristic elements typical for the *campo rupestre* complex are combinations of several

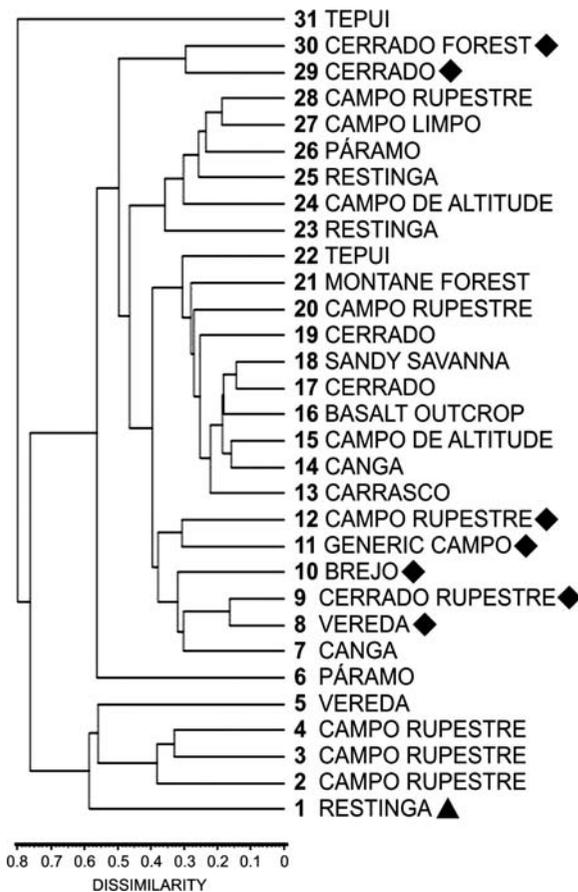


Fig. 2 Dendrogram comparing 29 neotropical open vegetation assemblages and two montane forests, based on hierarchical clustering analysis of species numbers within 1945 vascular plant genera using Sørensen similarity indices. Chord's coefficient was used with β -flexible clustering method ($\beta = -0.25$). Note the high dissimilarities, and that vegetation types designated by similar terms are not clustered together. Floristic sources are enumerated in the methods. *Full topped squares* vegetation subtypes from a single broad survey of the *Cerrado* biome by Mendonça et al. (1998). *Full triangle* broad survey of *restinga* coastal strand (Restinga-Net 2008). All remaining entries are geographically confined localities

species and genera of the Eriocaulaceae, Velloziaceae and Xyridaceae, usually along with *Aulonemia effusa* (Poaceae) and locally endemic species of *Acianthera* (Orchidaceae), *Cambessedesia*, *Chaetostoma*, *Lavoisiera* and *Microlicia* (Melastomataceae), *Diplusodon* (Lythraceae). When combined, these floristic elements distinguish *campo rupestre* from other shrubby/herbaceous outcrop vegetation types, though the latter may harbor a few *campo rupestre* floristic

elements (viz. Alves and Kolbek 2000; Borba et al. 2000, 2002; Giuliatti and Pirani 1988; Harley 1995; Rizzini 1997; Rutter et al. 2007). It is probable that many more exclusive species have been discovered during the last decade.

In this article, we compare *campo rupestre* surveys (Giuliatti et al. 1987; Harley and Simmons 1986; Peron 1989; Pirani et al. 1994; Stannard et al. 1995; Alves and Kolbek 2009) with other Neotropical vegetation bound to outcrops and sand based on their assemblages of vascular plant genera, and briefly address the main environmental variables and life forms which distinguish them.

Methods

We selected floristic checklists from open outcrop vegetation, one montane forest (Rodal and do Nascimento 2002) and one *cerrado* forest. We compared the numbers of species in 1945 vascular plant genera compiled from the 25 selected sources into a single database (numbered here as they appear in Fig. 2, for details see Supplementary material). The sources are: **1**: Restinga-Net (2008); **2**: Stannard et al. (1995); **3**: Alves and Kolbek (2009); **4**: Giuliatti et al. (1987); **5**: Araújo et al. (2002); **6**: Luteyn (1999); **7**: Silva et al. (1996); **8–12**: Mendonça et al. (1998); **13**: de Araújo et al. (1998, 1999); **14**: Mourão and Stehmann (2007); **15**: Safford (2007); **16**: Oliveira and Godoy (2007); **17**: da Costa et al. (2004); **18**: Magnusson et al. (2008); **19**: Weiser and Godoy (2001); **20**: Pirani et al. (1994); **21**: Rodal and do Nascimento (2002); **22**: Huber (1992); **23**: da Costa and Dias (2001); **24**: Caiafa and da Silva (2005); **25**: Zickel et al. (2007); **26**: Sklenář and Jorgensen (1999); **27**: Garcia and Pirani (2005); **28**: Anonymous (2008); **29–30**: Mendonça et al. (1998); and **31**: Huber et al. (1984).

Only the vascular plants determined to genus in each checklist were used for ordination. Due to the lack of species numbers in the Supplementary material for Safford (2007), all genera listed in that supplement were recorded as having a single species. Only surveys which included both herbaceous and woody layers were used. Taxa representing evident human introductions were removed from the data set. For checklists which distinguished the

occurrence of taxa in several vegetation subtypes or localities, each subgroup was recorded separately. Data on the *cerrado* biome was split into seven vegetation types as discerned by Mendonça et al. (1998). As species belonging to a single genus can have very different environmental preferences and the comparison presented is at genus level, we have not computed environmental variables. The genus assemblages for each locality were treated as relevés. Numbers of species in each genus and locality were converted into the Braun-Blanquet seven-index, respectively, discerning one, two, 3–4, 5–6, 7–8, 9–10 and >10 species. Data was pre-ordinated using JUICE 6.5.7 (Tichý 2002) and statistically analyzed in SYN-TAX 2000 software (Podani 2001), using the Sørensen index. We used a hierarchical classification algorithm (complete linkage, Euclidian distance) based on quantitative data, by β -flexible clustering method ($\beta = -0.25$). Chord's coefficient was used. Only the vascular epiphytes determined to genus were used for ordination. Nomenclature of all genera and species follows the Missouri Botanical Garden's VAST nomenclatural database Tropicos.org (2008). Authors of plant names follow Brummitt and Powell (1992). Species distribution data was obtained from literature, the R, RB, and SPF herbaria and complemented by access to the Clayton et al. (2007), GBIF (2007), JBRJ (2007), and USDA (2007) databases. The map (Fig. 1) was plotted using a mapmaking site on the Internet (Weinelt 2007) and edited by imaging software. The term *savanna* is interpreted herein strictly in the physiognomic sense, as usually zonal vegetation with a relatively contiguous herb layer and discontinuous or patchy tree and/or shrub layers. Definitions for *campo rupestre* and related vegetation units are compared based on our own field data and relevant literature.

Results

The resulting dendrogram separated floras with high dissimilarity (Fig. 2). The genus-level composition grouped the three most extensive *campo rupestre* floras (Giulietti et al. 1987, Stannard et al. 1995, Alves and Kolbek 2009) (Fig. 2: 2–4) together with one coastal strand (Fig. 2: 1) and one *vereda*

(marshland) in Minas Gerais (Fig. 2: 5). Another two *campo rupestre* sites, the Serra do Intendente (Fig. 2: 28) ([www.conceicaoomatodentro](http://www.conceicaoomatodentro.com.br) 2008) and the Serra do Ambrósio (Pirani et al. 1994; Fig. 2: 20) are grouped with distinct vegetation types. The last genus-level assemblage for *campo rupestre*, compiled for the entire *cerrado* biome by Mendonça et al. (1998) grouped with the remaining open vegetation types within that biome (Fig. 2: 12). Likewise the *Páramo* and *Tepui* floras (respectively, Fig. 2: 6, 26 and 22, 31) appear scattered throughout the cladogram, indicating that the classification of open vegetation relies heavily on physiognomy and that genus-level comparisons have limited applicability in vegetation classification.

Due to the great number of endemic and vicarious species, genera were expected to prove more useful than species as floristic elements for the circumscription of the *campo rupestre* concept (Table 1). However, this was not corroborated by the multivariate analysis. In the present survey, the combinations of genera alone were not sufficient to circumscribe *campo rupestre*, suggesting that species-level floristic and vegetation analyses incorporating environmental variables shall be necessary in order to better circumscribe currently used vegetation terms for open South American vegetation.

Though the term *campo rupestre* may be considered better circumscribed by the combination of floristic elements and habitat types, when compared, for instance, with the term *cerrado rupestre*, a distinction of vegetation types bound to outcrops within the studied region does not seem tangible to date. Due to the growing number of published data within the last two decades, the terms currently applied to open vegetation types in Brazil should be redefined in order to achieve greater precision.

A sound phytogeographic circumscription of outcrop vegetation types may not rely exclusively on a single character (i.e. floristics, physiognomy, woody species etc.) All these approaches to vegetation classification are complementary. Even when terms used for describing vegetation are relatively well circumscribed, they do not always refer to identical scales and zonalities, which may induce discrepancies in interpretation among users. The azonal types treated in the text are compared in Table 2.

From the currently available data, the following can be concluded:

Table 1 Examples of characteristic, exclusive (or nearly exclusive) genera of Brazilian montane vegetation complexes *campo rupestre* and *campo de altitude* on the Brazilian shield, and the *Tepui* complex of the Guayana shield, with approximate numbers of species

	<i>Campo rupestre</i>	<i>Campo de altitude</i>	<i>Tepuis</i>
Exclusive families	None	None	2
Exclusive genera and subgenera	4	6	39
Exclusive species estimate ^a	1,200	100	766
<i>Lychnophora</i> (Asteraceae)	70		
<i>Barbacenia</i> (Velloziaceae)	65		
<i>Paepalanthus</i> subgen. <i>Xeractis</i> (Eriocaulaceae)	27		
<i>Leiothrix</i> subgen. <i>Leiothrix</i> (Eriocaulaceae)	13		
<i>Svitramia</i> (Melastomataceae)	10		
<i>Acianthera teres</i> group (Orchidaceae)	6		
<i>Pseudotrimezia</i> (Iridaceae)	6		
<i>Burlemarxia</i> (Velloziaceae)	3		
<i>Cipocereus</i> (Cactaceae)	3		
<i>Morithamnus</i> (Asteraceae)	2		
<i>Bishopiella</i> (Asteraceae)	1		
<i>Raylea</i> (Sterculiaceae)	1		
<i>Prepusa</i> (Gentianaceae)		3	
<i>Glaziophyton</i> (Poaceae)		1	
<i>Worsleya</i> (Amaryllidaceae)		1	
<i>Itatiaia</i> (Melastomataceae)		1	
<i>Magdalenaea</i> (Scrophulariaceae)		1	
<i>Nothochilus</i> (Scrophulariaceae)		1	
<i>Lindmannia</i> (Bromeliaceae)			40
<i>Brocchinia</i> (Bromeliaceae)			20
<i>Tepuia</i> (Ericaceae)			10
Tepuianthaceae (all species)			8
<i>Connellia</i> (Bromeliaceae)			6
<i>Ayensua</i> (Bromeliaceae)			1
<i>Orectanthe</i> (Xyridaceae)			1
<i>Quelchia</i> (Asteraceae)			1

^a Compiled from several sources cited in Table 2

1. *Campo rupestre* can not be distinguished from other open vegetation types based exclusively on genus-level comparison of currently available data. For instance, the genus-level similarity between two distant localities with *canga* (vegetation on ironstone), one in Pará and another in Minas Gerais (viz. Jacobi et al. 2007; Secco and Mesquita 1983; Simmons 1963) did not prove to be significantly higher than that between *canga* and other *campo rupestre* outcrop vegetation (Fig. 2; Tables 1 and 2).
2. Currently, there is no reason supported by hard floristic data for the distinction of *cerrado rupestre* from *campo rupestre* (viz. Amaral et al. 2006; Felfili and Fagg 2007; Mendonça et al. 1998).

Discussion

Campo rupestre

As interpreted by recent authors, the *campos rupestres* are a peculiar, species-rich, vegetation complex forming an archipelago of isolated mountains of the Brazilian shield (rarely also on flat rock outcrops not protruding from the surrounding terrain), at altitudes ranging approximately from 800 to 2000 m a.s.l. in Brazil (Eiten 1978). The most constant feature mentioned by most authors as typical of *campo rupestre* is apparently the quartzite bedrock, though there are mentions of granitic-gneiss (Queiroz et al. 1996) and ironstone (Viana and Lombardi 2007). Outcrops of various sizes alternate with fissures and

Table 2 Scale and comparison of main characteristics of Brazilian and South American open vegetation referred in the text. A. Vegetation types with relatively uniform physiognomies. B. Vegetation complexes comprising several physiognomic types

A. Types based on physiognomy		
Amazon <i>caatinga</i> or <i>campina</i>	Species-poor white-sand savanna surrounded by Amazon rainforest. A few endemic woody species are known.	Anderson 1981, Magnusson et al. 2008 (18)
<i>Campo limpo</i>	Open grassy savanna with (almost) no woody species.	Loefgren 1890, 1898, Lindman 1906, Rizzini 1997, Munhoz and Felfili 2006, Garcia and Pirani 2005 (27)
<i>Campo sujo</i>	Open grassy savanna with few small woody species.	Munhoz and Felfili 2007
<i>Campo úmido</i>	Permanently wet savanna or field. Herb layer with Poaceae/Cyperaceae.	Eiten 1978, Tannus and Assis 2004
<i>Carrasco</i>	Arid white-sand savanna with deep sand layer, within the <i>Caatinga</i> biome. Annual rainfall <1,300 mm.	Andrade-Lima 1978, de Araújo et al. 1998, 1999 (13)
<i>Cerrado rupestre</i>	Savanna on rock outcrops lacking fine soil; floristic elements of <i>campo rupestre</i> (Velloziaceae etc.) occasionally present. Subtype of <i>Cerrado</i> biome.	Amaral et al. 2006, Mendonça et al. 1998 (9), Felfili and Fagg 2007, Ritter 2008, Oliveira and Godoy 2007 (16)
<i>Vereda</i>	Permanently wet savanna with <i>Mauritia flexuosa</i> palms. Subtype of <i>Cerrado</i> biome.	Munhoz and Felfili 2007, Eiten 1984, Filgueiras 1991, Araújo et al. 2002 (5), Mendonça et al. 1998 (8)
B. Vegetation complexes		
<i>Campo de altitude/páramo</i>	Stands of various physiognomies bound to igneous inselbergs (granite or nepheline-syenite), <i>Cortaderia</i> and many other taxa disjunct with high Andes; Monocotyledonous mats and giant rosette plants (<i>Alcantarea</i>). >1500 m a.s.l. Rain and mist all year long.	Martinelli 1989, Safford 1999, Luteyn 1999 (6), Caiafa and da Silva 2005 (15), Safford 2007 (24), Safford and Martinelli 2000, Sklenář and Jorgensen 1999 (26)
<i>Campo rupestre</i>	Stands of various physiognomies bound to montane quartzite outcrops and white sand. Many ericoid and cruciate subshrubs with lignotubers; monocotyledonous mats. 800–2,000 m a.s.l. Horizontal precipitation is an important factor.	Eiten 1978, Harley 1995, Conceição and Pirani 2007, Conceição and Giulietti 2002, Rizzini 1997, Alves et al. 2007, Stannard et al. 1995 (2), Alves and Kolbek 2009 (3), Giulietti et al. 1987 (4), Pirani et al. 1994 (28)
<i>Canga</i>	Stands of various physiognomies bound to ironstone outcrops and lateritic crusts. Many ericoid and cruciate subshrubs with lignotubers; monocotyledonous mats.	Simmons 1963, Secco and Mesquita 1983, Jacobi et al. 2007, Silva et al. 1996 (7), Mourão and Stehmann 2007 (14)
<i>Cerrado</i>	Generic savanna and associated vegetation (gallery forest, <i>campo</i> , etc.) on deep latossol.	Costa da et al. 2004 (17), Weiser and Godoy 2001 (19), Batalha and Mantovani 2001 (19), Mendonça et al. 1998 (8–12, 29, 30)
<i>Restinga</i>	Quaternary, Atlantic, psammic, coastal strand vegetation with distinct zonation, and various physiognomies. Many plant species present also occur in <i>campo rupestre</i> .	Costa da and Dias 2001 (1), Alves et al. 2007, Restinga-Net 2008 www.restinga.net/flora.asp , (23) Zickel et al. 2007 (25)
<i>Tepui</i>	Table mountains on the Guayana shield (usually quartzite or sandstone). Vegetation of various physiognomies. Caulirosette shrubs and hygrophilous herbs prevail. Surrounded by Amazon rainforest. 1,500–3,000 m a.s.l. Rainy all year.	Berry et al. 1995, Dinerstein et al. 1995, De Granville 1991, Maguire and Steyermark 1981, Maguire and Murça Pires 1978, Prance and Johnson 1991, Steyermark 1979, Huber et al. 1984 (22), Huber 1992 (31)

Numbers in parentheses correspond to references used in the multivariate analysis (Fig. 1)

white sand deposits. Local drainage systems dictated by topography further diversify this environment by creating relatively humid or arid sites, often separated from each other by a few centimeters. Possibly with the exception of large and homogenous white-sand grasslands described herein and occasional relict patches of typical *cerrado* (Eiten 1972), the plant communities form mosaics that can hardly be described in detail by traditional methods which use symmetrically distributed sample plots, regular plot shapes and sizes, or which rely exclusively on thick-stemmed woody species. Several distinct vegetation types comprise the *campos rupestres*, ranging from seasonally flooded grasslands on white-sand, sometimes covered by milky-quartz gravel, in which shrubs and trees usually do not form a closed canopy, to savanna tree-shrub formations with a contiguous herb layer, to communities on bare cliff faces. Special, species-poor epiphytic communities on shrubby *Vellozia* sp. div. (Werneck and Espírito-Santo do 2002, Alves et al. 2008) and rare patches of cloud forest (Menini Neto et al. 2007) also occur. Humid streamside vegetation includes dense, low stands in which the shrub and herb layer have many peculiar Melastomataceae (especially hygrophilous species of *Acisanthera*, *Clidemia*, *Lavoisiera*, *Microlicia*, *Rhynchanthera* and *Trembleya*).

Eiten (1978) considered the *campos rupestres* and the *cerrado* to be distinct floristic elements, but considered distinguishing one from the other “one of the most difficult problems”. The woody species of the former can be distinguished by “squarrose and cruciate herbs” and shrubs and small trees in with cruciately disposed leaves congested at the branch apices and candelabra-like branching, a growth form the author considers totally absent from *cerrado*. However, the author points out that several typical *cerrado* species often occur in adjacent *campo rupestre*. This may partly be explained by overlapping soils: we have observed several cases in which a layer of white sand, gradually transported down mountain slopes, overlies adjacent latossol. In these cases, *campo rupestre* species prevail in the herb layer, while most trees and shrubs are typical of *cerrado*. The underlying red–yellow latossol is often brought to the surface by ants and termites, and the color of their mounds contrasts with the white-sand surface. Our observations corroborate those of Eiten

(1978), in that woody species typical of *campo rupestre* are able to grow on outcrops and on oligotrophic sandy soils, whereas those from the *cerrado* usually cannot.

Campo rupestre can be rich in vascular plant species: 1626 species were found in the Cipó range, on roughly 200 km² (Giulietti et al. 1987) and 1053 species on the Pico das Almas, with ca. 170 km² (Stannard et al. 1995); In the São José range, 1144 vascular species were reported from less than 25 km² of *campo rupestre* (Alves and Kolbek 2009), and if these are combined with the forest species of the same range (Oliveira Filho and Machado 1993; Gonzaga et al. 2008) a total of 1500 species is reached in that small area. Distant *campos rupestres* can share similar many genera, but there are many cases of endemism with many vicarious species (Alves and Kolbek 1994; Conceição and Giulietti 2002; Conceição and Pirani 2007); hence *campo rupestre*, as currently circumscribed, can have quite distinct generic assemblages, as suggested by Fig. 2 and the Supplementary material. The notoriously high number of species restricted to isolated outcrop environments such as *campo rupestre* (when compared to the surrounding matrix of zonal vegetation) may be due to their isolation (Conceição et al. 2007a; Giulietti and Pirani 1988; Ibsch et al. 1995; Safford and Martinelli 2000). On the other hand, the large proportion of genera and families shared by the *campos rupestres* seems to be a consequence of their typically harsh environments (but see Körner 2003), the occupation of which demands special adaptations restricted to certain taxa (Burrows 1990; Conceição et al. 2007a). de Benites et al. (2003) comment on *campo rupestre*: “Morphological and physiological adaptation of plants to soil constraints and burning provide this ecosystem with a relevant genetic bank still to be investigated.” This isolation can be at least partly attributed to altitude (Alves and Kolbek 1994; Harley 1995), but available evidence points to edaphic isolation as the primary cause (Alves et al. 2007; Rizzini 1997).

Rizzini (1997) did not find it useful to distinguish *campo rupestre* from the so-called *campo limpo* (clean field), a term of earlier authors like Loefgren (1890, 1898) and later Lindman (1906), apparently conceived in allusion to lack of shrubs and trees.

Comparison with other outcrop vegetation types in Brazil (also see Supplementary materials)

One comparable vegetation type, the *campos de altitude* (Martinelli 1989 etc.) or “Brazilian páramos” (Safford 2007), are a vegetation complex which basically differs from *campo rupestre* (on quartzite) by occurring on other rocks such as granite or, in the case of the Itatiaia plateau, on Nepheline-syenite. de Benites et al. (2003) distinguish rupestrine soil complexes on quartzite from those on granite, following Semir (1991). The genera *Glaziophyton* (Poaceae), *Prepusa* (Gentianaceae) and *Worsleya* (Amaryllidaceae) are endemic to the *campos de altitude* (Martinelli 1989). As a consequence of altitudes (>1,500 m a.s.l.) and relative ocean proximity, there are far more hygropilous species and epiphytes per unit of area in the *campo de altitude* than in comparable areas of *campo rupestre*. In a recent genus-level comparison of three *campos de altitude* with 17, rather heterogeneous floristic lists, Safford (2007) concluded that: (1) The current floras of both the *campos de altitude* and the Andes are of mixed origin, derived of tropical, temperate and cosmopolitan evolutionary stock, and (2) That relatively low numbers of locally endemic genera exist in the *campos de altitude*. Using 334 typical genera, he further suggested that the floristic similarity is higher between the *campos de altitude* and very distant sites in the tropical Andes than between the *campos de altitude* and the much nearer low and middle-elevation sites in central and eastern Brazil. This floristic affinity of *campos de altitude* with the Andes is apparently not shared by the *campos rupestres*.

Cerrado rupestre (Amaral et al. 2006; Mendonça et al. 1998; Oliveira and Godoy 2007; Ritter 2008) or “*cerrado sensu stricto* on rocky soil” (Felfili and Fagg 2007) are azonal savannas on outcrops, litholic soils and lateritic/limonitic hardpans in the *cerrado* biome. *Cerrado rupestre* is very difficult to circumscribe because no consistent distinctive floristic element has been proposed (see Supplementary material), and the substrates emulate those of *campo rupestre*.

Several other terms are based purely on physiognomy. *Campo limpo* (sensu Lindman 1906; Loefgren 1890, 1898) means “clean field”. The same name was also applied to subtropical grasslands in Southern Brazil by Rodrigues et al. (2005). *Campo úmido* means “humid field”, while *vereda* refers small areas

of permanent grassy marshes with *Mauritia flexuosa* palms (Munhoz and Felfili 2007). *Campo sujo* (“dirty field” due to the presence of scattered woody species) is a predominantly herbaceous stand with sparse, low woody species. Though Eiten (1984) and Filgueiras (1991) are often cited as having defined these vegetation types, all these terms lack precise floristic and ecological circumscriptions. In the *cerrado*, *campo sujo* represent areas dominated by grasses, with the woody layer covering <10% (Munhoz and Felfili 2007). These terms are usually used to characterize stands within the *cerrado* biome (viz. Munhoz and Felfili 2006, 2007; Nemoto and Libeiro 2005).

Summits of the *Tepuis*, which are table mountains on the Guayana shield, can have a remarkably similar physiognomy to vegetation growing on outcrops in the *campos rupestres*. In comparison, the *Tepuis* have an even higher percentage of endemic species and uncommon adaptations (Berry et al. 1995; Dinerstein et al. 1995), but this discrepancy may be the result of distinct collection efforts and different intensities of human activity. De Granville (1991) suggested that the genus *Trilepis* and the species *Doryopteris sagittifolia* and *Banisteriopsis gardneriana* are floristic links of the *tepuis* and southernmost *campos rupestres*, but these taxa proved to be more widespread: herbarium data (NY, RB) indicate that all of these occur in several zonal biomes. Ibsch et al. (2001) consider *Vellozia andina* to be the only truly Andean species of the genus, but this curious taxon was not included in the phylogenetic classifications proposed by neither Salatino et al. (2001) nor Mello-Silva (2005). *Tepuis* have some exclusive plant families including the Tepuianthaceae and Saccifoliaceae (Maguire and Steyermark 1981; Maguire and Murça Pires 1978, Prance and Johnson 1991), and 39 genera are endemic to *tepuí* summits (De Granville 1991; Steyermark et al. 1995). The family Rapateaceae has its center of diversity in the *tepuí* region, while only one endemic species, *Cephalostemon riedelianus*, can be found in the *campos rupestres*, with the southern distribution limit apparently in the Serra do Cipó (Giulietti et al. 1997). A second species, *Cephalostemon angustatus* occurs in the *Veredas* of Minas Gerais (Araújo et al. 2002). Steyermark (1979) considered the presence of the *campo rupestre* elements *Comolia*, *Syngonanthus*, and *Paepalanthus* the result of centripetal immigration into the *Tepuis*.

Inselbergs are a geological term applied to igneous outcrops, which are frequently dome-shaped due to the distinct dissolution pattern the gneiss and/or granite. Isolated inselbergs are widespread throughout much of Latin America, in several distinct climatic zones. Consequently, inselberg vegetation is very variable, consisting mainly of tree/shrub communities on their summits and herbaceous/subshrub cliff-face assemblages including monocotyledonous mats (Porembski et al. 1996). The white-sand component of *campo rupestre* is not known from inselbergs.

Surrounding zonal vegetation

Cerrado, as defined by Eiten (1978) is “the general name given to the xeromorphic woodland scrub, savanna and grassfield vegetation of central Brazil”. It is the largest contiguous Neotropical savanna biome, forming a contiguous area in parts of the Brazilian states of Goiás, Tocantins, Distrito Federal, Bahia, Ceará, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Piauí, Rondonia, and São Paulo, and also occurring in isolated patches to the north in Amapá, Amazonas, Pará and Roraima, and to the south in small patches in Paraná (Ribeiro and Walter 1998). About two-thirds of the *Cerrado* vascular flora (ca. 4,000 species) grow exclusively in the *campos rupestres* (Alves et al. 2007; Sano and de Almeida 1998), outside its core region. Within the *cerrado* biome, various forms of open vegetation have been described.

Typical *cerrado* tree species have several peculiar growth strategies: their above-ground parts can resemble seedlings for many years after germination, while substantial growth occurs in their root systems. Above-ground growth begins only once the roots reach the deep water-table. Many tree species exhibit clonal growth: the apparent individuals are linked by underground rhizomes (Rizzini 1997). While there are probably hundreds of physiognomic subtypes in the *Cerrado* on latossol (including many forms of *campo*), the *campo rupestre* mosaic is apparently simpler because it is restricted to outcrops and shallow, litholic soils (Silva et al. 2004).

Caatinga is often savanna vegetation with an ephemeral rainy season, which occupies most of the 900,000 km² of semi-arid, Northeastern Brazil (Queiroz 2006a), into which the *campos rupestres* of the

northern half of the Espinhaço chain are inserted (Alves et al. 2007). Most of the vegetation seems dry and dead for long periods, while buds remain dormant. Both the woody and herbaceous layers can be discontinuous, and the herb layer is short-lived and mainly constituted by therophytes and geophytes that emerge only in the short rainy season (Queiroz 2006a). Despite the arid climate, the *caatinga* biome can have surprising species richness: with around 1,012 registered species of Angiosperms (Gamarrar-Rojas and Sampaio 2002), of which 18 genera and 318 species (ca. 31%) are considered endemic (Giulietti et al. 2002; Queiroz 2006b). As is true for the *Cerrado*, it is probable that a large part of the *Caatinga* alpha-diversity is really represented by *campo rupestre* species. However, the carrasco vegetation on deep quartz sand within this biome is species-poor (viz. de Araújo et al. 1998, 1999).

Prior to the current levels of deforestation of the Atlantic Rainforest, called “*Mata Atlantica*”, once surrounded the Ibitipoca range in Minas Gerais, some floristic elements of *campo rupestre* were also found in localities like the Serra de Ricardo Franco in Mato Grosso, within the domain of Pantanal zonal vegetation on the Bolivian border (Paulo G. Windisch, personal communication), the Serra do Cachimbo in the State of Pará, in contact with Amazonian rainforest (Pires and Prance 1985).

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