**UNIVERSIDADE FEDERAL DE MINAS GERAIS**
**INSTITUTO DE CIÊNCIAS BIOLÓGICAS**
Departamento de Botânica
**Programa de Pós-Graduação em Biologia Vegetal**

**LUIZA FONSECA AMORIM DE PAULA**

# COMUNIDADES VEGETAIS EM INSELBERG: ASPECTOS FLORÍSTICOS E FUNCIONAIS

**Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Mestre em Biologia Vegetal.**

**Área de Concentração: Florística e Biogeografia; Estrutura e Dinâmica de Comunidades Vegetais**

**BELO HORIZONTE – MG**

**2014**

**UNIVERSIDADE FEDERAL DE MINAS GERAIS**
**INSTITUTO DE CIÊNCIAS BIOLÓGICAS**
Departamento de Botânica
**Programa de Pós-Graduação em Biologia Vegetal**

**LUIZA FONSECA AMORIM DE PAULA**

# COMUNIDADES VEGETAIS EM INSELBERG: ASPECTOS FLORÍSTICOS E FUNCIONAIS

**Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Mestre em Biologia Vegetal.**

**Área de Concentração: Florística e Biogeografia; Estrutura e Dinâmica de Comunidades Vegetais**

**Orientador: Prof. Dr. João Renato Stehmann**
**Universidade Federal de Minas Gerais**

**Coorientador: Prof. Dr. Fernando Augusto O. Silveira**
**Universidade Federal de Minas Gerais**

**BELO HORIZONTE – MG**

**2014**

043 Paula, Luiza Fonseca Amorim de.
Comunidades vegetais em Inselberg : aspectos florísticos e funcionais [manuscrito] / Luiza Fonseca Amorim de Paula. – 2014.

98 f. : il. ; 29,5 cm.

Orientador: João Renato Stehmann. Co-orientador: Fernando Augusto O. Silveira.

Dissertação (mestrado) – Universidade Federal de Minas Gerais, Departamento de Botânica.

1. Inselberg – Mucuri, Vale do (MG) - Teses. 2. Afloramento granítico – Teses. 3. Biodiversidade – Conservação – Teses. 4. Ecologia funcional – Teses. 5. Mata Atlântica – Teses. 6. Endemismo – Teses. 7. Traços funcionais – Teses. 8. Comunidades vegetais – Teses. 9. Biologia vegetal – Teses. I. Stehmann, João Renato. II. Silveira, Fernando Augusto Oliveira e. III. Universidade Federal de Minas Gerais. Departamento de Botânica. IV. Título.

CDU: 581

**Dissertação defendida e aprovada, em 20 de janeiro de 2015, pela banca examinadora constituída pelos professores:**

Dr. João Renato Stehmann – orientador- UFMG

Bruno Rosado

Dr. Bruno Henrique Pimentel Rosado- Universidade do Estado do Rio de Janeiro

Flávio Fonseca do Carmo

Dr. Flávio Fonseca do Carmo- Instituto Prístino

Dedico esse trabalho aos meus pais e ao meu irmão,
trio inseparável da minha vida**.**

# AGRADECIMENTOS

Chego ao final dessa etapa com um imenso sentimento de gratidão. A natureza tem seus mistérios, sou grata por seus segredos, pela mágica da perfeição. Certamente não teria chegado até aqui sem a ajuda de diversas pessoas que fui encontrando nessa caminhada, todo o texto que se faz presente nas próximas páginas é fruto de troca de idéias, sonhos que se concretizaram e tornaram-se realidade.

Descobri que ciência se faz através de co-labor-ação. Por um lado, a solidão é a nossa maior companhia durante as infinitas horas na frente do computador, por outro, só existe conteúdo para ser preparado se idéias conjuntas são criadas. Sinto-me grata por ter encontrado pessoas tão especiais, que colaboraram profundamente na elaboração dessa dissertação.

Agradeço primeiramente aos meus pais, Marcelo e Ana Lúcia, por todo o carinho e atenção, por terem me ensinado a amar a Natureza com profundo respeito, e por terem participado efetivamente de cada etapa deste trabalho, desde a primeira expedição exploratória à Pedra em 2010 (acompanhada de Fortificante Sobe Pedra) até o segundo final da redação. Ao meu irmão, Marcelinho, por mesmo cansado de subir pedras, nunca ter se negado a dar aquela subidinha.

Ao meu orientador João Renato, por ter me dado a oportunidade de trabalhar com o que gosto, respeitar e sempre apoiar as minhas idéias.

Ao meu co-orientador Fernando Silveira (Lele), amigo de todas as horas, pela paciência infinita, disposição e pelos conselhos acadêmicos. Obrigada pelas diversas horas de discussão, por toda a sua atenção nesses últimos dois anos. Quem diria que uma conversa casual em um Congresso de Ecologia nos proporcionaria essa parceria tão especial. Vamos *vompliacar* o mundo todo, Lele!

Minha eterna gratidão à Lu e ao Renato, companheiros de jornada. Aprendi com eles que os detalhes fazem a diferença, que um pseudoescorpião mais vale que um diamante e que existe encanto em cada folha que cai. Prometo lavar as mãos sempre antes de comer, ok?

Ao Theo, por me mostrar que existe amor correspondido, pela compreensão de sempre, pela segurança, e por conhecer cada suspiro desse trabalho.

Ao Daniel, meus sinceros agradecimentos pelos inúmeros artigos compartilhados, pelos e-mails empolgantes com idéias, discussões fervorosas...ele me mostrou realmente o que é colaborar em um trabalho.

À Nilza, pelos caprichos, cuidados e pelo cafezinho à tarde.

À D. Mara, pelas comidinhas gostosas.

Aos doguitos, Tião e Cisco, pela companhia fiel.

À Nara e ao Pedrinho, pela iniciação botânica. Sem eles não teria conhecido o maravilhoso mundo das plantas.

Aos colegas do Laboratório de Sistemática Vegetal, obrigada pela vivência, pelas risadas e por todos os cafezinhos sem açúcar.

Aos colegas do Leept, obrigada pelos encontros, festinhas e discussões extremamente esclarecedoras.

Ao Eduardo Arcoverde e à Sara Colmenares, por terem sido tão atenciosos e pelas discussões a respeito de diversos aspectos funcionais das comunidades de inselbergs.

Aos companheiros de caminhada botânica, brejas, papo furado, imersões astrais, em especial à Mari Augsten, Tulio Jorge, Timão, Pablito e Felipe Leite .

À família Addiny, por permitir que coletássemos em sua propriedade e por todo apoio logístico.

Ao Lucas, Eline e Caique, obrigada pelos ovos cozidos e suporte de montaria ao longo desses quatro anos de coleta.

Ao Stefan Porembski, por decolar milhas e milhas para conhecer a Pedra do Bagão, obrigada pelas idéias e incentivos.

À todos que escalaram a Pedra do Bagão: Pai, Mãe, Cece, Creuso, Zé Carlos, Lucas, Nara M., Pedro V., Pablo B., Tulio J., Mariana A., Luiz Fernando L., Felipe L., Rafael D., Josme, Rafael P., Cristiano D., Samuel S., Luísa A., Renato F., Joyce T., João Renato S., Fernando S., Luiza C., Márcio, Saulo, Stefan P.

Ao D.A. Biologia, obrigada por todos os momentos filosóficos, de descontração, criação, revolução.....

Ao Conselho Nacional de Pesquisa e Desenvolvimento (CNPq), por ter sido meu fiel financiador durante o Mestrado.

À UFMG, minha segunda casa nesses últimos sete anos, espero que a graminha, a música e os diversos cantinhos secretos continuem a existir nesse espaço de efervescência de mentes.

Por fim, agradeço ao Manuel de Barros, por me encantar em cada detalhe escondido em seus poemas, e como diria ele: “Não tem altura o silêncio das pedras”.

ARVORES-SER

*“ Se-mentes efervescem, germinam!*
*Afloram belas flores e trazem feliz-idades!*
*O ciclo de mentes efervescentes entra em harmonia.*
*E dessa ressonância, se produz música, alegria!*
*Dos frutos, amadurecem sentimentos.*
*A amizade se consolida, lignifica-se!*
*Estrutura-se uma linha de crescimento,*
*Um novo momento! “*

Lu(í)Sa Azevedo

# SUMÁRIO

RESUMO GERAL……...........................................................................................................1
ABSTRACT……...……..........................................................................................................3
INTRODUÇÃO GERAL.........................................................................................................5

**CAPÍTULO I – Plant communities on an inselberg in Minas Gerais state, southeastern Brazil: species composition and ecological characterization**

Abstract .................................................................................................................20
Introduction...........................................................................................................21
Material and methods.........................................................................................23
Results....................................................................................................................27
Discussion..............................................................................................................37
Color guide.............................................................................................................54

**CAPÍTULO II – Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic Forest**

Abstract .................................................................................................................60
Introduction...........................................................................................................61
Material and methods.........................................................................................64
Results....................................................................................................................69
Discussion..............................................................................................................76
Suplementary information (Online Resource 1)...........................................89
Suplementary information (Online Resource 2)...........................................90
Suplementary information (Online Resource 3)...........................................91
Suplementary information (Online Resource 4)...........................................92
CONSIDERAÇÕES FINAIS ..................................................................................96

## Lista de figuras

### Introdução Geral

**Figura 1:** Número de artigos publicados resultantes da busca com o termo "inselberg" na base de dados do Web of Knowledge e Scielo, entre os anos de 1987 a 2013 (busca em 20 de Junho de 2014), artigos indexados em ambas as bases foram considerados apenas uma vez....9

**Figura 2:** Número de estudos publicados por continente, divididos por área de pesquisa, resultantes da busca com o termo "inselberg" na base de dados do Web of Knowledge e Scielo, entre os anos de 1987 a 2013 (busca em 20 de Junho de 2014). O total de artigos é maior do que 136 porque alguns artigos se encaixaram em mais de uma área de pesquisa.....10

### Capítulo I

**Figura 1:** Map of the biomes occurring in Minas Gerais state, southeastern Brazil. The study area, represented by a triangle, is inserted into an Atlantic Forest matrix, but it is considered a transition zone due to the proximity to both Caatinga and Cerrado biomes…………………..24

**Figura 2:** A. Overview of the inselberg studied in the Mucuri Valley, Minas Gerais state, southeastern Brazil; vegetation patches are visible on the flat part of the rock and in the the background the landscape is dominated by inselbergs. B. A typical vegetation patch of the inselberg studied, *Barbacenia tomentosa* Mart. is forming a mat in the border, the shrub *Cnidoscolus* aff. *lombardii* Fern.Casas is occupying the center region and the African invasive species *Melinis repens* (Willd.) Zizka is dominating the back part of the patch……………..25

**Figura 3:** Percentage of life-forms in each habitat record in an inselberg located in Minas Gerais state, southeastern Brazil. Life-form abbreviations: Ph=phanerophyte, Ch=chamephyte, Cr=criptophyte, H=hemicriptophyte, Th=therophyte. Habitat abbreviations: SD = shallow depression, MM = monocot mat, EFV = ephemeral flush vegetation, EV = epilithic vegetation, C = crevices……………………………………………………………..28

**Figura 4:** Cluster analysis, with the unweighted pair group method with arithmetic mean

(UPGMA), of the habitats found in an inselberg sampled in Minas Gerais state, southeastern Brazil, in relation to the presence of angiosperm species. Habitat abbreviations: EFV = ephemeral flush vegetation, EV = epilithic vegetation, MM = monocot mat, C= crevice, SD = shallow depression……………………………………………………………………31

**Capítulo II**

**Figura 1:** CSR classification showing the relative importance of the C (competitiveness), S (stress-tolerant) and R (ruderalism) axes in plant species (a) and in vegetation patches (b) from inselberg communities at Minas Gerais, south-eastern Brazil. Principal component analyses of 53 species (c) and patches (d) in inselberg plant communities. In panel (d) values of competitiveness, stress-tolerance, ruderalism, specific leaf area, leaf toughness, leaf area, leaf width, canopy height and seed mass correspond to the community mean trait values. In panels (b) and (d), each patch has a symbol specifying its predominant microhabitat, SD: shallow depression; M: mat; EFV: ephemeral flush vegetation; E: epilithic; and C: crevice…......................................................................................................................71

**Figura 2:** Results of the fourth corner test showing the connection between environmental parameters of vegetation patches and functional traits of species from inselberg plant communities at Minas Gerais, south-eastern Brazil. Significant positive associations are represented by red cells, and significant negative associations correspond to blue cells (* p<0,05;** p<0,01). Non-significant associations are shown in grey…………………………72

**Figura 3:** Results of the first two axes of RLQ analysis showing the relationship between environmental parameters of vegetation patches and functional traits from inselberg plant communities at Minas Gerais, south-eastern Brazil: Pearson's correlation between environmental parameters (a), functional traits (b) and the coordinates of the patches along axis 1. Pearson's correlation between environmental parameters (c), functional traits (d) and the coordinates of the patches along axis 2…………………………………………………...73

**Figura 4:** Schematic representation of the relationship between patch structure and functional traits of plants from inselberg communities. The triangle represents Grime's (2001) scheme of plant strategies: competitiveness (red), stress-tolerance (green) and ruderalism (blue). Soil depth and patch area increase from patch 1 towards patch 4. The arrows represent the leaf economics spectrum (Wright et al. 2004; Reich 2014) and show fundamental ecological trade-offs in ecological strategies. The arrows also emphasize that native species, occurring in patches set in flatter areas and with invasive presence, show higher SLA and less leaf toughness (patch 5). The icons of leaves represent the leaf size spectrum (Díaz et al. 2004). Figure credits: Fernando Levi…………………………………………………………...75

## Lista de tabelas

### Capítulo I

**Tabela 1:** List of lycophyte, monilophyte and angiosperm species (separated by the double black line) recorded on an inselberg in the Mucuri Valley, Minas Gerais state, southeastern Brazil. Phytogeographic domains: Am = Amazonia, Ca = Caatinga, Ce = Cerrado, AF = Atlantic Forest, Pm = Pampa, Pn = Pantanal, All = all Domains. Habitat types: SD = shallow depression, M = monocot mat, E = epilithic vegetation, C = crevice, EFV = ephemeral flush vegetation. Life-forms: Ph = phanerophyte, Cr = cryptophyte, Th = therophyte, Ch = chamephytes, Hc = hemicryptophytes. The following notations were also included: ! = endangered species, * = first record for Minas Gerais State. In bold, species endemic to inselbergs. Vouchers: L = Luiza Fonseca Amorim de Paula and A = Luísa A. Oliveira……………………………………….33

### Capítulo II

**Tabela 1:** Comparison between trait values of native plant community (mean ± SD; n = 52 species) and the invasive species *Melinis repens*, both native and invasive species occurred in inselberg vegetation at Minas Gerais, southeastern Brasil……………………………….…...70

## RESUMO GERAL

Inselbergs são montanhas monolíticas ou grupos delas, cuja formação geológica consiste predominantemente de rochas graníticas e/ou gnáissicas. Eles estão distribuídos principalmente nas regiões tropicais e subtropicais, podendo ser encontrados também em regiões temperadas. Geralmente, a vegetação é diferente daquela do seu entorno, devido à presença de fortes filtros ambientais, como altas variações térmicas diárias, ventos constantes, baixa retenção de água e solos superaquecidos. Tais fatores ajudam a explicar o alto grau de especificidade florística, onde são encontradas adaptações morfológicas, anatômicas e reprodutivas, consideradas vantajosas para a sobrevivência das plantas nesses ambientes. No primeiro capítulo, buscou-se, através de inventário florístico, caracterizações fisionômicas e espectro de formas de vida, descrever as comunidades vegetais em um inselberg localizado no Vale do Mucuri, nordeste de Minas Gerais. Foram registradas 88 espécies de plantas vasculares (pertencentes a 36 famílias), dessas, seis são novas espécies para a ciência e quatro são novos registros para o estado de Minas Gerais. As famílias mais ricas foram Bromeliaceae (10 spp.), seguidas de Cyperaceae (sete spp.), Orchidaceae e Poaceae (seis spp. cada). O espectro biológico indicou a predominância de fanerófitos (34 spp.), seguidos de hemicriptófitos (23 spp.) e caméfitos (14 spp.). Foi possível observar elevada taxa de endemismos e influência de outros biomas sobre a flora local estudada. Além disso, constatou-se que os habitats descritos nesse trabalho são compostos por comunidades vegetais específicas, que estão sob diferentes condições ambientais. No segundo capítulo, nós avaliamos a importância das estratégias CSR (competitividade:estresse-tolerância:ruderalidade) em diferentes habitats no inselberg, e testamos se havia uma conexão entre os parâmetros ambientais dos habitats e os traços funcionais das espécie vegetais, além de compararmos a variação entre traços das espécies nativas e uma espécie exótica.

Encontramos alta diversidade de estratégias ecológicas, mas a predominância foi de estratégias S e C. A espécie exótica foi funcionalmente distinta da comunidade nativa, com traços associados à ruderalidade. Além disso, a maioria dos traços funcionais foram significativamente correlacionados com pelo menos uma característica ambiental dos habitats, suportando o papel dos filtros ambientais na estruturação de comunidades vegetais nesses afloramentos. Ainda, por estarem sob distintas condições ambientais, e possuírem diferentes disponibilidades de recurso, alguns habitats foram mais susceptíveis à invasão biológica do que outros. Os resultados dessa dissertação, portanto, aumentam a nossa compreensão com relação à composição e estrutura das comunidades vegetais dos inselbergs e fornece *insights* sobre a dinâmica de invasão biológica, uma forte ameaça a esses ambientes. Argumentamos, assim, que o uso de abordagens mais amplas, tanto qualitativas quanto quantitativas, são fundamentais para o desenvolvimento de estratégias de conservação e manejo da vegetação única sobre os afloramentos graníticos e gnáissicos.

**Palavras-chave**: afloramentos graníticos, conservação, endemismo, ecologia funcional, Floresta Atlântica, traços funcionais, conservação da biodiversidade.

# ABSTRACT

Inselbergs are monolithic mountains or groups of them, whose geological formation consists especially of granitic and gneiss rocks. They are distributed mainly in tropical and subtropical regions, less common in temperate regions. Generally, the flora and vegetation of inselbergs are clearly distinguished from the surrounding matrix, due to harsh environmental filters, such as high daily temperature variations, constant winds, low retention of water and overheated soils. These factors help to explain the high degree of floristic specificity, in which are found morphological, anatomical and reproductive adaptations, considered advantageous to the survival of plants in these environments. In the first chapter, we sought to describe the plant communities in an inselberg located in the Mucuri Valley, northeast Minas Gerais, through floristic inventory, physiognomic characterization and life-form spectrum. A total of 88 species of vascular plants were recorded (belonging to 36 families), of which six were new species to science and four were new records for Minas Gerais state. The family with the highest number of species was Bromeliaceae (10 spp.), followed by Cyperaceae (seven spp.), Orchidaceae and Poaceae (six spp. each). The biological spectra indicated the predominance of phanerophytes (34 spp.), followed by hemicryptophytes (23 spp.) and chamephytes (14 spp.). It was observed high endemism rate and influence of other biomes on the local flora studied. In addition, it was found that the habitats described in this work were determined by specific plant community composition and variable degrees of environmental stress. In the second chapter, we evaluated the importance of CSR (competitiveness:stress-tolerance:ruderalism) ecological strategies in different habitat types on the inselberg, tested for a connection between habitat structure and functional traits, and compared the variation in functional traits between native and an exotic species. We found a relatively high diversity of ecological strategies, but most species lied between the S and C strategy. The invasive species was functionally distinctive from native communities, with the predominance of traits associated with ruderalism. We also found that, most functional traits significantly correlated with at least one environmental parameter of the habitats, highlighting the role of environmental filters in structuring plant communities in this heterogeneous environment. Yet, because the habitats are under different environmental conditions, and have different resource availability, some of them were more susceptible to biological invasion than others. The results of this Master thesis therefore increase our understanding regarding the composition and structure of inselberg plant communities and provides insights into the dynamics of biological invasion, a strong threat to these environments. We then argue that the use of broader approaches, both qualitative and quantitative, are fundamental to the development of conservation strategies and management of the unique vegetation on granitic and gneiss rock outcrops.

**Key words**: granite outcrops, conservation, endemism, functional ecology, Atlantic Forest, functional traits, biodiversity conservation

# INTRODUÇÃO GERAL

## *Inselbergs: sistemas modelo para abordar questões centrais da pesquisa em biodiversidade*

As questões a respeito da biodiversidade mundial vêm sendo foco no contexto político, cultural e biológico. Esse debate, cada vez mais, ganha grandes proporções à medida que cientistas, ambientalistas e autoridades alertam para a acelerada perda da diversidade a nível global, como uma consequência das mudanças climáticas, modificações no uso da terra e na composição atmosférica, o que vem trazendo sérias alterações nos processos e serviços ecossistêmicos, dos quais o homem se beneficia (Tilman 1999; Chapin *et al*. 2000 & Díaz & Cabido 2001; Díaz *et al*. 2007). Apesar de tamanha discussão, dados sobre diferentes aspectos da biodiversidade ainda são deficientes, especialmente porque diversos grupos de organismos são pouco estudados, o que dificulta até mesmo fazer-se estimativas do quanto já foi perdido em termos de espécies (Gaston 1996; Purvis & Hector 2000).

O Brasil tem a flora de plantas vasculares mais diversa no mundo, das quais 56% são endêmicas do país (Forzza *et al.* 2012). Estimativas que tentam quantificar a diversidade florística brasileira têm sido feitas, e novas plataformas virtuais, que integram as espécies e suas áreas de distribuição geográfica, estão sendo geradas com grande volume de dados (List of Species of the Brazilian Flora 2014; INCT 2014). Entretanto, ainda é preciso destacar as elevadas taxas de espécies novas descritas para o Brasil nos últimos anos, especialmente para o bioma Floresta Atlântica, o que pode ser uma maneira de estimar o conhecimento sobre a nossa flora (Sobral & Stehmann 2009). Tais constatações são corroboradas por Giulietti *et al.* (2005), onde os autores sugerem que os estudos científicos sobre a biodiversidade do Brasil ainda estão no estágio exploratório. Um reflexo desse estágio inicial de conhecimento da nossa flora é a insuficiência de dados observada pelo Ministério do Meio Ambiente (MMA

2002), ao buscarem áreas e ações prioritárias para a conservação dos biomas brasileiros, uma grande porcentagem das áreas foram classificadas como de "conhecimento insuficiente", mas de provável importância biológica.

Diante desse panorama, a Convenção sobre Diversidade Biológica (CBD), da qual o Brasil é signatário desde 2002 (Martinelli 2007), enfatizou a responsabilidade da humanidade de proteger e de fazer uso dos recursos naturais de uma maneira sustentável. Uma condição importante para se alcançar essa meta é buscar por uma compreensão mais abrangente das propriedades biológicas que distinguem os biomas tropicais ricos em espécies dos biomas menos diversos situados em latitudes mais altas **(**Porembski & Barthlott 2000a**).** Para tal, certos grupos de organismos e/ ou ecossistemas podem servir de modelos para estudos que tenham como foco a biodiversidade.

Nesse contexto, diversos pesquisadores vêm chamando a atenção para os "Inselbergs" (do alemão, insel = ilha e berg = montanha, Barthlott & Porembski 2000a), montanhas monolíticas ou grupos delas, que surgem abruptamente em meio às paisagens, cuja formação geológica consiste principalmente de rochas graníticas e/ou gnáissicas (Porembski *et al.* 1997; Porembski & Barthlott 2000b). Esses afloramentos representam um ecossistema peculiar e servem de excelentes sistemas modelo para abordar questões centrais da pesquisa em biodiversidade (Porembski & Barthlott 2000a**).** As principais áreas de distribuição dos inselbergs são as regiões tropicais e subtropicais, podendo ser encontrados também em regiões temperadas. Geralmente, a vegetação é diferente daquela do seu entorno, devido às suas características edáficas e aridez microclimáticas (Porembski *et al.* 1997), sendo, portanto, ecologicamente isolados e atribuídos como ilhas terrestres (Barthlott & Porembski 2000a). Esses sistemas geológicos relativamente uniformes, dessa forma, são fortemente adequados para análises comparativas ao longo de todos os continentes (Porembski & Barthlott 2000a).

Entretanto, no Brasil, no que diz respeito à biodiversidade de montanhas, o que inclui os afloramentos rochosos, não são feitas referências específicas nos documentos oficiais sobre a biodiversidade, embora o tema tenha sido considerado como um ponto importante da CDB (Martinelli 2007). Assim, ainda são grandes as lacunas a respeito da flora de várias regiões de montanhas em toda a extensão do território brasileiro (Safford 1999; Safford & Martinelli 2000). Esse fato é corroborado pelos dados sobre o número de espécies novas descritas para o Brasil nos últimos anos, dentre 1409 registros de espécies analisadas (representando aproximadamente 1/3 das espécies descritas entre 1990 e 2009; dados retirados de Sobral & Stehmann 2009), 419 (30%) são de vegetação sobre formações rochosas, dessas, 42 espécies (10%) ocorrem em inselbergs (de Paula *et al.*, dados não publicados).

O fator preocupante diante desse cenário é o fato dos afloramentos rochosos de maneira geral, o que inclui os inselbergs, estarem entre os ambientes mais ameaçadas e negligenciados no mundo (Ferreira *et al.* 2014). A crescente mineração, invasões biológicas, devido principalmente à retirada da vegetação circundante, e a coleta das espécies atrativas da flora (como Orchidaceae e Bromeliaceae) são descritas como as principais ameaças a esses afloramentos (Pigott 2000; Porembski 2000; Martinelli 2007; Ferreira *et al.* 2014). No entanto, os esforços para conservação destas espécies é baseado nas poucas abordagens qualitativas, que por sua vez têm limitado poder de previsão.

## *Comunidades vegetais em inselbergs*

Por um longo período, a vegetação dos afloramentos graníticos foi considerada como litofítica sem uma maior diferenciação entre seus habitats (Porembski *et al*. 2000). Entretanto, inselbergs formam ecossistemas que, apesar de diferenças na composição florística regional, compreendem comunidades vegetais circunscritas (Bathlott *et al.* 1993). As comunidades vegetais nesses afloramentos não são agregadas aleatoriamente e possuem um conjunto típico de habitats fisionomicamente definidos, que ocorrem quase de forma idêntica em todo o mundo (Porembski *et al.* 2000). Esse fato ocorre devido à existência de filtros ecológicos similares nesses ambientes, como exposição alta à radiação UV, variações térmicas diárias, ventos constantes, baixa retenção de água, solos impermeáveis e superaquecidos (Porembski & Barthlott 2000b; Scarano 2002). Tais fatores ajudam a explicar o alto grau de especificidade florística, onde são encontradas adaptações morfológicas, anatômicas e reprodutivas, consideradas vantajosas para a sobrevivência das plantas nesses afloramentos (Biedinger *et al.* 2000).

São reconhecidas três regiões no mundo com alta diversidade de plantas de inselberg: sudeste do Brasil, Madagascar e sudoeste da Austrália, sendo três áreas de importância global (Porembski 2007). Destacam-se na flora de inselbergs as plantas suculentas e as tolerantes à dessecação, essas últimas possuem a habilidade de, após longos períodos de desidratação, se rehidratarem sem perder a viabilidade, e tem os inselbergs como centros de diversidade e principais sítios de crescimento (Porembski *et al.*1998; Porembski & Barthlott 2000b). Ainda, é notável a elevada taxa de endemismo nesses afloramentos no Brasil (Meirelles *et al.* 1999; Porembski *et al.* 1997; Ribeiro *et al.* 2007), especialmente nas regiões dos estados do Rio de Janeiro, Minas Gerais, Espírito Santo e Bahia, onde os *pães de açúcar* formam elementos dominantes da paisagem (Porembski 2007).

O número de trabalhos desenvolvendo pesquisa em inselbergs aumentou consideravelmente nos últimos anos, em uma busca realizada nas bases de dados do Web of Knowledge e Scielo, com o tópico “inselberg“, foram encontrados 136 artigos publicados (Figura 1; de Paula *et al.*, dados não publicados). Apesar do número crescente de publicações envolvendo esses afloramentos, especialmente depois do ano 2000, quando foi feita uma compilação de estudos sobre inselbergs localizados em regiões tropicais e temperadas (Porembski & Barthlott 2000a), a maioria desses trabalhos foi concentrada nos continentes Africano e Americano (Figura 1, de Paula *et al*., dados não publicados). Nesses continentes, ecologia e taxonomia foram os principais temas de estudo, ao passo que na Ásia e na Oceania, o número de estudos de uma forma geral foi incipiente (Figura 2, de Paula *et al*., dados não publicados). Ainda, apesar de ecologia ter sido o principal foco de pesquisa, poucos trabalhos com uma abordagem funcional foram encontrados, sendo esses apenas qualitativos. Esse cenário mostra que, mesmo com a intensificação dos esforços de pesquisa em inselberg, ainda existe um grande déficit no que diz respeito às questões de estrutura e funcionamento de seu ecossistema, não sabemos como os atributos funcionais dos organismos e as características ambientais interagem em suas comunidades.

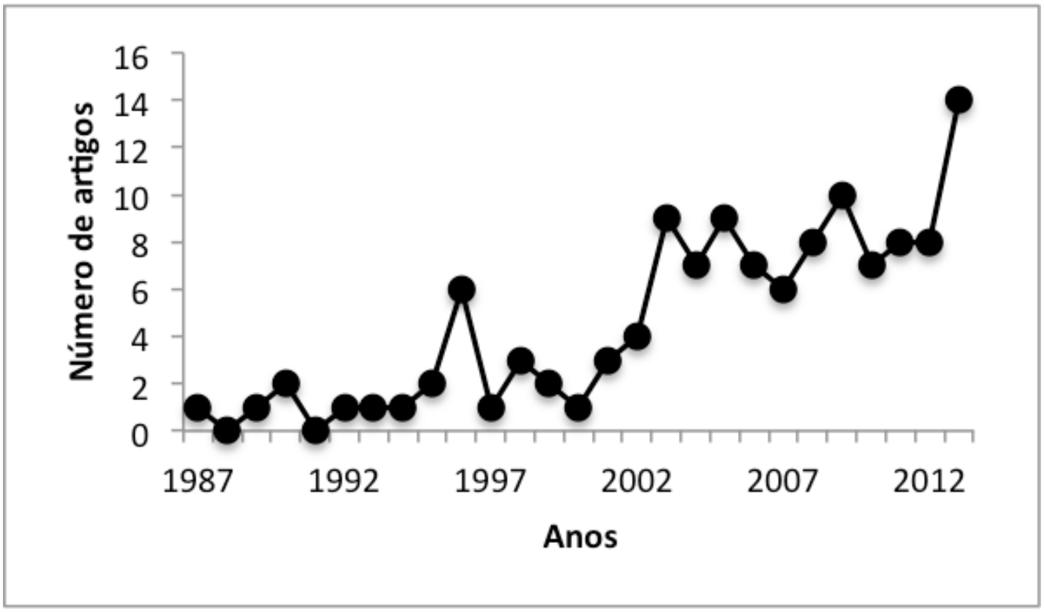


**Figure 1.** Número de artigos publicados resultantes da busca com o termo “inselberg” na base de dados do Web of Knowledge e Scielo, entre os anos de 1987 a 2013 (busca em 20 de Junho de 2014), artigos indexados em ambas as bases foram considerados apenas uma vez.

Atualmente, é crescente a aceitação de que a diversidade biológica abarca tanto o número quanto a composição de genótipos, espécies e tipos funcionais, o que antigamente era relacionado somente à riqueza de espécies (Grime 1997; Tilman *et al*. 1997; Díaz & Cabido 2001). Classificar as plantas somente por suas identidades taxonômicas tem fortes limitações quando se procura responder importantes questões ecológicas na escala do ecossistema, da paisagem ou de biomas (Keddy 1992). Dessa forma, estudos focados em biodiversidade passaram a incorporar o conceito de diversidade funcional (Díaz & Cabido 2001; Petchey & Gaston 2006), acreditando-se que os efeitos da diversidade sobre o funcionamento ecossistêmico devem ser conferidos especialmente aos traços funcionais das espécies e suas interações, do que simplesmente atribuído ao número de espécies isoladamente (Grime 1997; Tilman *et al*. 1997; Loreau 2000).

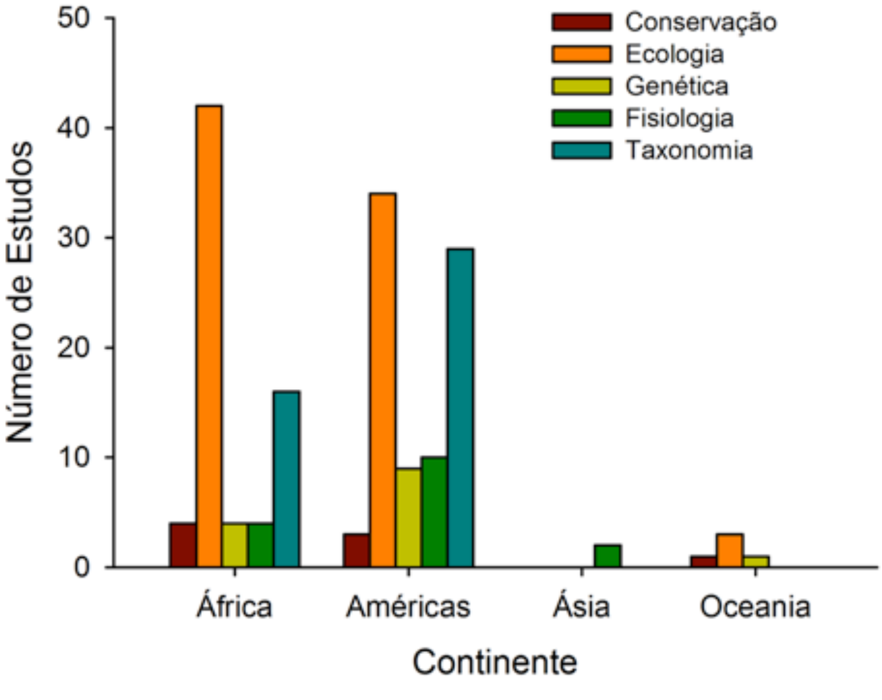


**Figure 2.** Número de estudos publicados por continente, divididos por área de pesquisa, resultantes da busca com o termo “inselberg” na base de dados do Web of Knowledge e Scielo, entre os anos de 1987 a 2013 (busca em 20 de Junho de 2014). O total de artigos é maior do que 136 porque alguns artigos se encaixaram em mais de uma área de pesquisa.

Em comunidades vegetais, traços funcionais são definidos como quaisquer características mensuráveis (morfológica, anatômica, bioquímica, fisiológica ou fenológica, Violle *et al.* 2007) que representam estratégias ecológicas das espécies (Grime 2001) e determinam como as plantas respondem aos fatores ambientais, afetam outros níveis tróficos e influenciam propriedades do ecossistema (Pérez-Harguindeguy *et al.* 2013). Todos esses componentes são cruciais na determinação dos processos ecossistêmicos (Hooper & Vitousek 1997; Tilman 1999; Loreau 2000). Entretanto, é um verdadeiro desafio identificar aqueles traços que variam em resposta às mudanças nas condições ambientais (Violle *et al.* 2007; Rosado *et al.* 2013), e eles são exatamente os elementos-chave na ecologia funcional (Dray *et al.* 2014).

Diversos trabalhos têm sido feitos a fim de analisar as relações entre a composição de traços de uma comunidade e suas condições ambientais (Doledéc *et al.* 1996; McInthyre & Lavorel 2001; Ackerly *et al.* 2002; Dray & Legendre 2008; Moretti *et al.* 2009; Dray *et al.* 2014), sendo os filtros ambientais foco em diversos temas de pesquisa (Cingolani *et al.* 2007; Pavoine *et al.* 2011; Negreiros *et al.* 2014). Levando-se em conta que os traços funcionais podem refletir as estratégias ecológicas das plantas (Grime 2001), através da quantificação desses traços (Pérez-Harguindeguy *et al.* 2013) é possível inferir a influência de filtros ambientais na condução da diversidade de estratégias em uma determinada comunidade vegetal (Grime *et al.* 1997; Díaz *et al.* 2004). Assim, acreditamos que através de abordagens da ecologia funcional (usando não só as identidades das espécies mas também os seus traços funcionais) poderemos entender melhor a estrutura e dinâmica das comunidades vegetais e o papel dos filtros nos afloramentos rochosos. Essas abordagens poderão, ainda, nos permitir predizer alterações nos serviços ecossistêmicos oriundos de distúrbios antropogênicos (Keddy 1992, Díaz & Cabido 1997, de Bello *et al.* 2010), incluindo mudanças na biodiversidade, e acessar a performance de espécies exóticas invasoras (Drenovsky *et al.* 2012).

Desse modo, no primeiro capítulo dessa dissertação, que está elaborado de acordo com as normas da Acta Botanica Brasilica, buscou-se através de inventário florístico, caracterizações fisionômicas dos habitats e espectro de formas de vida, descrever as comunidades vegetais em um inselberg localizado no Vale do Mucuri, nordeste de Minas Gerais. No segundo capítulo, que está em segunda rodada de revisão na Biodiversity and Conservation, avaliamos a importância das estratégias CSR (competitividade:estresse-tolerância:ruderalidade) (Grime 1977) em diferentes habitats no inselberg, e testamos se existia uma conexão entre os parâmetros ambientais dos habitats e os traços funcionais das espécie vegetais, além de compararmos a variação entre traços das espécies nativas e uma espécie exótica. Permearam como temas centrais desse capítulo as seguintes questões: Quais são os fatores ambientais que estruturam as comunidades de plantas nos inselbergs? Como as características ambientais estão relacionadas com os atributos das plantas? Quais são as características relacionadas à invasão biológica em ambientes com recursos limitados? Acreditamos que nossos dados podem ser usados em abordagens comparativas com estudos realizados em outras partes do mundo, já que os inselbergs compreendem comunidades vegetais circunscritas. Além disso, nosso trabalho inova o conhecimento científico na medida em que implementa simultaneamente várias abordagens inéditas em um ambiente com recursos limitados e tem implicações importantes para a restauração, conservação e gestão deste ecossistema ameaçado.

## Referências

Ackerly, D.D.; Knight, C.A.; Weiss, S.B.; Barton, K. & Starmer, K. P. 2002. Leaf size, specific leaf area and habitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. **Oecologia** 130: 449–457.

Barthlott, W.; Gröger, A. & Porembski, S. 1993. Some remarks on the vegetation of tropical inselbergs: diversity and ecological differentiation. **Compte rendu des séances de la société de biogéographie** 69: 105-124.

Barthlott, W. & Porembski, S. 2000a. Why Study Inselbergs?. Pp. 1-6. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Biedinger, N.; Porembski, S. & Barthlott, W. 2000. Vascular plants on inselbergs: Vegetative and reproductive strategies. Pp. 117-142. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Chapin, F.S. III *et al.* 2000. Consequences of changing biodiversity. **Nature** 405:234–242.

Cingolani, A. M. et al. 2007. Filtering processes in the assembly of plant communities: are species presence and abundance driven by the same traits? **Journal of Vegetation Science** 18: 911-920.

de Bello, F. *et al.* 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. **Biodiversity and Conservation** 19:2873-2893.

Díaz, S. & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. **Journal of Vegetation Science** 8:463-474

Díaz, S. & Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. **Trends in Ecology & Evolution** 16: 646-655.

Díaz, S. *et al.* 2004. The plant traits that drive ecosystems: Evidence from three continents. **Journal of Vegetation Science** 15:295-304.

Díaz, S.; Lavorel, S.; De Bello, F.; Quetier, F.; Grigulis, K. & Robson, M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. **Proceedings of the National Academy of Sciences of the United States of America** 104: 20684–20689.

Dolédec, S.; Chessel, D.; terBraak, C.J.F.; Champely, S. 1996. Matching species traits to environmental variables: A new three-table ordination method. **Environmental and Ecological Statistics** 3:143-166.

Dray, S. & Legendre, P. 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. **Ecology** 89: 3400–3412.

Dray, S.; Choler, P.; Dolédec, S.; Peres-Neto, PR.; Thuiller, W.; Pavoine, S.; ter Braak, C.J.F. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. **Ecology** 95:14-21.

Drenovsky, R.E. *et al.* 2012. A functional trait perspective on plant invasion. **Annals of Botany** 110:141-153.

Ferreira, J. *et al*. 2014. Brazil's environmental leadership at risk. **Science** 346: 706-707.

Forzza, R.C. *et al*. 2012. New Brazilian Floristic List Highlights Conservation Challenges. **Bioscience** 62: 39-45.

Gaston, K.J. 1996. **Biodiversity: A Biology of Numbers and Difference**. Black- well Science, Oxford.

Giulietti, A. M., R. M. Harley, L. P. De Queiroz, M. G. L. Wanderley, and C. Van Den Berg. 2005. Biodiversity and conservation of plants in Brazil. **Conservation Biology** 19:632–639.

Grime, J.P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. **The American Naturalist** 111: 1169-1194.

Grime, J.P. 1997. Biodiversity and ecosystem function: the debate deepens. **Science** 277: 1260–1261.

Grime, J. P. 2001. **Plant strategies, vegetation processes and ecosystem properties**. – Wiley.

Grime, J.P. *et al*. 1997. Integrated screening validates primary axes of specialisation in plants. **Oikos** 79:259-281.

Hooper, D.U. & Vitousek, P.M. 1997. The effects of plant composition and diversity on ecosystem processes. **Science** 277: 1302–1305.

INCT - **Virtual Herbarium of Plants and Fungi**. 2014. http://inct.florabrasil.net/en/herbario-virtual/.

Keddy, P.A. 1992. A pragmatic approach to fuctional ecology. **Functional Ecology** 6: 621-626.

**List of Species of the Brazilian Flora**. Rio de Janeiro Botanical Garden. http://floradobrasil.jbrj.gov.br (access on Oct 2014).

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical developments. **Oikos** 91: 3–17.

Martinelli, G. 2007. Mountain biodiversity in Brazil. **Brazilian Journal of Botany** 30: 587-597.

McIntyre, S. & Lavorel, S. 2001. Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. **Journal of Ecology** 89: 209–226.

Meirelles, S.T.; Pivello, V.R. & Joly, C.A. 1999. The vegetation of granite rock outcrops in Rio de Janeiro, Brazil, and the need for its protection. **Environmental Conservation** 26: 10-20.

MMA. 2002. **Biodiversidade Brasileira: Avaliação e Identificação de Áreas e Ações Prioritárias para Conservação, Utilização Sustentável e Repartição de Benefícios da Biodiversidade Brasileira**. Ministério do Meio Ambiente, Brasília.

Moretti, M.; de Bello, F.; Roberts, S.P.M. & Potts, S.G. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. **Journal of Animal Ecology** 78: 98–108.

Negreiros, D.; Le Stradic, S.; Fernandes, G.W.; Rennó, H.C. 2014. CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. **Plant Ecology** 215:379-388.

Pavoine, S.; Vela, E.; Gachet, S.; de Belair, G.; Bonsall, M.B. 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. **Journal of Ecology** 99:165-175.

Pérez-Harguindeguy *et al.* 2013. New handbook for standardised measurement of plant functional traits worldwide. **Australian Journal of Botany** 61:167-234.

Petchey, O. L. & Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. **Ecology Letters** 9:741–758.

Pigott, J.P. 2000. Environmental weeds and granite outcrops: possible solutions in the "too hard basket". **Journal of the Royal Society of Western Australia** 83: 135-137.

Porembski, S. 2000a. The invasibility of tropical granite outcrops ('inselbergs') by exotic weeds. **Journal of the Royal Society of Western Australia** 83: 131-137.

Porembski, S. 2007. Tropical inselbergs: habitat types, adaptive strategies and diversity patterns. **Brazilian Journal of Botany** 30: 579-586.

Porembski & Barthlott 2000a. **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Porembski, S. & Barthlott, W. 2000b. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. **Plant Ecology** 151: 19-28.

Porembski, S.; Seine, R. & Barthlott, W. 1997. Inselberg vegetation and the biodiversity of granite outcrops. **Journal of the Royal Society of Western Australia** 80: 193-199.

Porembski, S.; Martinelli, G.; Ohlemüller, R. & Barthlott, W. 1998. Diversity and ecology of saxicolous vegetation mats on inselbergs in the Brazilian Atlantic rainforest. **Diversity and Distributions** 4: 107-119.

Porembski, S.; Becker, U. & Seine, R. 2000. Islands on islands: habitats on inselbergs. Pp. 49-67. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Purvis, A. & Hector, A. 2000. Getting the measure of biodiversity. **Nature** 405: 212–219.

Raevel, V.; Violle, C. & Munoz, F. 2012. Mechanisms of ecological succession: insights from plant functional strategies. **Oikos** 121: 1761–1770.

Ribeiro, K.T.; Medina, B.M.O. & Scarano, F.R. 2007. Species composition and biogeographic relations of the rock outcrop flora on the high plateau of Itatiaia, SE-Brazil. **Brazilian Journal of Botany** 30: 623-639.

Rosado, B.H.P.; Dias, A.T.C. & Mattos, E.A. 2013. Going back to basics: importance of ecophysiology when choosing functional traits for studying. **Natureza & Conservação** 11:15-22.

Safford, H.D. 1999. Brazilian Paramos I. An introduction to the physical environment and vegetation of the campos de altitude. **Journal of Biogeography** 26: 693-712.

Safford, H.D. & Martinelli, G. 2000. Southeast Brazil. Pp 339-389. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. **Annals of Botany** 90: 517-524.

Sobral, M. & Stehmann, J. R. 2009. An analysis of new angiosperm species discoveries in Brazil. (1990–2006). **Taxon** 58: 227–232.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. **Ecology** 80: 1455–1474.

Tilman, D. *et al.* 1997. The influence of functional diversity and composition on ecosystem processes. **Science** 277: 1300–1302.

Violle, C. *et al.* 2007. Let the concept of trait be functional! **Oikos** 116:882–892.

# CAPÍTULO I

## A conservation perspective on inselberg plant communities: species composition and ecological characterization

---

Luiza F. A. de Paula[1], Nara F. O. Mota[2]; Pedro L.Viana[2], João Renato Stehmann[1]

[1] Departamento de Botânica, ICB/Universidade Federal de Minas Gerais, CP 486, 30161-970 Belo Horizonte, MG, Brazil

[2] Coordenação de Botânica. Museu Paraense Emílio Goeldi. Avenida Magalhães Barata, 376, São Braz, Belém - PA, 66040-170, Brazil

## ABSTRACT

Inselbergs are monolithic mountains or groups of them, whose geological formation consists mainly of granitic and gneiss rocks, distributed mainly in tropical and subtropical regions. They form ecosystems that, despite differences in regional floristic composition, comprise a set of circumscribed plant communities, clearly distinguished from the surrounding matrix. This distinction is due to the harsh environmental filters, such as high daily temperature variations, low retention of water and overheated soils. In this work, we sought to describe the plant communities in an inselberg located in Minas Gerais state, southeastern Brazil, through floristic inventory, physiognomic characterization and life-form spectrum. In addition, we compared species compositions and the percentage of invasibility of the different habitats observed. A total of 88 species of vascular plants were recorded (belonging to 36 families), of which six were new species to science and four were new records for Minas Gerais state. The family with the highest number of species was Bromeliaceae (10 spp.), followed by Cyperaceae (seven spp.). The biological spectra of the whole community indicated the predominance of phanerophytes (34 spp.), but each habitat showed a different life-form predominance. It was notable the high endemism rate and the influence of other biomes on the local flora studied. The habitats described here were determined by specific plant community composition and variable degrees of environmental stress. The percentage of invasibility was higher in habitats with relatively higher resource availability. We believe that our data can be used in comparative approaches in studies conducted in other parts of the world, since inselbergs comprise well defined plant communities.

**Keywords:** endemism, granitic and gneiss rock outcrops, life-forms, vascular plants

## Introduction

Brazil has the most diverse flora of vascular plants in the world, of which more than 50% are endemic to the country (Forzza *et al.* 2012). The Atlantic Forest biome greatly contributes for this high species richness, being internationally recognized as a center of biodiversity and endemism and considered a hotspot for conservation priorities (Myers *et al.* 2000; Mittermeier *et al.* 2004). Otherwise what is frequently overlooked is the fact that rock outcrops are not only widespread within this biome but also support large number of endemics (Safford & Martinelli 2000; Scarano 2002; Porembski 2007). Recent data revealed that from the 995 species of angiosperms occurring on outcrops inserted in the Atlantic Forest domain, 416 are endemic to these formations (Stehmann *et al.* 2009). Nevertheless, with regards to mountain biodiversity, no specific references are made in official documents on biodiversity in Brazil until recently (Martinelli 2007). The results are large gaps in our knowledge about the flora of various mountain regions in the fullest extent of the Brazilian territory (Safford 1999).

"Inselberg" was a term first used by Bornhardt in 1900, from the German language, insel = island and berg = mountain (Barthlott & Porembski 2000b), used to characterize monolithic mountains or groups of them, which appear abruptly in the landscape, whose geological formation consists mainly of granitic and gneiss rocks (Porembski *et al.* 1997; Porembski & Barthlott 2000). They have been considered as terrestrial habitat islands because of their strong spatial and ecological isolation, which provides a barrier against dispersal and migration (Porembski *et al.* 2000; Porembski 2007). These environments typically share a number of characteristics of stress, such as high exposure to UV radiation, daily temperature variations, winds, high rates of evapotranspiration, low water retention, and impermeable overheated soils (Porembski & Barthlott 2000; Scarano 2002). These factors help to explain the high degree of floristic specificity, in which are found morphological, anatomical and reproductive adaptations, considered advantageous to the survival of plants in these environments (Biedinger *et al.* 2000; de Paula *et al.* unpublished data). Outstanding is the high amount of succulents and vascular resurrection plants in which the plants can tolerate almost complete water loss in their vegetative tissues, being able to rehydrate without losing viability (Porembski & Barthlott 2000; Scott 2000).

There are three worldwide hotspots of inselberg plant diversity: southeastern Brazil, Madagascar and southwestern Australia (Porembski 2007). In Brazil, the core area compassing the states of Rio de Janeiro, Espírito Santo, southern Bahia and adjacent parts of Minas Gerais is extremely important, where inselbergs comprise high plant species richness and elevated rates of endemism (Porembski *et al.* 1998; Safford & Martinelli 2000; Taylor & Zappi 2004). Furthermore, it is noteworthy the high beta diversity of inselberg vegetation in this area, there is a considerable species turnover between individual outcrops (Porembski 2007). Nevertheless, our knowledge about the floristic composition and ecological aspects of inselberg vegetation are still not satisfactorily unexplored, despite their widespread occurrence in many tropical regions, inselbergs are still ignored as subjects of ecosystem research (Safford 1999; Barthlott & Porembski 2000b). This becomes more concerning when we take into account that threats to inselberg biodiversity are increasing (Meirelles *et al.* 1999; Burke 2003). The biological invasions, due to the removal of the buffer lowland vegetation in the surrounding areas of inselbergs (Pigott 2000; Porembski 2000a), quarrying, mining and extraction of attractive species of the flora (Martinelli 2007; Ferreira *et al.* 2014) have been described as the main threats for these rock outcrops. Moreover, it has also been shown that species restricted to rocky outcrops exhibited the highest extinction risk among vegetation types throughout the Brazilian Atlantic Forest domain (Leão *et al.* 2014), which coincides exactly with one of the richest areas with regards to inselberg plant species in Brazil.

The northern part of Minas Gerais state, especially the Mucuri Valley, is dominated by inselbergs that needs attention, either because there is a large gap of biological research (Oliveira-Filho *et al.* 2005) and almost nothing has been done with regards to floristic inventories. This region belongs to the Atlantic Forest domain but is inserted in an ecotonal area, under the influence of other adjacent biomes. Ecotones usually comprises high level of biodiversity (Risser 1995), especially those that are stable for prolonged period of time (Delcourt & Delcourt 1992), which is the case of the inselbergs, dating from the Precambrian granites and gneisses (Porembski *et al*. 1997). The aggravating factor is the increasing anthropogenic disturbance, mainly due to historical agricultural activities (MMA 2006), apart from the lack of conservation units in the zone. Studies conducted in this region already reinforced and even highlighted the need of enhancing efforts to inventory areas that comprise the inselbergs in this region (Martinelli 2007). This work aims, thus, to inventory the species of vascular plants, determine the floristic biological spectrum and describe ecological aspects of plant communities, including vulnerability to biological invasions, of an inselberg located in the Mucuri Valley, contributing to the knowledge and conservation of the flora of these unique outcrops.

## Material and methods

### *Study site*

This study was performed on an inselberg inserted into an Atlantic Forest matrix, in the Mucuri Valley, Minas Gerais state, southeastern Brazil (Fig. 1). This is a transition zone, due to the proximity to other biomes, such as Caatinga and Cerrado (Fig. 1), and inselbergs are typical landscape elements, surrounded by lowland fragments of semi-deciduous seasonal forest (Veloso *et al.* 1991) and degraded vegetation modified by farming and grazing (Fig. 2). The rock outcrop studied is located in a private area (17° 5' 09" S, 41° 15' 44" W) with altitudes ranging from 306 to 676 m a. s. l. The climate at the study area is tropical wet with dry season during winter (Aw), mean annual temperature is about 22.9°C and the annual rainfall is ca. 959.1 mm (INMET, historical data from 1961 to 1990; Alvares *et al*. 2013).

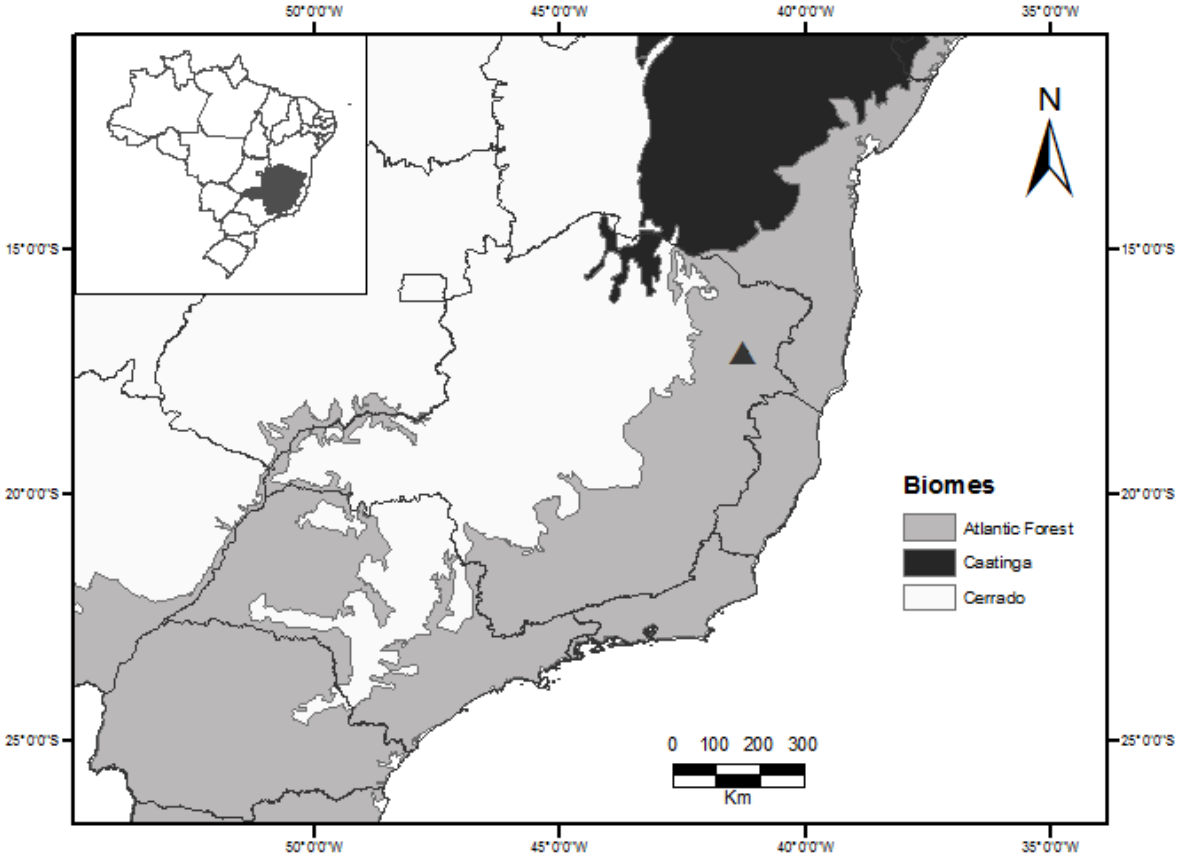


Figure 1. Map of the biomes occurring in Minas Gerais state, southeastern Brazil. The study area, represented by a triangle, is inserted into an Atlantic Forest matrix, but it is considered a transition zone due to the proximity to both Caatinga and Cerrado biomes.

### *Sampling*

The floristic survey consisted in the collection of fertile specimens and was conducted between January 2011 and April 2014. The sampling was restricted to vascular plant species arranged in vegetation patches, bounded by bare rock in many shapes and sizes, or directly seated on the bare rock (Caiafa & Silva 2005) (Fig. 2). The botanical material was processed according to the usual techniques for vascular plants (Fidalgo & Bononi 1989) and voucher specimens are kept in the BHCB herbarium (acronym according to Thiers 2010). Taxonomic identification was accomplished by means of specialized taxonomic literature, herbarium data and, when necessary, duplicates were sent to specialists. The circumscription adopted for angiosperm families is the one proposed by APG III (2009); for monilophytes and lycophytes we followed Smith *et al*. (2006) and Kramer & Green (1990), respectively. Spelling of the names, synonymy and authors follow List of Species of the Brazilian Flora (2014).

Species were also classified according to Raunkiaer (1934) life-forms, as phanerophytes, chamephytes, hemicryptophytes, cryptophytes, or therophytes. Species habitat were analyzed according to a classification established for the habitat types of inselbergs (Barthlott *et al*. 1993; Porembski 2007), and the following habitats were sampled: shallow depressions, monocot mats, epilithic vegetation, crevices, and ephemeral flush vegetation.

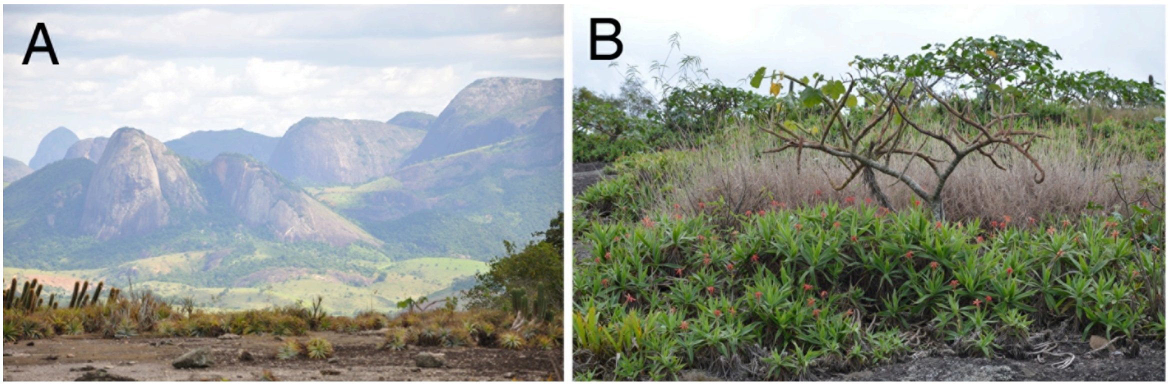


Figure 2. A. Overview of the inselberg studied in the Mucuri Valley, Minas Gerais state, southeastern Brazil; vegetation patches are visible on the flat part of the rock and in the the background the landscape is dominated by inselbergs. B. A typical vegetation patch of the inselberg studied, *Barbacenia tomentosa* Mart. is forming a mat in the border, the shrub *Cnidoscolus* aff. *lombardii* Fern.Casas is occupying the center region and the African invasive species *Melinis repens* (Willd.) Zizka is dominating the back part of the patch.

To compare species compositions and the percentage of invasibility of the habitats, 17 50-m long transects were set in five different areas of the inselberg to cover the variation in habitats on the inselberg. We placed four transects in areas 1-4, plus an additional transect in area five. In each transect, we surveyed up to five randomly chosen patches. For some transects, it was not possible to sample five patches due to steepness of the surveyed areas. In total, we randomly selected 61 patches and categorized them as one of the habitats abovementioned. Patch sampling reflected patch occurrence in the study area, therefore we sampled different numbers of patch per category. Patch area ranged from 0.03 to 79.12 $m^2$ (11.97 ± 19.2; SD).

### *Data analysis*

To compare angiosperm species composition between the five habitat sampled, we performed cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA), based on the Sørensen similarity index. The calculation of the Sørensen similarity index and the UPGMA were both achieved with the software Past (Hammer *et al.* 2001).

### *Distribution, Endemisms and Conservation*

Distribution of the species by phytogeographical domain and endemism to inselbergs were determined based on literature (whenever possible original manuscripts of species descriptions were reviewed), databases of List of Species of the Brazilian Flora (2014), INCT Virtual Herbarium of Plants and Fungi (2014), and also determined by specialists. Information of threatened species was based on the Brazilian official list (MMA 2008) and Red Book of Brazilian Flora (Martinelli & Moraes 2013).

## Results

### *Floristics*

A total of 88 species of vascular plants belonging to 36 families and 73 genera were found, consisting of 10 pteridophytes (three lycophytes and seven monilophytes) and 78 angiosperms (one magnoliid, 38 monocots and 39 eudicots) (Table 1). A color guide of the most representative species is available at http://fieldguides.fieldmuseum.org/sites/default/files/rapid-color-guides-pdfs/378.pdf (de Paula *et al*. 2013). The family with the highest number of species was Bromeliaceae (10 spp.), followed by Cyperaceae (seven spp.), Orchidaceae and Poaceae (six spp. each), Apocynaceae and Asteraceae (five spp. each) and Velloziaceae (four spp.). The richest genera were *Mandevilla* (Apocynaceae), *Selaginella* (Selaginellaceae) and *Tillandsia* (Bromeliaceae) (three spp. each). The African invasive species *Melinis repens* was recorded on the area.

Six inventoried species on the sampled inselberg patches were determined as new to science: the recently described grass *Axonopus graniticola* (Viana & de Paula 2013); a species of *Bradea* (Rubiaceae), which is a genus restricted to de Atlantic Forest in the states of Minas Gerais, Rio de Janeiro and Espírito Santo; a species of *Mandevilla* (Apocynaceae), also known from inselbergs of Espírito Santo state; a species of *Schwenckia* (Solanaceae), growing in Minas Gerais and Bahia states; and species belonging to the genera *Anthurium* (Araceae) and *Scleria* (Cyperaceae), so far only found in the study area.

Four new records for Minas Gerais state were recognized: *Pitcairnia azouryi*, *Begonia aguiabrancensis* (Begoniaceae), *Sinningia aghensis* (Gesneriaceae) and *Encyclia spiritusanctensis* (Orchidaceae). These species were previously considered endemic to Espírito Santo state, except for *P. azouryi*, also occurring in Rio de Janeiro state. Two species are considered rare for the Brazilian flora (Giulietti *et al*. 2009): *Stigmaphyllon crenatum* (Malpighiaceae) and *Tabebuia reticulata* (Bignoniaceae).

*Life-forms*

The biological spectra indicated the predominance of phanerophytes (34 spp./38.63%), followed by hemicryptophytes (23 spp./26.13%) and chamephytes (14 spp./15.90%). Life forms were distributed in different proportion in the habitats analyzed, with the predominance of phanerophytes (44.7%) in shallow depressions, chamephytes (57.1%) in monocot mats, phanerophytes (52.9%) in crevices, chamephytes (40%) in epilithic vegetation and terophytes (50%) in ephemeral flush vegetation (Fig. 3).

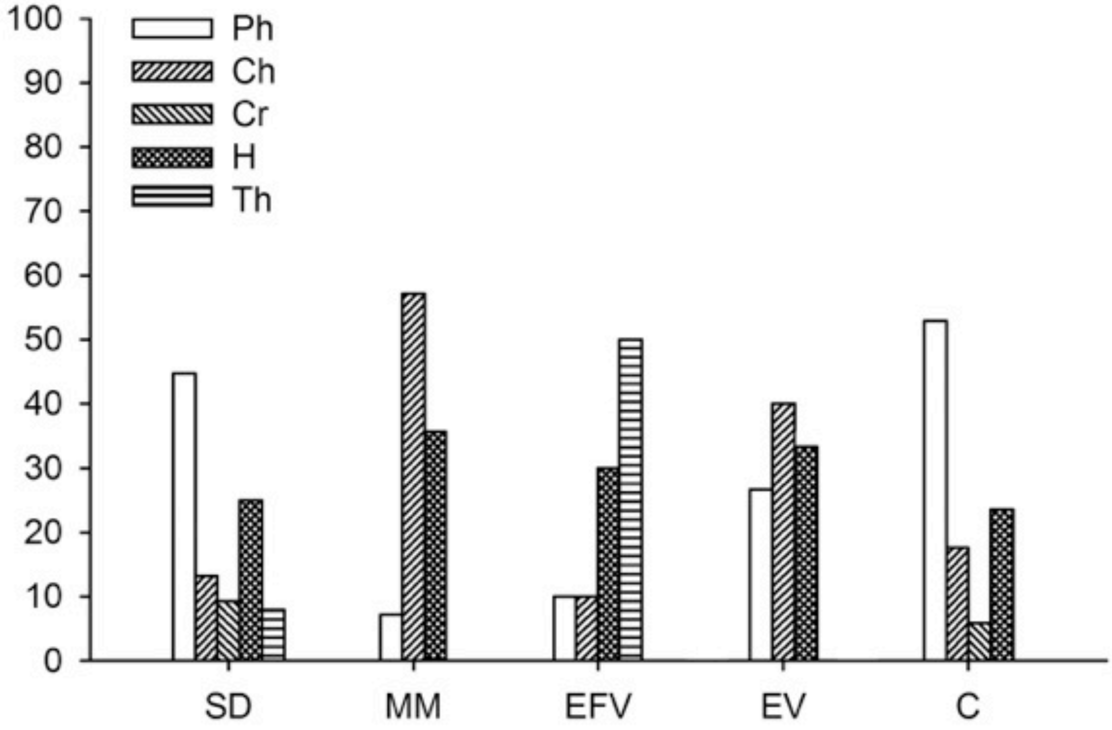


Figure 3. Percentage of life-forms in each habitat record in an inselberg located in Minas Gerais state, southeastern Brazil. Life-form abbreviations: Ph=phanerophyte, Ch=chamephyte, Cr=criptophyte, H=hemicriptophyte, Th=therophyte. Habitat abbreviations: SD = shallow depression, MM = monocot mat, EFV = ephemeral flush vegetation, EV = epilithic vegetation, C = crevices.

*Habitat types*

Shallow depressions were the richest habitat in the studied inselberg, with 76 species being recorded, of which 45 were exclusive. This habitat consisted of depressions on the rock filled with shallow soil, colonized by herbs, shrubs and trees, giving a heterogeneous aspect to the vegetation cover. On the depressions with a thin layer of soil it was common to find subshrubs like *Begonia aguiabrancensis* (Begoniaceae), *Vernonanthura* sp. (Asteraceae), *Cuphea sessilifolia* (Lythraceae), *Marsdenia* sp. (Apocynaceae), many monocots like *Axonopus graniticola* (Poaceae), *Anthurium* sp. nov., *Philodendron edmundoi* (Araceae), *Cyrtopodium glutiniferum* (Orchidaceae), *Vellozia* spp. (Velloziaceae) and some cacti, such as *Coleocephalocereus* spp. and *Pilosocereus brasilensis* subsp. *ruschianus*. On the depressions with deeper substrate, shrubs were dominant, such as *Cnidoscolus* aff. *lombardii*, *Croton nepetifolius*, *Stillingia argutedentata* (Euphorbiaceae), *Mandevilla* spp. (Apocynaceae), *Stachytarpheta gesnerioides* var. *gesnerioides* (Verbenaceae), *Tibouchina* spp. (Melastomataceae), and trees were also found: *Erythroxylum* aff. *vaccinifolium* (Erythroxylaceae), *Tabebuia reticulata* (Bignoniaceae) and *Wunderlichia azulensis* (Asteraceae).

Monocot mats were composed by 14 species, which formed carpets on both flat and inclined open rocky slopes. The most representative mat-forming species were *Alcantarea simplicisticha, Encholirium gracile*, *Pitcairnia azouryi*, *Portea petropolitana, Vriesea neoglutinosa*, (Bromeliaceae), *Trilepis lhotzkiana* (Cyperaceae), *Barbacenia* spp. and *Vellozia* spp. (Velloziaceae). Species of the lycophyte genus *Sellaginela* were also a remarkably common mat-former in the study area.

In the narrow, shallow-soil crevices, although not very common in the studied inselberg, were found 17 species, but none of them were exclusive to this habitat. Shrub species (*Mandevilla grazielae*, *Vernonanthura* sp., *Cnidoscolus* aff. *lombardii*), cacti

*Coleocephalocereus* spp.) and bromeliads (*Alcantarea simplicisticha*, *Encholirium gracile*, *Orthophytum compactum*) were common components recorded.

The exposed rock surface was covered by lichens and cyanobacteria (Büdel *et al.* 2000), though some vascular plants could grow directly on the rock. In this work, 15 species were identified as epilithic, such as the orchids *Acianthera prolifera, Pseudolaelia geraensis* and *P. vellozicola* (Orchidaceae) - the latter also occur as epiphyte on *Vellozia* spp. -, *Coleocephalocereus* spp. (Cactaceae) and *Philodendron edmundoi* (Araceae).

In turn, the ephemeral flush vegetation was formed by a wet substrate, due to the proximity of a natural pond and to an artificial dam. Ten species were found in this habitat, of which seven were exclusive. The families identified were usually composed by annual species, such as Burmanniaceae (*Burmannia capitata*), Cyperaceae (*Cyperus luzulae*, *Bulbostylis lagoensis*, *Fuirena umbellata*, *Rynchospora tenuis*), Lentibulariaceae (*Utricularia subulata*), Poaceae (*Andropogon bicornis*, *Melinis repens*, *Paspalum paniculatum*) and Plantaginaceae (*Achetaria crenata*).

From the sampling to compare species compositions between the habitats, 58 species of angiosperms were recorded; from the 61 selected patches, 23 patches were categorized as shallow depressions, 22 were monocot mats, 7 were ephemeral flush vegetation, 5 were epilithic vegetation and 4 were crevices. The UPGMA cluster analysis identified a cluster between monocot mats and crevices, ephemeral flush vegetation was the most different habitat with regards to species composition. The cophenetic correlation was 0.9436 (Fig. 4).

### *Endemisms, Distribution and Conservation*

Regarding endemism, 20 species were considered possibly endemic to inselbergs. We can highlight *Axonopus graniticola* (Viana & de Paula 2013), once its known distribution is restricted to the study area – the type locality - and an inselberg in Espírito Santo state

(Filgueiras & Rodrigues 2014), *Achetaria crenata* (Souza *et al.* 2009), *Alcantarea simplicisticha* (Leme *et al.* 2008), *Barbacenia purpurea* (Suguiyama *et al.* 2014), *Begonia aguiabrancensis* (Kollmann 2008), *Coleocephalocereus buxbaumianus*, *C. fluminensis* and *Pilosocereus brasiliensis* ssp. *ruschianus* (Taylor & Zappi 2004), *Encholirium gracile* (Martinelli & Moraes 2013), *Encyclia spiritusanctensis* (Menezes 1991), *Mandevilla grazielae* (Sales *et al.* 2006), *Paliavana prasinata* (Araujo *et al.* 2005), *Pitcairnia azouryi* (Martinelli *et al.* 2006), *Pseudolaelia geraensis* (Menini Neto *et al.* 2013), *Sinningia aghensis* (Martinelli & Moraes 2013), *Stigmaphyllon crenatum* (Anderson 1993), *Stillingia argutedentata* (Jablonski 1967), *Vellozia candida* (Mello-Silva 2004), *Vriesea vellozicola* (Siqueira-Filho & Leme 2006) and *Wunderlichia azulensis* (Mauad *et al.* 2014).

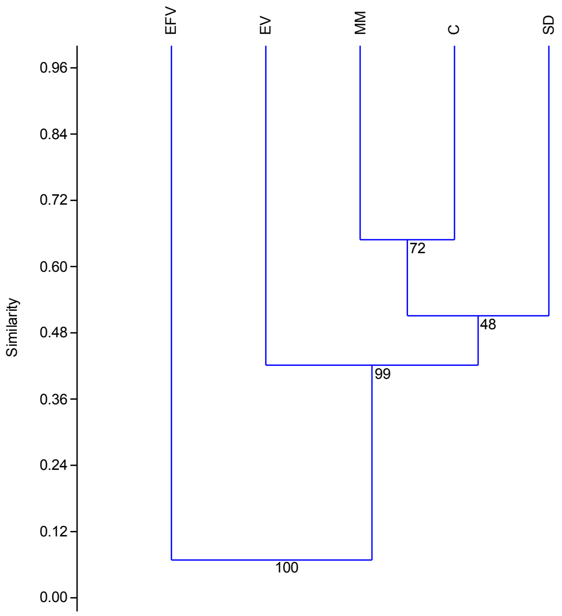


Figure 4. Cluster analysis, with the unweighted pair group method with arithmetic mean (UPGMA), using Sørensen similarity index, of the habitats found in an inselberg sampled in Minas Gerais state, southeastern Brazil, in relation to the presence of angiosperm species. Habitat abbreviations: EFV = ephemeral flush vegetation, EV = epilithic vegetation, MM = monocot mat, C= crevice, SD = shallow depression. The cophenetic correlation was 0.9436

The pattern of distribution of the inselberg flora showed that most species (67.05%) were not exclusive from the Atlantic Forest Domain. It was verified that 47.72 % of the species co-occurred in Cerrado Domain and 36.36 % also occurred in Caatinga Domain. None of the inventoried species were included in the Official List of Threatened Species of the Brazilian Flora (MMA 2008), but six species were present in the Red Book of the Brazilian Flora (Martinelli & Morais 2013): *Coleocephalocereus buxbaumianus*, *C. fluminensis*, *Encholirium gracile*, *Sinningia aghensis*, *Stigmaphyllon crenatum* and *Wunderlichia azulensis*.

With regards to biological invasion, invasive proportion was null in patches categorized as epilithic vegetation, monocot mats and crevices. However, the invasive species *Melinis repens* could indeed establish in the ephemeral flush vegetation (14.3% of the patches were invaded) and dominate in shallow depressions (30% of the patches were invaded) (Fig. 2B).

**Table 1.** List of lycophyte, monilophyte and angiosperm species (separated by the double black line) recorded on an inselberg in the Mucuri Valley, Minas Gerais state, southeastern Brazil. Phytogeographic domains: Am = Amazonia, Ca = Caatinga, Ce = Cerrado, AF = Atlantic Forest, Pm = Pampa, Pn = Pantanal, All = all Domains. Habitat types: SD = shallow depression, M = monocot mat, E = epilithic vegetation, C = crevice, EFV = ephemeral flush vegetation. Life-forms: Ph = phanerophyte, Cr = cryptophyte, Th = therophyte, Ch = chamephytes, Hc = hemicryptophytes. The following notations were also included: ! = endangered species, * = first record for Minas Gerais State. In bold, species endemic to inselbergs. Vouchers: L = Luiza Fonseca Amorim de Paula and A = Luísa A. Oliveira.

| **FAMILY - specialist**<br>***Species*** | **Habitat type** | **Life-form** | **Voucher** | **Phytogeografic Domain** |
|---|---|---|---|---|
| SELAGINELLACEAE – T.E. Almeida & A. Salino | | | | |
| *Selaginella convoluta* (Arn.) Spring | SD, M | Ch | L 97 | Ca, Ce, AF |
| *S. jungermannioides* (Gaudich.) Spring | SD, M | Hc | L 390 | AF |
| *S. sellowii* Hieron. | SD,M | Hc | L 306 | Ca, Ce, AF |
| ANEMIACEAE – T.E. Almeida & A. Salino | | | | |
| *Anemia ferruginea* Humb. & Bonpl. ex Kunth | SD | Hc | L 147 | Am, Ca, Ce, AF |
| *A. villosa* Humb. & Bonpl. ex Willd. | SD | Hc | L 133 | Ce, AF |
| BLECHNACEAE – T.E. Almeida & A. Salino | | | | |
| *Blechnum occidentale* L. | SD | Hc | L 352 | Am, Ca, Ce, AF |
| POLYPODIACEAE – T.E. Almeida & A. Salino | | | | |
| *Microgramma vaccinifolia* (Langsd. & Fisch.) Copel. | SD | Ph | L 343 | Ce, AF |
| *Serpocaulon latipes* (Langsd. & Fisch.) A.R.Sm. | SD | Hc | L 686 | AF |
| PTERIDACEAE – T.E. Almeida & A. Salino | | | | |
| *Cheilanthes geraniifolia* (Weath.) R.M.Tryon & A.F.Tryon | E, SD | Hc | L 135 | Ce, AF |
| *Doryopteris collina* (Raddi) J.Sm. | E, SD | Hc | L 93 | Am, AF |
| MAGNOLIIDS | | | | |
| PIPERACEAE – D.L. Ambrosio | | | | |
| *Peperomia incana* (Haw.) Hook. | SD | Ph | L 139 | AF |
| MONOCOTS | | | | |
| AMARYLLIDACEAE – J. Dutilh | | | | |

**Table 1.** Continuation.

| **FAMILY - specialist**<br>***Species*** | **Habitat type** | **Life-form** | **Voucher** | **Phytogeografic Domain** |
|---|---|---|---|---|
| *Hippeastrum glaucescens* (Mart.) Herb. | SD | Cr | L 636 | Ca, Ce, AF |
| ARACEAE – E.G. Gonçalves | | | | |
| *Anthurium* sp. nov. | SD, C | Hc | L 136 | AF |
| *Philodendron edmundoi* G.M. Barroso | SD, E | Ch | L 328 | AF |
| BROMELIACEAE – L.M. Versieux, R. Forzza and R. Lousada | | | | |
| ***Alcantarea simplicisticha*** Leme & A.P.Fontana | M, C, SD,E | Hc | L 87 | AF |
| ***Encholirium gracile*** L.B.Sm.! | M, C, SD,E | Ch | L 234 | AF |
| *Orthophytum compactum* L.B.Sm. | SD, C, E | Hc | L 86 | Ce, Ce, AF |
| ***Pitcairnia azouryi*** Martinelli & Forzza * | M | Ch | L 607 | AF |
| *Portea petropolitana* (Wawra) Mez | M | Ch | L 331 | AF |
| *Tillandsia gardneri* Lindl. | SD | Ph | L 249 | Ca, Ce, Af, Pm |
| *T. recurvata* (L.) L. | SD | Ph | L 375 | Ca, Ce, AF, Pm |
| *T. stricta* Sol. | SD | Ph | L 326 | Ca, Ce, AF, Pm |
| ***Vriesea vellozicola*** Leme & J.A.Siqueira | SD | Hc | L 639 | AF |
| *V. neoglutinosa* Mez | M, C, SD | Hc | L 124 | AF |
| BURMANNIACEAE – M.O. Pivari | | | | |
| *Burmannia capitata* (Walter ex J.F.Gmel.) Mart. | EFV | Th | L 357 | Am, Ce, AF |
| COMMELINACEAE | | | | |
| *Tradescantia* sp. | SD | Ch | L 154 | - |
| CYPERACEAE – R. Trevisan | | | | |
| *Bulbostylis lagoensis* (Boeckeler) Prata & M.G.López | SD, EFV | Th | L 690 | Ce, AF |
| *Cyperus coriifolius* Boeckeler | M, SD | Hc | L 282 | Ce, AF |
| *C. luzulae* (L.) Retz | EFV | Hc | L 637 | All |
| *Fuirena umbellata* Rottb. | EFV | Th | L 806 | All |
| *Rhynchospora tenuis* Link | EFV | Th | L 807 | All |
| *Scleria* sp. nov | SD | Hc | L 653 | AF |
| *Trilepis lhotzkiana* Nees ex Arn. | M, C, SD,E | Ch | L 134 | Am, Ca, Ce, AF |
| ORCHIDACEAE – J. A. N. Batista & P.L. Viana | | | | |
| *Acianthera prolifera* (Herb. ex Lindl.) Pridgeon & M.W.Chase | E, SD | Hc | L 346 | Ce, AF |
| *Cyrtopodium glutiniferum* Raddi | SD | Hc | L 115 | AF |
| ***Encyclia spiritusanctensis*** L.C.Menezes * | SD | Ch | L 140 | AF |
| ***Pseudolaelia geraensis*** Pabst | E | Ch | L 338 | AF |
| *P. vellozicola* (Hoene) C.Porto & Brade | SD, E | Ch | L 245 | Ce, AF |
| *Prescottia montana* Barb.Rodr. | SD | Hc | L 333 | |

**Table 1.** Continuation.

| **FAMILY - specialist**<br>***Species*** | **Habitat type** | **Life-form** | **Voucher** | **Phytogeografic Domain** |
|---|---|---|---|---|
| POACEAE – P.L. Viana | | | | |
| *Andropogon bicornis* L. | EFV | Hc | L 298 | All |
| ***Axonopus graniticola*** P.L. Viana | SD | Hc | L 145 | AF |
| *Ichnanthus* cf. *dasycoleus* Tutin | SD | Th | L 356 | Am, Ca, AF |
| *Melinis repens* (Willd.) Zizka | SD, EFV | Ch | L 395 | Ca, Ce, AF |
| *Paspalum paniculatum* L. | EFV | Hc | L 678 | Am, Ce, AF, Pm, Pn |
| *Setaria* sp. | SD | Th | L 673 | - |
| VELLOZIACEAE – R. Mello-Silva | | | | |
| ***Barbacenia purpurea*** Hook. | M | Ch | L 640 | AF |
| *B. tomentosa* Mart. | M, SD, C | Ch | L 288 | Ce, AF |
| ***Vellozia candida*** J.C.Mikan | SD | Ph | L 90 | Ca, AF |
| *V. plicata* Mart. | M, C, SD,E | Ph | L 287 | Ca, Ce, AF |
| EUDICOTS | | | | |
| APOCYNACEAE – I. Koch | | | | |
| *Ditassa* cf. *longicaulis* (E.Fourn.) Rapini | SD | Ph | L 397 | CE, AF |
| ***Mandevilla grazielae*** M.F.Sales *et al.* | SD, C | Cr | L 153 | Ca, AF |
| *M. tenuifolia* (J.C.Mikan) Woodson | SD | Cr | L 606 | Am, Ca, Ce, AF |
| *Mandevilla* sp. nov**.** | SD | Cr | L 611 | AF |
| *Marsdenia* sp. | SD | Ph | L 137 | - |
| ASTERACEAE – E.K.O. Hattori & A.C. Fernandes | | | | |
| *Baccharis salicifolia* (Ruiz & Pav.) Pers. | SD | Ph | L 645 | Am, Ce, AF |
| *Lepidaploa cotoneaster* (Willd. ex Spreng.) H.Rob. | SD | Ph | L 248 | Ce, AF |
| *Mikania microcephala* DC. | SD | Ph | L 396 | Ce, AF |
| *Vernonanthura* sp. | SD, C | Ph | L 359 | - |
| ***Wunderlichia azulensis*** Maguire & G.M.Barroso! | SD, C | Ph | L 131 | AF |
| BEGONIACEAE - L. Kollmann | | | | |
| ***Begonia aguiabrancensis*** L.Kollmann * | SD, C | Ph | L 141 | AF |
| BIGNONIACEAE | | | | |
| *Tabebuia reticulata* A.H.Gentry | SD, C | Ph | L 401 | Ca, AF |
| CACTACEAE – D. Zappi | | | | |
| ***Coleocephalocereus buxbaumianus*** Buining ! | SD, E, C | Ph | L 320 | AF |
| ***C. fluminensis*** (Miq.) Backeb.! | SD, E, C | Ph | L 629 | AF |
| ***Pilosocereus brasiliensis* ssp. *ruschianus*** (Buining & Brederoo) Zappi ! | SD, E | Ph | L 321 | Ca, AF |
| DIOSCORIACEAE – D. Araújo | | | | |

**Table 1.** Continuation.

| **FAMILY - specialist**<br>***Species*** | **Habitat type** | **Life-form** | **Voucher** | **Phytogeografic Domain** |
|---|---|---|---|---|
| *Dioscorea polygonoides* Humb. & Bonpl. ex Willd. | SD | Cr | L 683 | Ca, AF |
| ERYTHROXYLACEAE | | | | |
| *Erythroxylum* cf. *vaccinifolium* Mart. | SD | Ph | L 91 | Ca, Ce, AF |
| EUPHORBIACEAE - R. Riina | | | | |
| *Cnidoscolus* aff. *lombardii* Fern.Casas | SD, C | Ph | L 130 | AF |
| *Croton nepetifolius* Baill. | SD | Ph | L 138 | Ca, AF |
| ***Stillingia argutedentata*** Jabl. | SD | Ph | L 132 | AF |
| FABACEAE | | | | |
| *Aeschnomene* sp. | SD | Ph | L 144 | - |
| GESNERIACEAE – A. Chautems and M. Peixoto | | | | |
| ***Sinningia aghensis*** Chautems ! * | SD | Cr | L 642 | AF |
| *S. brasiliensis* (Regel & Schmidt) Wiehler & Chautems | SD | Cr | L 676 | Ca, AF |
| ***Paliavana prasinata*** (Ker Gawl.) Benth. | SD | Ph | L 283 | AF |
| LENTIBULARIACEAE – M.O. Pivari | | | | |
| *Utricularia subulata* L. | EFV | Th | L 162 | Am, Ca, Ce, AF |
| LOASACEAE | | | | |
| *Aosa parviflora* (Schrad. ex DC.) Weigend | SD | Th | L 105 | AF |
| LYTHRACEAE | | | | |
| *Cuphea sessilifolia* Mart. | SD | Ph | L 152 | Ca, Ce, AF |
| MALPIGHIACEAE – A. Amorim | | | | |
| ***Stigmaphyllon crenatum*** C.E.Anderson ! | SD | Hc | A 75 | AF |
| MALVACEAE | | | | |
| *Melochia* cf. *morongii* Britton | SD | Ph | L 677 | Ce, AF |
| *Pseudobombax* cf. *crassipes* Ravenna | SD | Ph | L 378 | Ce, AF |
| MELASTOMATACEAE – P.J.F. Guimarães | | | | |
| *Cambessedesia eichleri* Cogn. | SD | Ph | L 241 | Ce, AF |
| *Tibouchina heteromalla* (D.Don) Cogn. | SD, C | Ph | L 168 | Ce, AF |
| *Tibouchina* sp. | SD | Ph | L 163 | - |
| PLANTAGINACEAE | | | | |
| ***Achetaria crenata*** (Ronse & Philcox) V.C.Souza | EFV, SD | Ph | L 157 | Ca, AF |
| PORTULACACEAE | | | | |
| *Portulaca hirsutissima* Cambess. | SD, E, M | Ch | L 394 | Ca, Ce, AF |
| RUBIACEAE – R. Salas | | | | |
| *Bradea* sp. nov. | SD | Ph | L 303 | AF |

**Table 1.** Continuation.

| **FAMILY - specialist**<br>***Species*** | **Habitat type** | **Life-form** | **Voucher** | **Phytogeografic Domain** |
|---|---|---|---|---|
| SOLANACEAE – J.R. Stehmann | | | | |
| *Schwenckia* sp.nov. | SD | Th | L 239 | Am, Ca, Ce, AF |
| TALINACEAE | | | | |
| *Talinum paniculatum* (Jacq.) Gaertn. | SD | Th | L 178 | Am, Ca, Ce, AF |
| VERBENACEAE | | | | |
| *Stachytarpheta gesnerioides* var. *gesnerioides* Cham. | SD | Ph | L 166 | Ce, AF |

## Discussion

The richest families found in this study were also well represented in other surveys of inselberg flora (Barthlott & Porembski 2000a; Safford & Martinelli 2000; Caiafa & Silva 2005; Ribeiro *et al.* 2007; Gomes & Alves 2009). Among the monocots, Bromeliaceae, Orchidaceae, Cyperaceae and especially Velloziaceae consist of rupicolous and saxicolous representants (Smith & Ayensu 1976; Benzing 2000; Menini Neto *et al*. 2013). The first two families are also represented by species that can be either epiphytic or rupicolous (Safford & Martinelli 2000). Desiccation tolerance, vegetative propagation and water-storing tissues are typical features of the species belonging to these families (Porembski *et al*. 1998; Porembski & Barthlott 2000), which may contribute to their establishment on the rock outcrops.

Within the Bromeliaceae, typical genera of rock outcrops were found here, *e.g*., *Alcantarea*, *Encholirium*, *Orthophytum*, *Pitcairnia*, *Tillandsia* and *Vriesea*. These genera dominate inselberg landscapes in the Brazilian territory and some have been subject of studies regarding molecular and evolutionary biology (Barbará *et al.* 2007; Palma-Silva *et al.* 2011), which reinforced the island-like character of inselberg flora, and supported the idea that intraspecific gene flow among inselbergs is unusually low (Palma-Silva *et al*. 2011).

The presence of some Apocynaceae species may be related to the requirements for the colonization of xeric environments such as inselbergs. Adaptations to water stress and high temperatures are common among this family (Barthlott & Porembski 2000a). The genus *Mandevilla*, among the three most specious genera found in this study, are often cited as common elements of granitic otucrops, many of them being endemic (Porembski *et al*. 1998; Sales *et al*. 2006). Interestingly, Martins & Alves (2008) identified anatomical features of *Mandevilla* spp., particularly in the leaves, that could be related to resistance against high temperature, insolation and water stress.

Poaceae has also common members of the world's inselbergs flora, well represented in outcrops of South America, Africa, Madagascar, Australia and the United States (Barthlott & Porembski 2000a). The native species *Axonopus graniticola* appeared to be more specialized to this type of environment, showing adaptations of protection against high temperatures, such as the persistence of leaf sheaths on the culms and the readily deciduous leaf blades during the dry season (Viana & de Paula 2013). However, many grasses are ecologically generalists, and its occurrence may be due to the fact that they have more ecological tolerance than habitat specificity (Safford & Martinelli 2000).

Regarding biological invasions, it seemed that inselberg environmental heterogeneity implicated in differences in invasibility, as there were some habitats more invasive-prone than others. In habitats with relatively higher resource availability and favorable characteristics to the invasion, such as shallow depressions (de Paula et al, unpublished data), *Melinis repens* was found in large clumps. This species and other weeds were found throughout southeastern Brazil in several inselbergs studied, being considered a serious threat for inselberg vegetation (Porembski *et al*. 1998; Porembski 2000a). The critical point is that, when disturbance regimes are altered, rock outcrops become extreme vulnerable to invasion by non-native exotic organisms (Hooper 2009). The reason is that, after disturbances, inselberg plant communities, as well as other types of outcrop vegetation (Jacobi *et al.* 2007), have low ability to persist and recover, especially because its species have reduced growth rates and low dispersability (Hooper 2009). Consequently, the opportunity for invasive organisms become higher and the chances of repair and restoration are significantly more challenging for this type of vegetation (Hopper 2009).

Many studies on rocky outcrops have found phanerophytes and hemicriptophytes as the predominant life-forms (Safford & Martinelli 2000; Caiafa & Silva 2005; Ribeiro *et al.* 2007; Gomes & Alves 2009), although other studies of vegetation patches showed a greater proportion of chamephytes species (Porembski *et al.* 1998; Conceição & Giulietti 2002; Conceição *et al.* 2007). The proportion of life-forms can be influenced by climate and edaphic conditions (Cain 1950), though there is no obvious pattern in the proportion of life forms in many studies about rupicolous vegetation within the Atlantic Forest domain (Ribeiro *et al.* 2007). The greatest representativeness of phanerophytes found in this study may be related to the geomorphology of the inselberg studied, which comprises many depressions. This habitat allows the accumulation of larger amounts of soil, enabling the establishment of woody species from the surrounding vegetation. These species, then, possibly decrease insolation in the lower stratum of the patches (Conceição *et al.* 2007), which favors the gradual replacement by other phanerophytes that do not support direct insolation throughout the day.

Despite the fact that phanerophytes were the most predominant life-form on the inselberg as a whole, this was not the case for all habitats. It was notable that in most resource limited habitats, such as epilithic vegetation and monocot mats, chamephytes were most representative. Usually, this plant life-form reflect harsh environmental conditions (Cain 1950). Moreover, in the ephemeral flush vegetation prevailed the therophytes, during the rainy season the annual species are conspicuous, while in the dry season the vegetation patches are covered by desiccated plant remnants. Commonly, Brazilian inselbergs have low representation of annual plants, whereas in African inselbergs, therophytes are dominant (Porembski 2000b). The reasons for these difference in life-form proportion are still not very clear, and it might be related to ecological competition and past climatological change (Safford & Martinelli 2000), we point out that it might also be related to trait-environmental relationships (de Paula *et al*., unpublished data).

It has been already shown that inselbergs have a typical set of physiognomically defined communities, which occur very similar throughout the world (Porembski *et al*. 2000). The habitats described in these work were also reported on other inselbergs in tropical and temperate regions (Porembski *et al*. 1997; Porembski 2000b; Porembski *et al.* 2000), determined by specific plant community composition and variable degrees of environmental stress. Shallow depressions were the richest habitat in the study area, which can be possibly explained by the high nutrient availability, deeper soils and shading that allows the establishment of various life-forms, but especially phanerophytes. Most of the species occurring on the other habitats, except the ones from the ephemeral flush vegetation, could establish on these depressions, so its floristic composition has some similarity with monocot mats and crevices. However, these depressions comprise a high number of exclusive species, which can be related to the fact that some trees and shrubs are not able to develop on habitats under more extreme conditions, so they are concentrated on these more favorable environments.

Ephemeral flush vegetation was the most distinct habitat regarding species composition, with high floristic specificity due to its seasonal aspect. Floristically, this habitat is relatively uniform on inselbergs in tropical and temperate zones (Poremski 2007). Usually, carnivorous plants (Lentibulariaceae), which are indicative of poor soils, belong to the most prominent species of this community, as a consequence of low nutrient availability (Porembski *et al*. 2000). Also, the vegetation consists of annual species including grasses and sedges, represented by typical generalist species (Porembski 2000b).

The Bromeliaceae, Cyperaceae and Velloziaceae families are described in the literature as the most typical mat-formers, the latter two families comprise desiccation-tolerant species (Porembski & Barthlott 2000). In southeastern Brazil, *Alcantarea*, *Vriesea* and *Encholirium* species are commonly cited for inselberg monocot mats (Porembski *et al.* 1998; Porembski 2007), as well as *Trilepis lhotzkiana*, a widely distributed Cyperaceae species in Brazil (Safford & Martinelli 2000). The high diversity of monocots presented in this work and also in other Brazilian inselbergs seems to reflect the high diversity of the matrices they are inserted (Porembski *et al.* 1998). In the Atlantic Forest domain, for example, there is a large 'pool' of regional species able to associate forming mats, in contrast with other tropical regions, for example the West African inselbergs, where just a few species are mat-forming (Porembski 2000b). The close floristic similarity between monocot mats and crevices might be related to the fact that both habitats share similar envirionmental conditions, they are not as poor in resource availability as the epilithic vegetation, and are not as rich as the shallow depresions. So, species with similar recource requirements might develop on these habitats.

The species recorded for the mats and especially for the epilithic vegetation are ecologically important in the colonization of the bare rock, and thus for the formation of inselberg plant communities (Porembski *et al.* 1997). It is possible to speculate that these pioneer species could be enabling the establishment of other species incapable to attach to the exposed rock. Thereby, through interspecific facilitation, an increase in functional and taxonomic diversity could have being promoted by these nurse plants (Franco & Nobel 1989), enhancing ecosystem functioning (Díaz & Cabido 2001; Cardinale *et al.* 2002). Usually, species are not equally important in their participation to ecosystem processes, these species could be accounting for a considerable fraction of ecosystem functioning in these rock outcrops. Even though inselberg research has increased over the past years, we still do not understand basic attributes of this ecosystem, there is a large gap concerning questions of its ecosystem structure and function (Barthlott & Porembski 2000b).

Another observation confirmed in this work was the strong influence of both Cerrado and Caatinga phytogeographical domains on the inselberg flora studied. These domains are also subjected to harsh environmental conditions, and the mosaic vegetation of both comprise xerophytic plants adapted to intense dry seasons (Sampaio 1995; Ratter *et al.* 1997; Leal *et al.* 2005). It is possible to infer that inselbergs in this area represent a discontinuous and scattered stepping stones for a xeric vegetation, which has been already observed in other tropical parts of the world (Burke 2002; Gröger & Huber 2007). Inselbergs can be important sources for species adapted to stressful conditions, from many biomes, and can also serve as maintainer of the genetic diversity of several species that comprise disjunction populations (Hopper 2009), especially those with short dispersal ranges (Burke 2002). This character of refuge of the inselbergs (Porembski *et al*. 2000) might be emphasized particularly in the context of the increasing natural resource extraction in Brazil (Ferreira *et al*. 2014) and the rapid habitat loss and fragmentation of the Brazilian Atlantic Forest (Tabarelli *et al.* 2004). In this aforementioned domain species restricted to rocky outcrops exhibited the highest extinction risk among various vegetation types, it seems that species adapted to resource-limited environments, such as inselbergs, are more extinction-prone than other environments (Leão *et al*. 2014).

Due to the difficulty of access and the fact that many inselbergs are inserted into areas of grassland or forest remnants, the botanical community has overlooked the great potential of these outcrops. With regards to conservation, every remnant of native vegetation of rocky outcrops, no matter how small, is worth retaining, and should be investigated and preserved (Hooper 2009). Remnants can house populations of some organisms showing unexpected persistence (e.g., old lineages and old individuals, like some members of Velloziaceae family) and enhanced resilience (Hopper 2009), new species and endemics, despite massive fragmentation and loss of surrounding vegetation. Moreover, to achieve any chance of success, repair and restoration of rock outcrop communities should definitely include control of exotic species (Cramer & Hobbs 2007).

The results here presented reveal new species, new records for Minas Gerais state, high plant species richness, elevated endemism and high beta-diversity in a single inselberg. Together with our results on life-form spectra and biological invasions, we ague on the importance of increasing efforts on inselberg research, which still lack studies both with respect to their floristic composition and in relation to various ecological aspects. We believe that our data can contribute to comparative approaches worldwide, since inselbergs comprise well defined plant communities, and will consequently improve management and conservation of this unique flora.

## Acknowledgments

First of all, we thank Fernando A.O. Silveira for the valuable suggestions on the manuscript and for collaboration in the data sampling. We thank Ana L. Fonseca, Marcelo Amorim, Marcelo Fonseca, Luísa Azevedo, Renato Fernandes, Theo Mota, Lucas, Eliane, Caique, Pablo Burkowski, Túlio Jorge, Felipe Leite, Mariana Augsten and Stefan Porembski for logistical support and help in the field work. We express our gratitude to the Addiny family for kindly providing permission for the field work on its property. We are also thankful for the botanical specialists who gently helped with many identifications. Finally, we thank de Paula Foundation for the financial support to the project and the grants from the CNPq (Conselho Nacional de Pesquisa e Desenvolvimento), this study was in partial fulfillment of the master requirements of L.F.A. de Paula in Plant Biology, who received a scholarship from

CNPq.

## References

Alvares, C.A.; Stape, J.L.; Sentelhas, P.C.; Gonçalves, J.L.M. & Sparovek, G. 2013. Köppen's climate classification map for Brazil. **Meteorologische Zeitschrift 22**:711-728.

Anderson, C. 1993. Novelties in Stigmaphyllon (Malpighiaceae) from South America. **Contr. University of Michigan Herbarium 19**: 415-429.

APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. **Botanical Journal of the Linnaean Society 161**:105-202.

Araujo, A.O.; Souza, V.C. & Chautems, A. 2005. Gesneriaceae of Cadeia do Espinhaço in Minas Gerais, Brasil. **Brazilian Journal of Botany 28**: 109-135.

Barbará, T.; Martinelli, G.; Fay, M.F.; Mayo, S.J. & Lexer C . 2007. Population differentiation and species cohesion in two closely related plants adapted to neotropical high altitude 'inselbergs', Alcantarea imperialis and Alcantarea geniculata (Bromeliaceae). **Molecular Ecology 16**: 1981-1992.

Barthlott, W.; Gröger, A. & Porembski, S. 1993. Some remarks on the vegetation of tropical inselbergs: diversity and ecological differentiation. **Compte rendu des séances de la société de biogéographie 69**: 105-124.

Barthlott, W. & Porembski, S. 2000a. Vascular plants on inselbergs: systematic overview. Pp. 103-116. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Barthlott, W. & Porembski, S. 2000b. Why Study Inselbergs?. Pp. 1-6. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Benzing, D.H. 2000. **Bromeliaceae: profile of an adaptive radiation**. Cambridge, Cambridge University Press.

Biedinger, N.; Porembski, S. & Barthlott, W. 2000. Vascular plants on inselbergs: Vegetative and reproductive strategies. Pp. 117-142. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Büdel, B.; Becker, U.; Follmann, G & Sterflinger, K. 2000 . Algae, Fungi and Lichens on Inselbergs. Pp. 69-90. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Burke, A. 2002. Are Namibian inselbergs conservation islands? A floral perspective: research in action. **South African Journal of Science 98**: 560.

Burke, A. 2003. Inselbergs in a changing world - global trends. **Diversity and Distributions 9**: 375-383.

Caiafa, A.N. & Silva, A.F. 2005. Composição florística e espectro biológico de um campo de altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais—Brasil. **Rodriguésia 56**: 163-173.

Cain, S.A. 1950. Life-forms and phytoclimate. **The Botanical Review 16**: 1-32.

Cardinale, B.J.; Palmer, M.A. & Collins, S.L. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. **Nature 415**: 426-429.

Conceição, A.A. & Giulietti, A.M. 2002. Floristic composition and structural aspects of campo rupestre on two plateaus in Pai Inacio Hill, Chapada Diamantina, Bahia, Brazil. **Hoehnea 29**: 37-48.

Cramer, V.A. & Hobbs, R.J. 2007. Old fields dynamics and restoration of abandoned farmland, science and practice of ecological restoration series. Washington DC, Island.

Conceição, A.A.; Pirani, J.R. & Meirelles, S.T. 2007. Floristics, structure and soil of insular vegetation in four quartzite-sandstone outcrops of" Chapada Diamantina", Northeast Brazil. **Brazilian Journal of Botany 30**: 641-656.

de Paula, L.F.A.; Viana, P.L; Mota, N.; Augsten, M.; Leite, F. & Stehmann, J.R. 2013. **Saxicolous Plants of an Inselberg in the Mucuri Valley**. Chicago, Rapid Color Guides, The Field Museum. http://fieldguides.fieldmuseum.org/sites/default/files/rapid-color-guides-pdfs/378.pdf (access Oct 2014)

Delcourt, P.A. & Delcourt, H.R.1992. Ecotone Dynamics in space and time. Pp. 19-51. In: Hansen, A.J. & di Castri, F. (eds) **Landscape Boundaries: Consequences for Biotic Diversity and Landscape Flows**. New York, Ecological Studies, Springer-Verlag.

Díaz, S. & Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. **Trends in Ecology & Evolution 16**: 646-655.

Ferreira, J. *et al*. 2014. Brazil's environmental leadership at risk. **Science 346**: 706-707.

Fidalgo, O. & Bononi, V.L.R. 1989. **Técnicas de coleta, preservação e herborização de material botânico**. Governo do Estado de São Paulo, Secretaria do Meio Ambiente, Instituto de Botânica.

Filgueiras, T.S. & Rodrigues, R.S. *Axonopus* in **Lista de Espécies da Flora do Brasil**. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB1303 (access on Oct 2014).

Forzza, R.C. *et al*. 2012. New Brazilian Floristic List Highlights Conservation Challenges. **Bioscience 62**: 39-45.

Franco, A.C. & Nobel, P.S. 1989. Effect of nurse plants on the habitat and growth of cacti. **The Journal of Ecology 77**: 870-886.

Giulietti, A.M.; Rapini, A.; Andrade, M.J.G; Queiroz, L.P & Silva, J.M.C. 2009. **Plantas raras do Brasil**. Belo Horizonte, Conservação Internacional.

Gomes, P. & Alves, M. 2009. Floristic and vegetational aspects of an inselberg in the semi-arid region of Northeast Brazil. **Edinburgh Journal of Botany 66**: 329-346.

Gröger, A. & Huber, O. 2007. Rock outcrop habitats in the Venezuelan Guayana lowlands: their main vegetation types and floristic components. **Brazilian Journal of Botany 30**: 599-609.

Hammer, Ø., Harper, D.A.T., Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 9.

Hopper, S.D. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. **Plant and Soil 322**: 49-86.

INCT - **Virtual Herbarium of Plants and Fungi**. 2014. http://inct.florabrasil.net/en/herbario-virtual/ (access on Oct 2014).

INMET. 1992. **Normais climatológicas (1961-1990)**. National Institute of Meteorology, Brasília, Brasil.

Jablonski, E. 1967. Notes on Neotropical Euphorbiaceae. 2. New species and transfers. **Phytologia 14**: 450-456.

Jacobi, C.M.; do Carmo, F.F.; Vincent, R.C. & Stehmann, J.R. 2007. Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. **Biodiversity and Conservation** 16:2185-2200.

Kollmann, L.J.C. 2008. Duas novas spécies de Begonia (Begoniaceae) do Espírito Santo, Brasil. **Rodriguésia 59**: 155-160.

Kramer, K. U. & Green, P. S. 1990. Pteridophytes and Gymnosperms. In: Kubitzki, K. **The Families and Genera of Vascular Plants**. New York, Springer-Verlag.

Leal, I.R.; Silva, J.M.C.; Tabarelli, M. & Lacher, T.E. 2005. Changing the course of biodiversity conservation in the Caatinga of northeastern Brazil. **Conservation Biology 19**: 701-706.

Leão, T.C.; Fonseca, C.R.; Peres, C.A. & Tabarelli, M. 2014. Predicting Extinction Risk of Brazilian Atlantic Forest Angiosperms. **Conservation Biology 28**:1349-1359.

Leme, E.M.C.; Fraga, C.N.; Kollmann, L.J.C. & Fontana, A.P. 2008. Three new Alcantarea species from Espírito Santo and Minas Gerais, Brazil. **Journal of the Bromeliad Society 58**: 205-216.

**List of Species of the Brazilian Flora**. Rio de Janeiro Botanical Garden. http://floradobrasil.jbrj.gov.br (access on Oct 2014).

Martinelli, G. 2007. Mountain biodiversity in Brazil. **Brazilian Journal of Botany 30**: 587-597.

Martinelli, G. & Forzza, R.C. 2006. Pitcairnia L'Hér.(Bromeliaceae): a new species, P. azouryi Martinelli & Forzza, and notes on P. encholirioides LB Sm. **Brazilian Journal of Botany 29**: 603-607.

Martinelli, G. & Moraes, M.A. 2013. **Red Book of Brazilian Flora**. Jardim Botânico do Rio de Janeiro. http://cncflora.jbrj.gov.br/portal/pt-br/livro (access on Oct 2014).

Martins, S. & Alves, M. 2008. Aspectos anatômicos de espécies simpátridas de Mandevilla (Apocynaceae) ocorrentes em inselbergues de Pernambuco—Brasil. **Rodriguésia 59**: 369-380.

Mauad, L.P.; Buturi, F.O.S.; Souza, T.P.; Nascimento, M.T. & Braga, J.M.A. 2014. New distribution record and implications for conservation of the endangered *Wunderlichia azulensis* Maguire & GM Barroso (Asteraceae: Wunderlichieae). **Check List 10**: 706-708.

Meirelles, S.T.; Pivello, V.R. & Joly, C.A. 1999. The vegetation of granite rock outcrops in Rio de Janeiro, Brazil, and the need for its protection. **Environmental Conservation 26**: 10-20.

Mello-Silva, R. 2004. Sistemática de Vellozia candida (Velloziaceae). **Rodriguesia 55**: 59-64.

Menezes, L.C. 1991. A large and showy new species from Brazil from northern Espirito Santo, Encyclia spiritusanctensis LC Men. **Orchid Dig 55**: 23.

Menini Neto, L.; Forzza, R.C. & van den Berg, C. 2013. Taxonomic revision of *Pseudolaelia* Porto & Brade (Laeliinae, Orchidaceae). **Acta Botanica Brasilica 27**: 418-435.

Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., & Fonseca, G.A.B. 2004. **Hotspots Revisited. Earth's biologically richest and most endangered terrestrial ecorregions**. Mexico, CEMEX.

MMA – Ministério do Meio Ambiente. 2006. **Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira– PROBIO. Biodiversidade e conservação nos Vales dos Rios Jequitinhonha e Mucuri**. Brasília – DF. http://sistemas.mma.gov.br/sigepro/pub/display_bibliografias.php?%20vId_Gerenciamento= 1001&Destaque=7 (access on Oct 2014).

MMA – Ministério do Meio Ambiente. 2008. **Espécies da flora brasileira ameaçadas de extinção**. Instrução normativa n.6, de 23 de setembro de 2008, Brasília – DF.

Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. **Nature 403**:853-858

Oliveira-Filho, A.T. *et al* .2005. Análise florística do compartimento arbóreo de áreas de Floresta Atlântica sensu lato na região das Bacias do Leste (Bahia, Minas Gerais, Espírito Santo e Rio de Janeiro). **Rodriguésia 56**: 185-235

Palma-Silva, C. *et al*. 2011. Sympatric bromeliad species (Pitcairnia spp.) facilitate tests of mechanisms involved in species cohesion and reproductive isolation in Neotropical inselbergs. **Molecular Ecology 20**: 3185-3201

Pigott, J.P. 2000. Environmental weeds and granite outcrops: possible solutions in the "too hard basket". **Journal of the Royal Society of Western Australia 83**: 135-137.

Porembski, S. 2000a. The invasibility of tropical granite outcrops ('inselbergs') by exotic weeds. **Journal of the Royal Society of Western Australia 83**: 131-137.

Porembski, S. 2000b. West African inselberg vegetation. Pp. 177-211. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Porembski, S. 2007. Tropical inselbergs: habitat types, adaptive strategies and diversity patterns. **Brazilian Journal of Botany 30**: 579-586.

Porembski, S. & Barthlott, W. 1997. Seasonal dynamics of plant diversity on Inselbergs in the Ivory Coast (West Africa). **Botanica Acta 110**: 466-472.

Porembski, S. & Barthlott, W. 2000. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. **Plant Ecology 151**: 19-28.

Porembski, S.; Becker, U. & Seine, R. 2000. Islands on islands: habitats on inselbergs. Pp. 49-67. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of**

**isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Porembski, S.; Martinelli, G.; Ohlemüller, R. & Barthlott, W. 1998. Diversity and ecology of saxicolous vegetation mats on inselbergs in the Brazilian Atlantic rainforest. **Diversity and Distributions 4**: 107-119.

Porembski, S.; Seine, R. & Barthlott, W. 1997. Inselberg vegetation and the biodiversity of granite outcrops. **Journal of the Royal Society of Western Australia 80**: 193-199.

Ratter, J.A.; Ribeiro, J.F. & Bridgewater, S. 1997. The Brazilian cerrado vegetation and threats to its biodiversity. **Annals of Botany 80**: 223-230.

Raunkiaer, C. 1934. The life forms of plants and statistical geography. **The life forms of plants and statistical geography**. Oxford, Clarendon.

Ribeiro, K.T.; Medina, B.M.O. & Scarano, F.R. 2007. Species composition and biogeographic relations of the rock outcrop flora on the high plateau of Itatiaia, SE-Brazil. **Brazilian Journal of Botany 30**: 623-639.

Risser, P.G., 1995. The status of the science examining eco- tones. Bioscience 45, 318–325.

Safford, H.D. 1999. Brazilian Paramos I. An introduction to the physical environment and vegetation of the campos de altitude. **Journal of Biogeography 26**: 693-712.

Safford, H.D. & Martinelli, G. 2000. Southeast Brazil. Pp 339-389. In: Porembski, S. & Barthlott, W. (eds.) **Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions**. Berlin, Ecological Studies, Springer-Verlag.

Sales, M.F.; Kinoshita, L.S. & Simões, A.O. 2006. Eight new species of Mandevilla Lindley (Apocynaceae, Apocynoideae) from Brazil. **Novon: A Journal for Botanical Nomenclature 16**: 112-128.

Sampaio, E.V.S. 1995. Overview of the Brazilian Caatinga. Pp. 35–63. In: Bullock, S.H.; Mooney, H.A. & Medina, E. **Seasonally dry tropical forests**. Cambridge, Cambridge University Press.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. **Annals of Botany 90**: 517-524.

Scott, P. 2000. Resurrection plants and the secrets of eternal leaf. **Annals of Botany 85**: 159-166.

Siqueira-Filho, J.A. & Leme, E.M. 2006. **Fragmentos de Mata Atlântica do nordeste: biodiversidade, conservação e suas bromélias**. Rio de Janeiro, Andrea Jackobsson Estúdio Editorial Ltda.

Smith, A.R.; Pryer, K.M.; Schuettpelz, E.; Korall, P.; Schneider, H. & Wolf, P.G. 2006. A classification for extant ferns. **Taxon 55**: 705-731.

Smith, L.B. & Ayensu, E.S. 1976. A revison of American Velloziaceae. **Smithsonian Contributions to Botany 30**: i–viii + 1–172.

Souza. V.C. & Giulietti, A.M. 2009. Levantamento das espécies de Scrophulariaceae sensu lato nativas do Brasil. **Pesquisas, Botânica 60**: 7-288.

Stehmann, J.R.; Forzza, R.C.; Salino, A.; Sobral, M.; Costa, D.P. & Kamino, L.H.Y. 2009. **Plantas da Floresta Atlântica**. Jardim Botânico do Rio de Janeiro, Rio de Janeiro.

Suguiyama, V.F.; Silva, E.A.; Meirelles, S.T.; Centeno, D.C. & Braga, M.R. 2014 Leaf metabolite profile of the Brazilian resurrection plant *Barbacenia purpurea* Hook.(Velloziaceae) shows two time-dependent responses during desiccation and recovering. **Frontiers in Plant Science 96**: 1-13.

Tabarelli, M.; Silva, M.J.C. & Gascon, C. 2004. Forest fragmentation, synergisms and the impoverishment of neotropical forests. **Biodiversity and Conservation 13**: 1419-1425.

Taylor, N.P. & Zappi, D.C. 2004. **Cacti of eastern Brazil**. Kew, Royal Botanic Gardens.

Thiers, B. [continuously updated]. **Index Herbariorum: a global directory of public herbaria and associated staff**. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/ (access on Oct 2014).

Veloso, H.P.; Rangel Filho, A.L.R. & Lima, J.C.A. 1991. **Classificação da vegetação brasileira, adaptada a um sistema universal**. Rio de Janeiro, Fundação Instituto Brasileiro de Geografia e Estatística.

Viana, P.L. & de Paula, L.F.A. 2013. *Axonopus graniticola*, a new species of *A.* ser. *Suffulti* (Poaceae, Panicoideae, Paspaleae) from Minas Gerais, Brazil. **Phytokeys 21**: 7-16.

## Minas Gerais, BRASIL

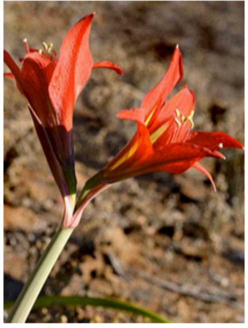
# Plantas Saxícolas em Inselbergue no Vale do Mucuri

1

**Luiza Fonseca A. de Paula, Pedro Lage Viana, Nara Mota, Mariana Augsten, Felipe Leite e João Renato Stehmann**

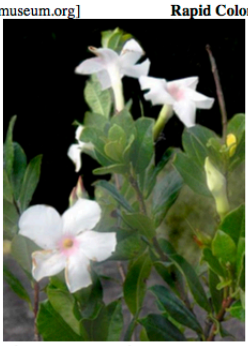
Fotos dos autores, exceto onde indicado: Produzido por: Tyana Wachter, R. Foster, J. Philipp. Apoio de Connie Keller, Hyndman Fund & A. Mellon Foundation. Agradecimentos a Universidade Federal de Minas Gerais , C. Addiny, M. Amorim, A. L. Fonseca, C. Dalcin, P. Burkowski e T. Jorge pelo apoio logístico e ajuda em campo; assim como aos botânicos A. Chautems, A. Salino, A.C. Fernandes, D. Zappi, E. Gonçalves, E. Hattori, J. Dulith, L. Versieux, L. Giacomin, L. Kollmann, R. Lousada, R. Mello-Silva e T. Almeida pela ajuda nas identificações taxonômicas.

[http://fieldmuseum.org/IDtools] [rrc@fieldmuseum.org] **Rapid Color Guide # 378** versão **1** 08/2013


1 **Hippeastrum** glaucescens
AMARYLLIDACEAE


2 **Mandevilla** grazielae
APOCYNACEAE


3 **Mandevilla** grazielae
APOCYNACEAE


4 **Mandevilla** sp. nov.
APOCYNACEAE


5 **Anthurium** sp. nov.
ARACEAE


6 **Anthurium** sp. nov.
ARACEAE


7 **Philodendron** edmundoi
ARACEAE

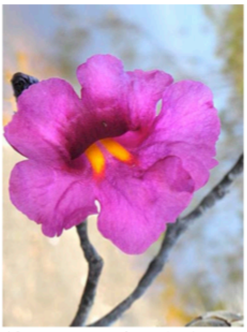

8 **Philodendron** edmundoi
ARACEAE


9 **Wunderlichia** azulensis
ASTERACEAE


10 **Begonia** aguiabrancensis
BEGONIACEAE


11 **Begonia** aguiabrancensis
BEGONIACEAE

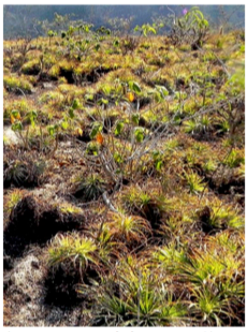

12 **Tabebuia** reticulata
BIGNONIACEAE


13 **Tabebuia** reticulata
BIGNONIACEAE


14 **Alcantarea** simplicisticha
BROMELIACEAE


15 **Alcantarea** simplicisticha
BROMELIACEAE


16 **Alcantarea** simplicisticha
BROMELIACEAE


17 **Encholirium** gracile
BROMELIACEAE


18 **Encholirium** gracile
BROMELIACEAE


19 **Encholirium** gracile
BROMELIACEAE


20 **Encholirium** gracile
BROMELIACEAE

# Minas Gerais, BRASIL
# Saxicolous Plants of an Inselberg in the Mucuri Valley 2

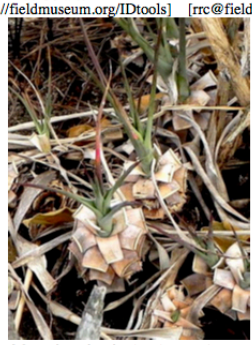
**Luiza Fonseca A. de Paula, Pedro Lage Viana, Nara Mota, Mariana Augsten, Felipe Leite e João Renato Stehmann**

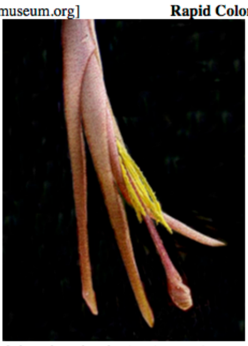
Fotos dos autores, exceto onde indicado: Produzido por: Tyana Wachter, R. Foster, J. Philipp. Apoio de Connie Keller, Hyndman Fund & A. Mellon Foundation. Agradecimentos a Universidade Federal de Minas Gerais , C. Addiny, M. Amorim, A. L. Fonseca, C. Dalcin, P. Burkowski e T. Jorge pelo apoio logístico e ajuda em campo; assim como aos botânicos A. Chautems, A. Salino, A.C. Fernandes, D. Zappi, E. Gonçalves, E. Hattori, J. Dulith, L. Versieux, L. Giacomin, L. Kollmann, R. Lousada, R. Mello-Silva e T. Almeida pela ajuda nas identificações taxonômicas.

[http://fieldmuseum.org/IDtools] [rrc@fieldmuseum.org] **Rapid Color Guide # 378** version 1 08/2013


21 **Orthophytum** compactum
BROMELIACEAE


22 **Orthophytum** compactum
BROMELIACEAE


23 **Pitcairnia** barbatostigma
BROMELIACEAE


24 **Pitcairnia** barbatostigma
BROMELIACEAE

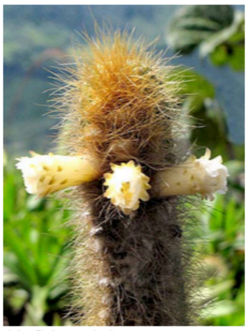

25 **Pitcairnia** barbatostigma
BROMELIACEAE

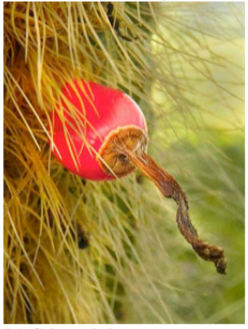

26 **Portea** petropolitana
BROMELIACEAE


27 **Vriesea** neoglutinosa
BROMELIACEAE


28 **Vriesea** neoglutinosa
BROMELIACEAE


29 **Coleocephalocereus** buxbaumianus
CACTACEAE


30 **Coleocephalocereus** buxbaumianus
CACTACEAE


31 **Coleocephalocereus** buxbaumianus
CACTACEAE

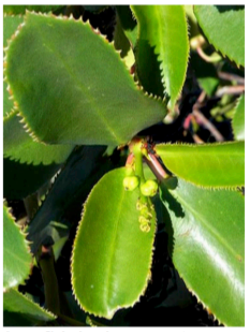

32 **Coleocephalocereus** fluminensis
CACTACEAE


33 **Pilosocereus** brasilensis
CACTACEAE


34 **Cyperus** coriifolius
CYPERACEAE


35 **Cnidoscolus** cf. lombardii
EUPHORBIACEAE


36 **Cnidoscolus** cf. lombardii
EUPHORBIACEAE


37 **Stillingia** argutedentata
EUPHORBIACEAE


38 **Paliavana** prasinata
GESNERIACEAE


39 **Sinningia** aghensis
GESNERIACEAE


40 **Sinningia** aghensis
GESNERIACEAE

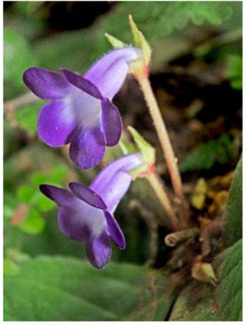
## Minas Gerais, BRASIL

# Plantas Saxícolas em Inselbergue no Vale do Mucuri

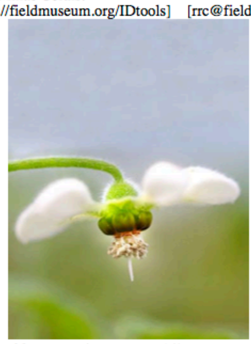
**Luiza Fonseca A. de Paula, Pedro Lage Viana, Nara Mota, Mariana Augsten, Felipe Leite e João Renato Stehmann**

Fotos dos autores, exceto onde indicado: Produzido por: Tyana Wachter, R. Foster, J. Philipp. Apoio de Connie Keller, Hyndman Fund & A. Mellon Foundation. Agradecimentos a Universidade Federal de Minas Gerais , C. Addiny, M. Amorim, A. L. Fonseca, C. Dalcin, P. Burkowski e T. Jorge pelo apoio logístico e ajuda em campo; assim como aos botânicos A. Chautems, A. Salino, A.C. Fernandes, D. Zappi, E. Gonçalves, E. Hattori, J. Dulith, L. Versieux, L. Giacomin, L. Kollmann, R. Lousada, R. Mello-Silva e T. Almeida pela ajuda nas identificações taxonômicas.

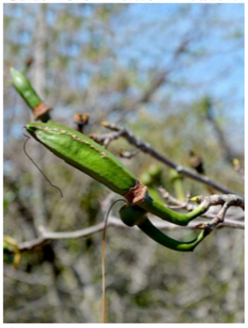
[http://fieldmuseum.org/IDtools] [rrc@fieldmuseum.org] **Rapid Color Guide # 378** versão **1** 08/2013

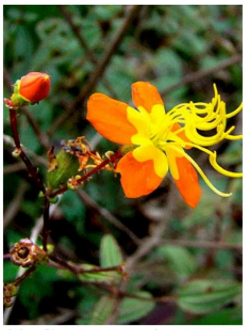

41 **Sinningia** macrophylla
GESNERIACEAE


42 **Aosa** parviflora
LOASACEAE


43 **Aosa** parviflora
LOASACEAE


44 **Pseudobombax** cf. crassipes
MALVACEAE


45 **Pseudobombax** cf. crassipes
MALVACEAE


46 **Cambessedesia** eichleri
MELASTOMATACEAE

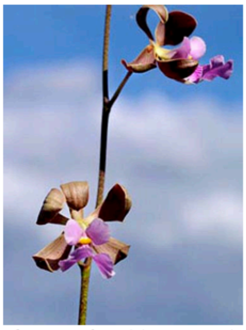

47 **Tibouchina** heteromalla
MELASTOMATACEAE

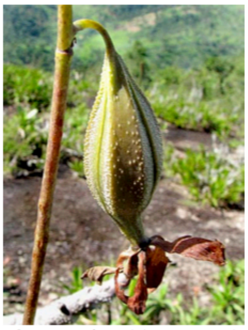

48 **Acianthera** prolifera
ORCHIDACEAE


49 **Cyrtopodium** glutiniferum
ORCHIDACEAE


50 **Cyrtopodium** glutiniferum
ORCHIDACEAE


51 **Cyrtopodium** glutiniferum
ORCHIDACEAE


52 **Encyclia** spiritusanctensis
ORCHIDACEAE

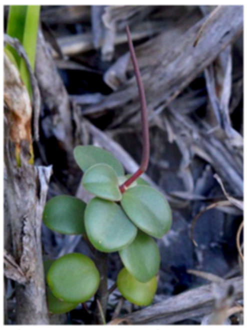

53 **Encyclia** spiritusanctensis
ORCHIDACEAE


54 **Pseudolaelia** geraensis
ORCHIDACEAE


55 **Pseudolaelia** geraensis
ORCHIDACEAE


56 **Pseudolaelia** vellozicola
ORCHIDACEAE


57 **Pseudolaelia** vellozicola
ORCHIDACEAE


58 **Peperomia** sp.
PIPERACEAE


59 **Peperomia** sp.
PIPERACEAE


60 **Achetaria** crenata
PLANTAGINACEAE

## Minas Gerais, BRASIL

# Saxicolous Plants of an Inselberg in the Mucuri Valley

## 4

**Luiza Fonseca A. de Paula, Pedro Lage Viana, Nara Mota, Mariana Augsten, Felipe Leite e João Renato Stehmann**

Fotos dos autores, exceto onde indicado: Produzido por: Tyana Wachter, R. Foster, J. Philipp. Apoio de Connie Keller, Hyndman Fund & A. Mellon Foundation. Agradecimentos a Universidade Federal de Minas Gerais , C. Addiny, M. Amorim, A. L. Fonseca, C. Dalcin, P. Burkowski e T. Jorge pelo apoio logístico e ajuda em campo; assim como aos botânicos A. Chautems, A. Salino, A.C. Fernandes, D. Zappi, E. Gonçalves, E. Hattori, J. Dulith, L. Versieux, L. Giacomin, L. Kollmann, R. Lousada, R. Mello-Silva e T. Almeida pela ajuda nas identificações taxonômicas.

[http://fieldmuseum.org/IDtools] [rrc@fieldmuseum.org] **Rapid Color Guide # 378** versão **1** 08/2013

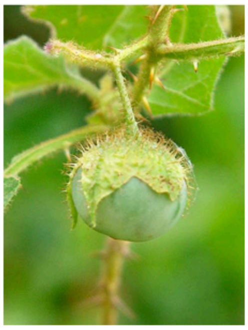

61 **Axonopus** graniticola
POACEAE


62 **Axonopus** graniticola
POACEAE


63 **Portulaca** hirsutissima
PORTULACACEAE


64 **Solanum** sp. nov.
SOLANACEAE

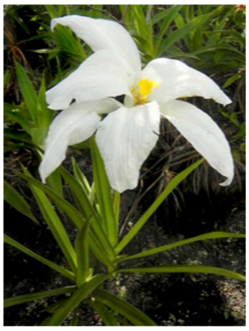

65 **Solanum** sp. nov.
SOLANACEAE


66 **Solanum** sp. nov.
SOLANACEAE foto: Cláudio Nicoletti

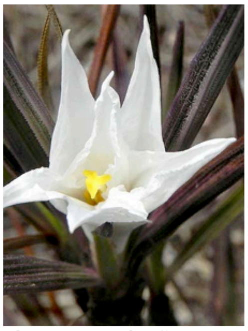

67 **Barbacenia** tomentosa
VELLOZIACEAE


68 **Barbacenia** tomentosa
VELLOZIACEAE


69 **Vellozia** candida
VELLOZIACEAE


70 **Vellozia** candida
VELLOZIACEAE


71 **Vellozia** candida
VELLOZIACEAE


72 **Vellozia** plicata
VELLOZIACEAE


73 **Vellozia** plicata
VELLOZIACEAE


74 **Stachytarpheta** gesnerioides
VERBENACEAE


75 **Stachytarpheta** gesnerioides
VERBENACEAE


76 **Cheilanthes** geraniifolia
PTERIDOPHYTA


77 **Doryopteris** collina
PTERIDOPHYTA


78 **Microgramma** vaccinifolia
PTERIDOPHYTA


79 **Selaginella** convoluta
PTERIDOPHYTA


80 **Selaginella** sellowii
PTERIDOPHYTA

## Minas Gerais, BRASIL

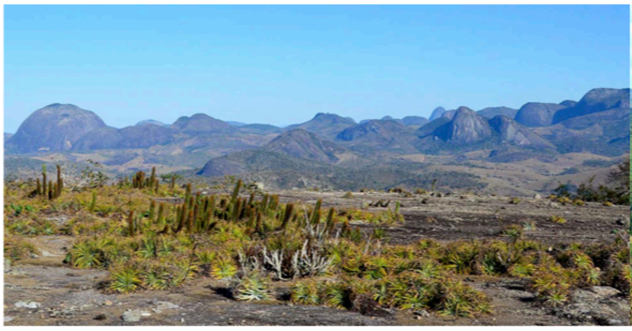
# Plantas Saxícolas em Inselbergue no Vale do Mucuri

**Luiza Fonseca A. de Paula, Pedro Lage Viana, Nara Mota, Mariana Augsten, Felipe Leite e João Renato Stehmann**

Fotos dos autores, exceto onde indicado: Produzido por: Tyana Wachter, R. Foster, J. Philipp. Apoio de Connie Keller, Hyndman Fund & A. Mellon Foundation. Agradecimentos a Universidade Federal de Minas Gerais , C. Addiny, M. Amorim, A. L. Fonseca, C. Dalcin, P. Burkowski e T. Jorge pelo apoio logístico e ajuda em campo; assim como aos botânicos A. Chautems, A. Salino, A.C. Fernandes, D. Zappi, E. Gonçalves, E. Hattori, J. Dulith, L. Versieux, L. Giacomin, L. Kollmann, R. Lousada, R. Mello-Silva e T. Almeida pela ajuda nas identificações taxonômicas.

[http://fieldmuseum.org/IDtools] [rrc@fieldmuseum.org] **Rapid Color Guide # 378** versão **1** 08/2013

Vista do inselbergue na estação seca



Ilhas de vegetação em superfície plana do inselbergue

Ilhas de vegetação em superfície íngreme do inselbergue

Típicas ilhas de vegetação delimitadas por rocha nua

Vista do inselbergue na estação chuvosa

# CAPÍTULO II

# Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic Forest

Luiza F. A. de Paula[1]*, Daniel Negreiros[2], Luísa A. Oliveira[1], Renato L. Fernandes[1], João Renato Stehmann[1], Fernando A. O. Silveira[1]

[1] Departamento de Botânica, ICB/Universidade Federal de Minas Gerais, CP 486, 30161-970 Belo Horizonte, MG, Brazil

[2] Departamento de Biologia Geral, ICB/UFMG, Brazil.

**ARTIGO EM REVISÃO NA BIODIVERSITY & CONSERVATION**

## Abstract

The Atlantic forest is among the hottest hotspots for biodiversity conservation. Inselbergs are isolated granitic and gneiss rocks that rise sharply above the lowland surrounding forests. Due to prevailing stressful conditions and resource paucity of inselbergs, distinguished plant communities are formed in these rocky-associated vegetation, which comprise unusually high levels of endemic and threatened species. Here, we evaluated the importance of CSR (competitiveness:stress-tolerance:ruderalism) ecological strategies in different vegetation patches on the inselberg, tested for a connection between patch structure and functional traits, and compared the variation in functional traits between native and an exotic species which represents a major threat to inselberg communities. Despite the stressful conditions of inselbergs, we found a relatively high diversity of ecological strategies, but most species and patches lied between the S and C strategy. The invasive *Melinis repens*, in turn, was functionally distinctive from native communities, with the predominance of traits associated with ruderalism. We also found that, most functional traits significantly correlated with at least one environmental parameter, highlighting their role in structuring plant communities in this heterogeneous environment. Since inselberg patches were spatially heterogeneous, and the variation in resource availability implies in favouring different ecological strategies, some patch types were more invasive-prone than others. Our data provide significant advances for identifying the environmental drivers of biological invasion in resource-limited environments. We argue that further trait-based approaches will become critical for developing conservation and management strategies for inselberg plant communities, especially in the context of rapid habitat loss and fragmentation of the Atlantic Forest.

**Keywords:** comparative ecology, ecological strategies, inselberg, leaf economics spectrum, rocky outcrops, trait-environment relationship.

## Introduction

The Atlantic Forest is renowned worldwide for being a biodiversity hotspot (Myers et al. 2000), and its rapid habitat loss and fragmentation are raising concerns on the scientific community (Galindo-Leal et al. 2003; Tabarelli et al. 2004; Joly et al. 2014). The Atlantic Forest covers most of the Brazilian coast and goes up to 700 km inward the continent, extending into eastern Paraguay, Bolivia and north-eastern Argentina (Oliveira-Filho and Fontes 2000). The causes of habitat loss have started with deforestation since the colonisation of Brazil and proceeded with the overexploitation of forest resources (wood, charcoal), agriculture, grazing and urbanisation, since the Atlantic Forest range coincides with the most urbanised areas of the country (Tabarelli et al. 2005). Despite legal protection, many threats persist, which lead to the fact that most species officially threatened with extinction in Brazil are elements from the Atlantic Forest (Tabarelli et al. 2003; Martinelli and Moraes 2013).

The Atlantic Forest is a very heterogeneous environment encompassing tropical and subtropical regions, with a wide variation in altitude, temperature and rainfall (Oliveira-Filho and Fontes 2000). This biome comprises the coastal rain forests of Brazil, semi-deciduous forests, *Araucaria* mixed forests, cloud forests and the north-eastern altitudinal forests enclaves (Oliveira-Filho and Fontes 2000). In addition to these forest physiognomies, some plant communities of the Atlantic Forest are associated with stressful environmental factors and often exposed to either flooding, drought or cold winter temperatures (Scarano 2002). A remarkable vegetation type included in these marginal habitats is the one growing on rocky outcrops. Inselbergs (i.e., monolithic mountains or groups of them), whose geological formation consists mainly of granitic and gneiss rocks (Porembski and Barthlott 2000; Porembski et al. 1997), are widespread throughout the Atlantic Forest and support large number of endemic plants contributing to the high biodiversity of this biome (Safford and Martinelli 2000; Porembski 2007). The vegetation associated with these rocks can be considered a conservation priority in the vegetation mosaic of the Atlantic Forest, due to their high degree of diversity, endemism and extinction threats (Porembski and Barthlott 2000, Porembski 2007; Leão et al. 2014).

In many tropical and subtropical regions, threats to inselberg biodiversity are steeply increasing (Meirelles et al. 1999; Burke 2003). Besides the removal of the buffer lowland vegetation in the surrounding areas of inselbergs, which facilitates biological invasion (Pigott 2000; Porembski 2000), inselbergs are also experiencing a particular set of threats including quarrying, mining and unsustainable extraction of attractive species of the flora (Martinelli 2007). The critical point is that inselberg plant communities, as well as other types of outcrop vegetation (Jacobi et al. 2007) are especially vulnerable to soil removal since their species usually have reduced growth rates and reduced dispersability (Hopper 2009). Thus, the ability of inselberg plant communities to persist and recover after disturbance is very low and consequently, the opportunity for invasive organisms is high (Hopper 2009). In this way, this fragility makes the chances of repair and restoration significantly more challenging for this vegetation type, which is aggravated by the high number of endemic and threatened species (Martinelli and Moraes 2013). Even more critical is that species restricted to rocky outcrops exhibited the highest extinction risk among vegetation types throughout the Brazilian Atlantic Forest domain (Leão et al. 2014). Since plant species adapted to resource-limited environments, such as inselbergs, are more extinction-prone compared to species in other environments, some functional traits increase vulnerability to extinction more than others (Leão et al. 2014).

Plant communities in inselbergs are not randomly assembled. They are better described as terrestrial islands since community composition is clearly distinguished from the surrounding matrix (Porembski et al. 2000), due to the prevailing ecological filters, including lack of soil and water, high temperatures and constant winds (Porembski and Barthlott 2000;

Scarano 2002). These filters may also have a role in structuring different vegetational habitats on inselbergs (Barthlott et al. 1993; Porembski 2007; Porembski et al. 2000), though studies focusing on quantitative functional ecology of plant communities in outcrops are virtually inexistent. Taking into account the increasing destruction of natural systems, a trait-based approach (by using species traits instead of their identities) can be a powerful way to understand the structure and dynamics of inselberg plant communities. This approach can also predict changes in ecosystem services delivery due to human disturbances (Díaz and Cabido 1997; de Bello et al. 2010), and assess the performance of exotic invasive species (Drenovsky et al. 2012). Given the high vulnerability of inselbergs to biological invasions (Porembski 2000; Hopper 2009) it is extremely important to identify the combinations of advantageous traits that could explain variation in invasiveness, seeking invasive species management and restoration in the scenario of global environmental changes (Drenovsky et al. 2012).

Here, the role of functional traits in structuring inselberg plant communities is investigated for the first time. The use of functional traits provides insights to understand how communities respond to changing environmental conditions and thus has implications for conservation and restoration. First, we evaluated the importance of ecological strategies in different vegetation patches on the inselberg. Since the patches had particular environmental characteristics, we expected environmental filters selecting distinct functional strategies in each patch type. Thereafter we tested for a connection between the patch structure and plant functional traits, by estimating the strength of trait-environment relationships. We expected a strong link between functional traits and environmental drivers as a result of the harsh environmental conditions of inselbergs. We also compared the variation in functional traits between native and an exotic invasive species and looked for habitat preference by the invader in order to gain insight into invasibility in resource-limited communities. We expected non-native species to have particular traits, which could give them some advantage over native species, and also to display habitat preference leading to heterogeneity in invasion.

## Material and methods

### *Study area and sampled species*

This study was performed on an inselberg inserted into an Atlantic Forest matrix, in Teófilo Otoni city, south-eastern Brazil. In this region, inselbergs are characteristic landscape elements, occurring in large numbers with different degrees of connectivity, surrounded by lowland fragments of semi-deciduous seasonal forest (Veloso et al. 1991) and degraded vegetation modified by farming and grazing. The studied inselberg is located in a private area (17° 5' 09" S, 41° 15' 43.9" W) with altitudes ranging from 306 to 676m a. s. l. The climate at the study area is tropical wet with dry season during winter (Aw), mean annual temperature is about 22.9°C and the annual rainfall is ca. 959.1 mm (INMET 1992, historical data from 1961 to 1990; Alvares et al. 2013).

Inselberg vegetation is distributed as isolated patches with well delimited borders. The sampling was restricted to angiosperms occurring in patches surrounded by bare rock or directly establishing on it. To sample vegetation, 17 50-m long transects were set in five different areas of the inselberg to cover the variation in habitats on the inselberg. We placed four transects in areas 1-4, plus an additional transect in area five (Online Resource 1). In each transect, we surveyed up to five randomly chosen patches. For some transects, it was not possible to sample five patches due to steepness of the surveyed areas. In total, we randomly selected 61 patches and categorised them following Porembski (2007): crevices, ephemeral flush vegetation , epilithic vegetation , mats  and shallow depressions (Online Resource 2 and 3). Patch sampling reflected patch occurrence in the study area, therefore we sampled different numbers of patch per category (Online Resource 1). Patch area ranged from 0.03 to 79.12 $m^2$ (11.97 ± 19.2; SD). These patches are determined by specific plant community composition and variable degrees of environmental stress (de Paula et al, unpublished data). 58 species of angiosperms occurred on the selected patches (out of 88 species in the studied inselberg; de Paula et al. unpublished data) (Online Resource 4), but we sampled functional traits for only 53 species, due to the fact that data on leaf traits were lacking for five species, either because they were too small to allow measurements (*e.g.* Lentibulariaceae) or because they were modified (*e.g.* Cactaceae).Voucher specimens were deposited at the Herbarium BHCB. Species identification was accomplished by means of specialised literature and herbarium data. Taxa classification followed Bremer et al. (2009).

*Environmental parameters and functional trait measurements*

For each patch, we determined species richness and measured the following environmental parameters: patch area (calculated as the ellipse area), soil depth and slope. Soil depth and slope measurements were taken at the patch centre, using a caliper and a clinometer, respectively. These parameters were chosen because they were used in different studies as the basis for the classification of habitats on inselbergs (Barthlott et al. 1993; Seine et al. 1998; Porembski et al. 2000; Porembski 2007) and are already known for being key variables in structuring species diversity in plant communities arranged in vegetation patches (Michelangeli 2000; Ribeiro and Medina 2002; Oliveira et al. 2004; Ribeiro et al. 2007).

Functional traits were carefully selected to reflect plant ecological strategies (Grime et al. 1997; Díaz et al. 2004; Negreiros et al. 2014) in the harsh environmental conditions of inselbergs. We sampled seven functional traits (leaf area, leaf width, leaf toughness, leaf dry matter content [LDMC], specific leaf area [SLA], plant height and seed dry mass) following Pérez-Harguindeguy et al. (2013) in April 2014, the end of the rainy season when leaves were fully mature. These traits are related to resource use and conservation, growth and dispersal, which are considered the main axes of plant ecological strategies, and are highly correlated with ecological processes and ecosystem services (Westoby 1998; Grime 2001; Díaz et al. 2004). For leaf functional traits, whole ramets were collected from six randomly chosen mature individuals per species in the selected patches. For monocots, we avoided collecting individuals on the same patch to prevent sampling in the same genet. Shoots were immediately placed in moist paper bags to avoid desiccation, subsequently packed in plastic bags and kept in a cooler until they were placed in a refrigerator. After a minimum of 12 h under 4°C in the refrigerator, measurements were taken from two undamaged, full-grown leaves (including the petiole) per individual.

Leaf area was obtained by scanning each leaf and measurements were done with the software Leaf Area Measurement available at: www.nucleodiversus.org/uploads/file/leafarea.zip. Leaf area was calibrated using graph-paper squares of known area. Leaf fresh weight was obtained from the turgid leaves and leaf dry weight was determined with an analytic scale (precision of 0.01 mg) after 96 h of drying in an oven at 60°C. Leaf toughness was measured using a digital penetrometer (Chatillon® model DFE-010, Largo, Florida, USA) coupled to a cone-shaped tip (model SPK-FMG-009A), according to Silva and Batalha (2011). The values of leaf toughness were standardised using leaf thickness (obtained with the use of a digital micrometer, Mitutoyo® series 293, precision of 0.0001 mm) (Negreiros et al. 2014). Leaf width was obtained using a digital caliper (Mitutoyo® 500-144B, precision of 0.01 mm), measuring the maximum leaf blade width.

We assessed plant height during the growth period (November 2013 to May 2014) in 10 individuals per species. Seeds were collected from August 2013 to June 2014. The number of collected seeds per species varied according to seed availability. When necessary, plant height and seed mass were sampled outside the selected patches to increase sampling. For species with tiny seeds (*e.g. Begonia aguiabrancensis*, *Paliavana prasinata*, *Sinningia brasiliensis*, *Tibouchina* spp.) more than 300 seeds per individual were required to be weighed. Some of the dust-like seeds of orchids could not be weighed and we used an average weight for the family (Arditti 1979), except for *Acianthera prolifera*, for which we obtained empirical data. For *Barbacenia purpurea* we used the weight of the congeneric occurring in the study site under the assumption that seed size is phylogenetically conserved (Moles et al. 2005). For two species (*Bradea* sp. nov. and *Portea petropolitana*) there were no available data, then we used the median of the existing values for the other species, and assigned to these species without seed weight.

### *CSR classification*

The plant ecological strategy scheme known as CSR (C: competitive; S: stress-tolerant; R: ruderal; Grime 2001) was applied following Pierce et al. (2013). SLA, LDMC and leaf area values were used to calculate the CSR strategies. These values were inputted into the 'CSR Triangulator Vascular Plants' (Pierce et al. 2013) to calculate the mean CSR strategy for each species. For succulent species (>5 g water per $dm^2$ of leaf area) higher water content indicates stress-tolerance, not higher LDMC, and therefore we used the leaf water content instead of LDMC in the calculation of CSR strategies for succulents (Pierce et al. 2013). The representation of the CSR categories using colours was performed by converting the C, S, and R coordinates into red, green, and blue, respectively (Pierce et al. 2007).

### *Factorial Analyses*

At the species level, a principal component analysis (PCA) was used to look for the main axes of variation between functional traits and to seek the trends in correlation between species functional trait values, and thus to identify the position of the African invasive species *Melinis repens* (Poaceae) in respect to the rest of the native plant community. A one sample *t* test was performed to compare trait values of native plant community and the invasive species. At the patch level, a PCA was also run to identify the main axes of variation and to seek trends in correlation between environmental parameters and community mean trait value (also known as community mean, CM) for each functional trait. A varimax (orthogonal) rotation of the eigenvectors was employed to facilitate the interpretation and simplify the structure of the principal components retained by the PCA (Quinn and Keough 2002). To meet the assumptions of the parametric analyses, we log-transformed CM species richness, soil depth, patch area, ruderalism and seed mass; for leaf area and width we square-root transformed data.

### *Fourth-corner and RLQ analysis, trait–environment relationships*

A powerful method of accessing trait response to environmental gradients analyses simultaneously evaluates the information contained in three tables: L (species presence/absence across samples), R (environmental parameters of samples), and Q (species traits) (Dray et al. 2014). The fourth-corner approach (Legendre et al. 1997) and RLQ (R-mode linked to Q-mode) analysis (Dolédec et al. 1996) represent the most integrated methods to analyse trait-environment relationships. We followed Dray et al. (2014) who recently showed the complementarity between these two approaches and proposed some methodological adjustments to combine them into a single framework. To meet parametric assumptions, soil depth, patch area, SLA, leaf toughness and seed mass were log-transformed. To account for strong positive skewness, a fourth root transformation was applied to leaf area, leaf width and height (Quinn and Keough 2002). To conduct the RLQ analysis, a correspondence analysis was used for the community presence/absence (L) matrix, while a principal component analysis (PCA) was used for the functional (Q) and environmental (R) matrices. Significance was obtained through a test based on the total co-inertia with 50,000 permutations. In the functional PCA, the species were weighted by their overall relative frequency over the patches (number of patches that each species occurred), whereas in the environmental PCA, the patches were weighted by the relative plant richness (Dolédec et al. 1996; Dray and Dufour 2007; Pavoine et al. 2011). Both analyses were carried out in the R (R Development Core Team 2012) software with the ''ade4'' package (Chessel et al. 2004; Dray and Dufour 2007) and some functions provided by Pavoine et al. (2011). Fourth-corner and RLQ tests were performed using the combined null models 2 and 4 (Dray et al. 2014). We excluded *M. repens* from the community (L) and functional (Q) matrices, since in both analyses we treated the presence/absence of this species as an environmental parameter (R matrix).

## Results

The CSR strategies of the species in inselberg plant communities were relatively diverse (Fig. 1a). The species generally occupied a region of the CSR triangle from S-corner to C-corner. Species at the S-corner of the triangle consisted of succulents and species with smaller leaves, higher LDMC and lower SLA. The C-corner of the triangle included species with larger leaves, lower LDMC and higher SLA values. Few species occupied the R-corner. The invasive *M. repens* exhibited a CSR strategy quite near the central point of the triangle (C:S:R = 37:30:32 %). The CSR strategies at patch-level showed that inselberg patches also occupied the region between the C and S corners of the triangle, with a strong overlap among different microhabitats, except for ephemeral flush vegetation which was more variable (Fig. 1b).

In the species-level PCA (Fig. 1c), the PC1 correlated positively with competitiveness, canopy height, leaf width, leaf area, and seed mass, whereas it was negatively correlated with stress-tolerance. PC2 was positively correlated with ruderalism, SLA, and concentrated some of the native species and the invasive *M. repens.* PC2 was negatively correlated with leaf toughness, stress tolerance and concentrated a great part of the native species. The average trait values of invaded patches differed significantly from the *M. repens*' trait values, with the invasive species showing more ruderalism, higher SLA, smaller and narrower leaves, less competitiveness, less stress tolerance and smaller seeds (Table 1).

**Table 1** Comparison between native plant community of invaded patches (mean ± SE; n = 36 species) and *Melinis repens* trait values, both native and the invasive species occurred in inselberg vegetation at Minas Gerais, south-eastern Brazil

| | Invaded patches | *M. repens* | one-sample *t* test |
|---|---|---|---|
| Ruderalism (%) | 4.4 ± 1.7 | 32.2 | -13.792** |
| Specific leaf area ($mm^2$ $mg^{-1}$) | 11.9 ± 0.7 | 23.1 | -10.512** |
| Leaf width (mm) | 38.7 ± 6.3 | 4.6 | 8.052** |
| Leaf area ($cm^2$) | 110.7 ± 25.3 | 7.3 | 5.835** |
| Competitiveness (%) | 51.6 ± 3.8 | 37.5 | 3.744* |
| Stress-tolerance (%) | 44.0 ± 4.2 | 30.3 | 3.291* |
| Seed mass (mg) | 5.2 ± 2.0 | 0.2 | 3.170* |
| Canopy height (mm) | 824.3 ± 111.8 | 441.5 | 2.368 |
| Leaf toughness (gF $mm^{-1}$) | 5.8 ± 0.8 | 5.1 | -1.043 |

Significantly different at *$p< 0.01$; **$p< 0.001$.

In the patch-level PCA (Fig. 1d), the PC1 correlated positively with slope, patch area, species richness and soil depth. Shallow depressions and mats were either positively or negatively associated with PC1. Ephemeral flush vegetation and epilithic patches were negatively associated with PC1, whereas crevices were positively association with PC1. The PC2 was positively correlated with SLA and ruderalism and negatively correlated with leaf toughness and stress-tolerance. This axis concentrated shallow depressions in the positive side while mats and epilithic vegetation were concentrated in the negative side (Fig. 1d).

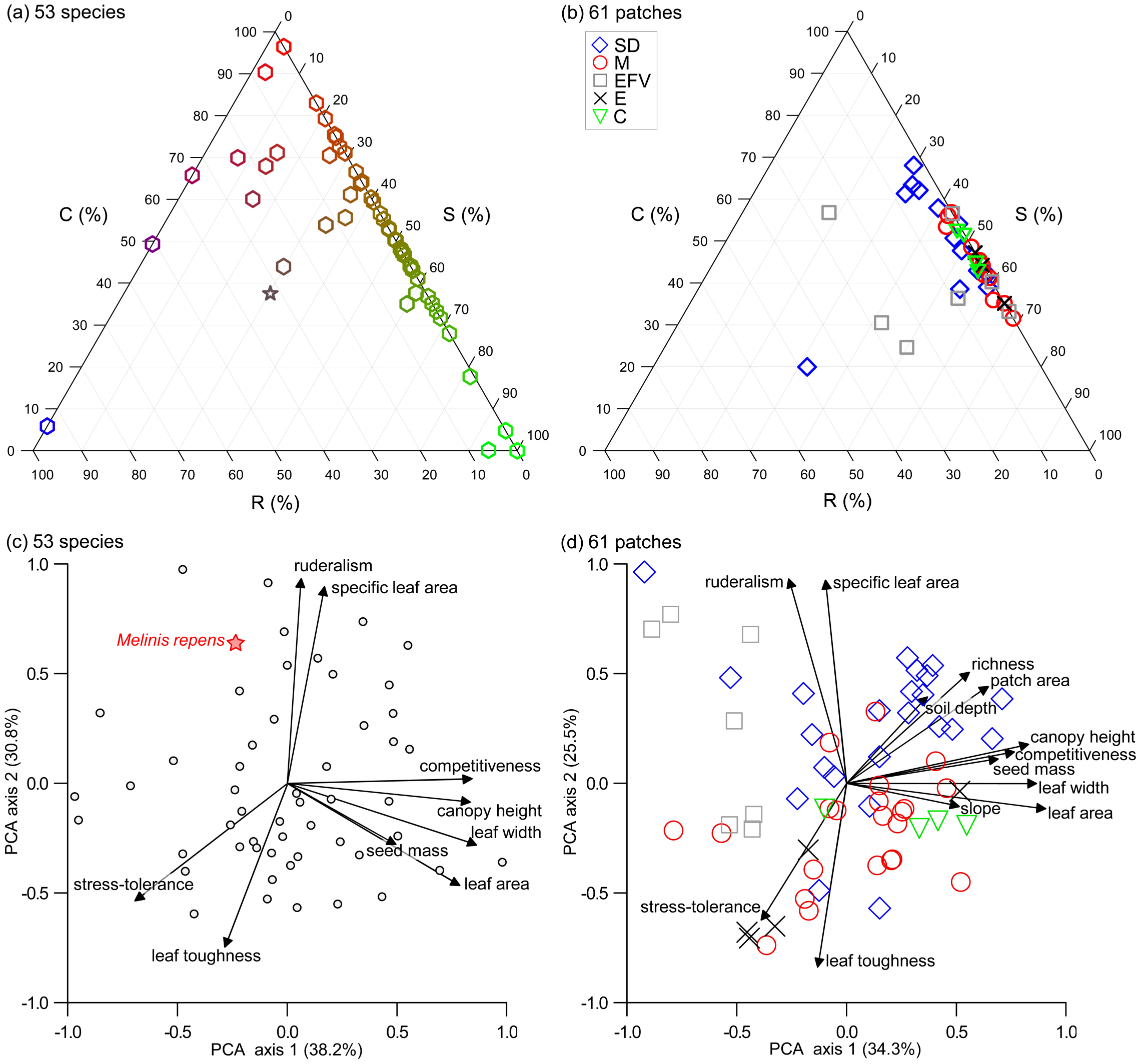
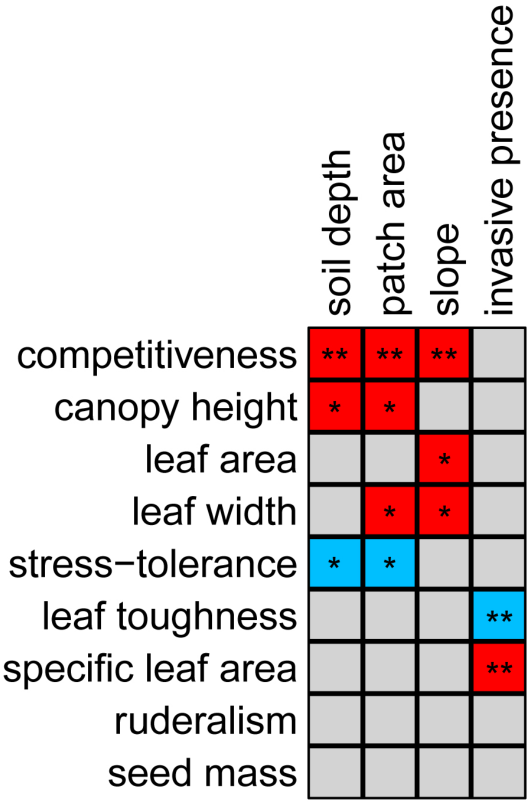


**Fig. 1** CSR classification showing the relative importance of the C (competitiveness), S (stress-tolerant) and R (ruderalism) axes in plant species (a) and in vegetation patches (b) from inselberg communities at Minas Gerais, south-eastern Brazil. Principal component analyses of 53 species (c) and patches (d) in inselberg plant communities. In panel (d) values of competitiveness, stress-tolerance, ruderalism, specific leaf area, leaf toughness, leaf area, leaf width, canopy height and seed mass correspond to the community mean trait values. In panels (b) and (d), each patch has a symbol specifying its predominant habitat, SD: shallow depression; M: mat; EFV: ephemeral flush vegetation; E: epilithic; and C: crevice

Plant functional traits and environmental drivers were not randomly distributed among patches. Seven functional traits significantly correlated with at least one environmental driver (Fig. 2). The fourth-corner statistics showed that patch area and soil depth were positively correlated with competitiveness, plant height and negatively correlated with stress-tolerance. Patches in steeper sites correlated positively with competitiveness, leaf area and leaf width. In addition, the invasive presence correlated positively with SLA and negatively with leaf toughness. Seed mass and ruderalism were not significantly correlated to any environmental driver (Fig. 2).



| | soil depth | patch area | slope | invasive presence |
|---|---|---|---|---|
| competitiveness | 🟥 ** | 🟥 ** | 🟥 ** | ⬜ |
| canopy height | 🟥 * | 🟥 * | ⬜ | ⬜ |
| leaf area | ⬜ | ⬜ | 🟥 * | ⬜ |
| leaf width | ⬜ | 🟥 * | 🟥 * | ⬜ |
| stress−tolerance | 🟦 * | 🟦 * | ⬜ | ⬜ |
| leaf toughness | ⬜ | ⬜ | ⬜ | 🟦 ** |
| specific leaf area | ⬜ | ⬜ | ⬜ | 🟥 ** |
| ruderalism | ⬜ | ⬜ | ⬜ | ⬜ |
| seed mass | ⬜ | ⬜ | ⬜ | ⬜ |

**Fig. 2** Results of the fourth corner test showing the connection between environmental parameters of vegetation patches and functional traits of species from inselberg plant communities at Minas Gerais, south-eastern Brazil. Significant positive associations are represented by red cells, and significant negative associations correspond to blue cells (* p<0,05;** p<0,01). Non-significant associations are shown in grey

The RLQ analysis provided the global ordination of species traits and environmental variables along independent axes. The overall association between the species traits and the habitat structure was highly significant (p = 0.0032). The correlations between the environmental variables and the first RLQ axes showed that the positive side of the axis 1 was strongly correlated with larger patches with deeper soils (Fig. 3a). In these patches, species showed less stress-tolerance, higher competitiveness, greater height and had wider, larger and softer leaves (Fig. 3b). The second RLQ axis outlined species with greater ruderalism, higher SLA and smaller leaves with less toughness (Fig. 3d). These species were mostly found in flatter patches (lower slope) and with greater presence of *M. repens* (Fig. 3c). Seed mass was not correlated with any RLQ axes (Fig. 3).

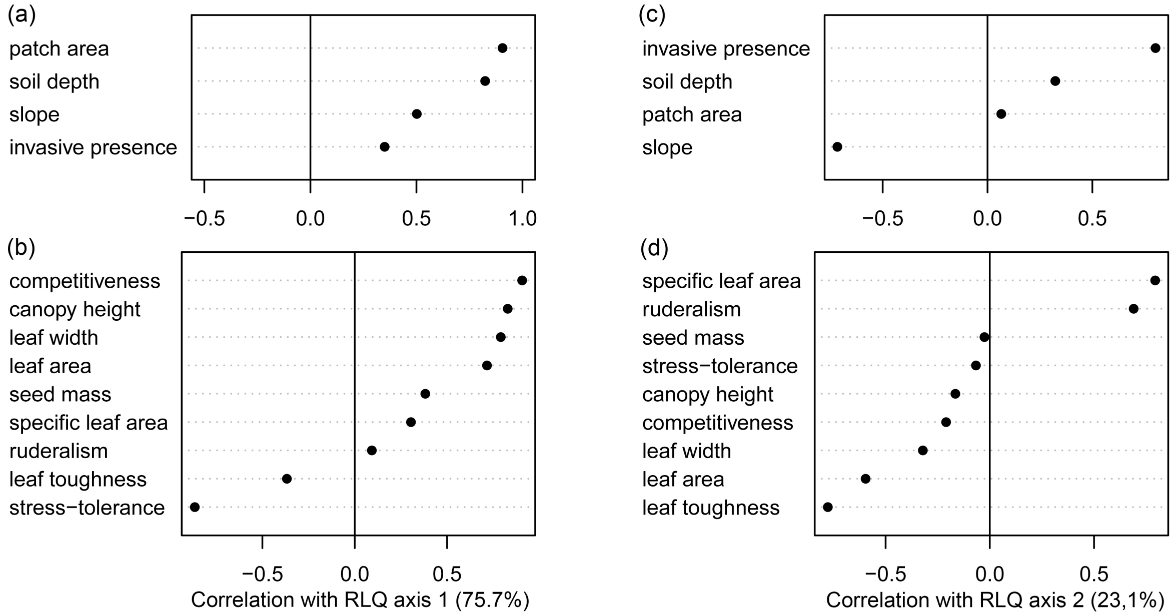


**Fig. 3** Results of the first two axes of RLQ analysis showing the relationship between environmental parameters of vegetation patches and functional traits from inselberg plant communities at Minas Gerais, south-eastern Brazil: Pearson's correlation between environmental parameters (a), functional traits (b) and the coordinates of the patches along axis 1. Pearson's correlation between environmental parameters (c), functional traits (d) and the coordinates of the patches along axis 2

The results of the analyses described above, especially those from the RLQ, were summarised in a schematic framework highlighting the environmental drivers, the respective predominant ecological strategy and functional traits in five theoretical patches (Fig. 4).

Larger patches with deeper soils filter species with greater competitiveness, higher height, with wider, larger and softer leaves (patch 1 towards patch 4). In the opposite direction, smaller patches with shallower soils filter shorter, more stress-tolerant species which have narrower, smaller and tougher leaves. Patch 5 represents the vulnerability of inselbergs to biological invasions: *Melinis repens* (brownish colour, with intermediate CSR strategy) usually coexists with more ruderal native species in patches set in flatter areas.

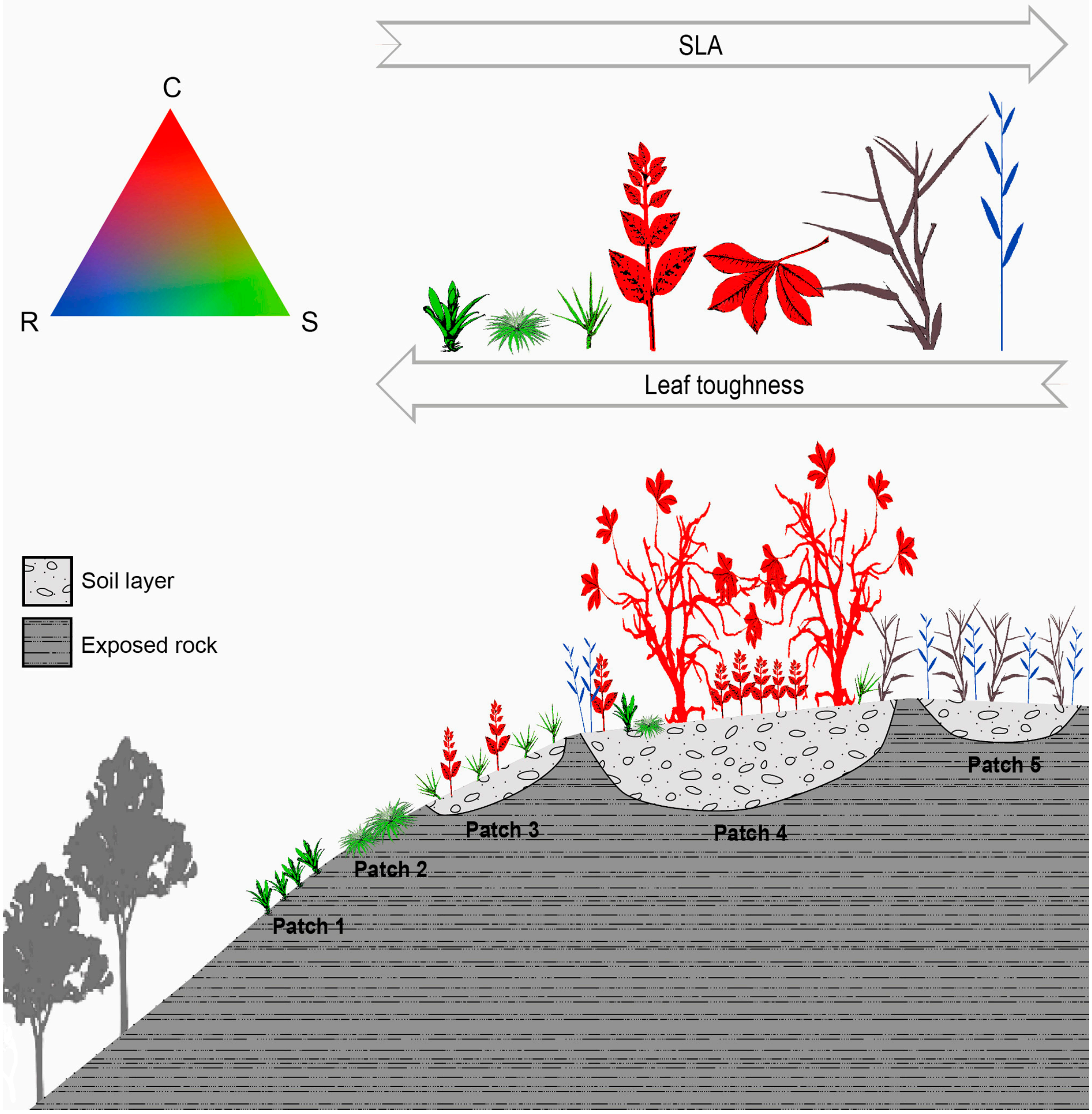


**Fig. 4** Schematic representation of the relationship between patch structure and functional traits of plants from inselberg communities. The triangle represents Grime's (2001) scheme of plant strategies: competitiveness (red), stress-tolerance (green) and ruderalism (blue). Soil depth and patch area increase from patch 1 towards patch 4. The arrows represent the leaf economics spectrum (Wright et al. 2004; Reich 2014) and show fundamental ecological trade-offs in ecological strategies. The arrows also emphasize that native species, occurring in patches set in flatter areas and with invasive presence, show higher SLA and less leaf toughness (patch 5). The icons of leaves represent the leaf size spectrum (Díaz et al. 2004). Figure credits: Fernando Levi

## Discussion

We found strong evidence supporting the role of environmental filters in structuring plant communities in heterogeneous inselberg patches. We also identified two independent trait combinations, assigned as specialisation axes. A first axis was associated to size-related traits, and highlighted traits connected with competitiveness and stress tolerance. More interestingly, a second axis revealed a set of traits related to resource-use strategies, as patches located in flatter sites were more invasive-prone and shoed species with higher SLA and less leaf toughness. Both RLQ analysis and the fourth corner approach pointed to relationships between invasiveness and leaf economic traits. Yet, in the context of invasibility, both CSR strategies and the factorial analyses were consistent in indicating the invasive species *M. repens* as functionally distinct from the rest of the native community.

The diversity in functional traits reflects the response of inselberg communities to resource availability. Despite the general overlap in patch ecological strategies, the RLQ analysis and the fourth corner approach consistently showed a strong and significant association between patch structure and functional traits, including CSR strategies. Larger patches with deeper soils (resource-rich environments, such as shallow depressions) filtered taller species with greater competitiveness, wider, larger and softer leaves, and consequently with less stress-tolerance (Fig. 4). On the other hand, smaller patches with lack of soil (resource-poor environments, such as epilithic patches) filtered species with greater stress tolerance and traits usually related to this strategy, such as low height and high leaf toughness. These results reflected both leaf economics (Wright et al. 2004; Reich 2014) and size spectra (Díaz et al. 2004; Cerabolini et al. 2010; Negreiros et al. 2014) and represent the axis of specialisation of the world's flora, stress-tolerant species showing conservative traits and competitors/ruderals showing acquisitive traits (Reich 2014). It is also worthy to point out that seed mass had low associations with the other functional traits and with the environmental drivers. This result agrees with plant ecological schemes that have proposed independence between vegetative and reproductive strategies (Westoby 1998; Grime 2001; Westoby et al. 2002).

The opposition between competitiveness and stress tolerance was also found in resource-limited quartzitic outcrops in a *campo rupestre* (rupestrian grassland) vegetation in south-eastern Brazil (Negreiros et al. 2014). The heterogeneity in ecological strategies in the different studied patches suggested that distinct CSR strategies may coexist in the microhabitats of the inselberg. In the context of rocky outcrops, the range of strategies could relate to the niche complementary hypothesis (Huston 1997; Loreau 2000), which proposes that ecological differences among species result in more complete resource use. From the functional point of view, this could be interpreted as the greater the range of functional traits, the greater the opportunity for more efficient resource use in a spatially or temporally variable environment (Loreau 1998; 2000; Díaz and Cabido 2001). So, the fine-scale variability in slope, area and soil depth of the patches combined with the interspecific differences in traits related to resource use (Fridley et al. 2011) could have enabled the existence of different strategies in inselberg plant communities, indicating the link between functional diversity and resource dynamics (Díaz and Cabido 2001).

Inselberg environmental heterogeneity also implicates in differences in invasibility, as there were some microhabitats more invasive-prone than others. Since invasive species are not able to withstand stressful conditions of inselbergs, biological invasion has been argued to be of less concern in these habitats (Meirelles et al. 1999). However, low-resource environments are also vulnerable to biological invasion (Funk 2013). Our data suggest that in some microhabitats, such as nutrient-poor environment patches (*e.g.* mat and epilithic patches), invasive species may not be able to establish and/or persist (invasive proportion is null in epilithic patches; de Paula et al., unpublished data). However, in other microhabitats, with relatively higher resource availability and favourable characteristics to the invasion, such as shallow depressions in inselberg flat areas, *M. repens* could indeed establish and dominate (30% of the shallow depression patches were invaded by *M. repens*; de Paula et al., unpublished data), although the impact magnitude in native community composition remains to be evaluated. Similar results were found for the biological invasion in Florida (David and Menges 2011). They looked for the presence and performance of *M. repens* in different microhabitats and found habitat preferences for sites with higher litter volume. Thus, there seems to exist preference for certain types of microhabitats by *M. repens*, leading to variation in the invasion.

The understading on the dynamics on plant invasion has important implications for biodiversity conservation in both high- and low-resource environments. Two contrasting views have been put forward to explain whether coexisting native and invasive species should show converging or diverging functional traits. The “try-harder” view sustains that invasive species should show more aquisitive functional trait syndromes than resident species in high-resource environments. The “join-the-locals” view, on the other hand, stresses the importance of filtering by environmental factors and predicts strong functional trait similarities between invasive and resident species (Tecco et al. 2010). In our study, *M. repens* was functionally distinct from the native community, with traits more related to ruderalism, such as higher SLA and lower leaf area, width and seed mass, therefore providing moderate support for the “try-harder” at least in the more productive and less-stressful habitats. This functional syndrome is typical from invasive plants, and is thought to increase colonisation success in disturbed areas (van Kleunen et al. 2010; Funk 2013; Ordonez and Olff 2013).

In more-productive, lowland Atlantic forest, *M. repens* is an important invasive species colonising and establishing in both ombrophilous and semideciduous disturbed sites (Zenni and Ziller 2011). In resource-limited environments, as the case of the inselbergs, invasive grasses are also often restricted to frequently disturbed and nutrient-enriched sites (Barbosa et al. 2010). Some life-history traits of *M. repens*, such as C4 photosynthesis and short life-cycles (David and Menges 2011), may favour its persistence in more favourable microhabitats (such as shallow depressions), enabling them to replace resident species after disturbances, *e.g.* cattle, which is common in the study area. In this case, biological invasion may alter the functional composition of the patches, resulting in deep modifications in ecosystem processes, including water and nutrient dynamics and trophic transfers (Chapin et al. 2000; Díaz and Cabido 2001). In this sense, *M. repens* could be causing a huge impact with serious consequences for inselberg ecosystem functioning (Burke 2003). Moreover, we also argue that trait filtering in flatter patches could be selecting traits associated with ruderalism (*i.e.* selecting species with higher SLA, lower leaf toghness and leaf area), filtering *M. repens* and species similar to it. However, we were not able to detect if these filters occur after disturbances or not, and in this situation the "join the locals" view is also partially supported. Then, we ague that more studies foccused in plant invasion, taking into account species abundance, should be done in order to elucidate whether plant invasion on inselbergs is mediated by converging or diverging functional syndromes.

In addition to our own data, several studies have reinforced the widespread impact that invaders are causing in tropical and temperate inselberg plant communities (Hussey 1993; Hopper et al. 1997; Pigott and Sage 1997; Wyatt 1997; Pigott 2000; Porembski 2000; Hopper 2009). This scenario is even more worrying given that inselbergs within the Atlantic Forest are inserted into increasingly smaller and disconnected forest fragments (Tabarelli et al. 2004), enhancing the chances of invasiveness. Therefore, we contend that exotic invasive species are a major threat to the unique vegetation of inselbergs and must be considered in the management plans of these outcrops.

In recent years, studies on inselberg habitat types typically focused on floristic lists, phytosociological analyses, physiognomic determinations and qualitative aspects of functional ecology, such as life-form spectra (Barthlott et al. 1993; Seine et al. 1998; Porembski et al. 2000; Porembski 2007). We argue that a deeper quantitative functional perspective on the ecology of these plant communities will improve our ability to understand how they are structured and to predict how they respond to environmental changes. Therefore, investigating connections between patch structure and functional traits have practical implications for the conservation of this resource-limited flora (Funk 2013). First, the heterogeneity in ecological strategies found here can be useful for restoration of inselbergs after disturbance. Since species have different tolerance to abiotic stresses, restorationists can select species based on their functional role. Second, predicting plant invasion and its impact on ecosystems is complex and challenging (Drenovsky et al. 2012), and our results contribute to better predict invasion dynamics in resource-limited communities. All these information will be critical for developing conservation and management strategies in inselberg vegetation, especially in the context of rapid habitat loss and fragmentation of the Atlantic Forest.

## Conflict of interest

The authors declare that they have no conflict of interest.

## Acknowledgments

We thank Ana L. Fonseca, Marcelo Amorim, Marcelo Fonseca, Theo Mota, Luiza C. Martins, Lucas, Eliane and Caique for logistical support and help in the field work. We express our gratitude to the Addiny family for kindly providing permission to do field work on its property. J.P. Lemos-Filho and G.W. Fernandes gently loaned us equipments, S. Dolédec gave statistical advice and F. de Bello, B.H.P. Rosado and F.F. Carmo provided insightful discussions. Finally, we thank the grants from the CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, 163020/2013-2, 482720/2012), CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) and FAPEMIG (Fundação de Amparo à Pesquisa de Minas Gerais). This study was in partial fulfillment of the master requirements of L.F.A. de Paula in Plant Biology, who received a scholarship from CNPq. F.A.O. Silveira receives a research productivity fellowship from CNPq.

## References

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22:711-728

Arditti J (1979) Aspects of the physiology of orchids. Academic Press, London

Barbosa NPU, Fernandes GW, Carneiro MAA, Júnior LAC (2010) Distribution of non-native invasive species and soil properties in proximity to paved roads and unpaved roads in a quartzitic mountainous grassland of southeastern Brazil (rupestrian fields). Biological Invasions 12:3745-3755

Barthlott W, Gröger A, Porembski S (1993) Some remarks on the vegetation of tropical inselbergs: diversity and ecological differentiation. Biogeographica 69:105-124

Bremer B, Bremer K, Chase MW et al (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161:105-121

Burke A (2003) Inselbergs in a changing world - global trends. Diversity and Distributions 9:375-383

Cerabolini BEL, Brusa G, Ceriani RM, de Andreis R, Luzzaro A, Pierce S (2010) Can CSR classification be generally applied outside Britain? Plant Ecology 210:253-261

Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S (2000) Consequences of changing biodiversity. Nature 405:234-242

Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package-I-One-table methods. R news 4:5-10

David AS, Menges ES (2011) Microhabitat preference constrains invasive spread of non-native natal grass (*Melinis repens*). Biological Invasions 13:2309-2322

de Bello F, Lavorel S, Díaz S, Harrington R, Cornelissen JHC, Bardgett RD, Berg MP, Cipriotti P, Feld CK, Hering D (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. Biodiversity and Conservation 19:2873-2893

Díaz S, Cabido M (1997) Plant functional types and ecosystem function in relation to global change. Journal of Vegetation Science 8:463-474

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16:646-655

Díaz S, Hodgson JG, Thompson K et al (2004) The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15:295-304

Dolédec S, Chessel D, ter Braak CJF, Champely S (1996) Matching species traits to environmental variables: A new three-table ordination method. Environmental and Ecological Statistics 3:143-166

Dray S, Dufour AB (2007) The ade4 package: Implementing the duality diagram for ecologists. Journal of Statistical Software 22:1-20

Dray S, Choler P, Dolédec S, Peres-Neto PR, Thuiller W, Pavoine S, ter Braak CJF (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95:14-21

Drenovsky RE, Grewell BJ, D'Antonio CM, Funk JL, James JJ, Molinari N, Parker IM, Richards CL (2012) A functional trait perspective on plant invasion. Annals of Botany 110: 141–153.

Fridley JD, Grime JP, Askew AP, Moser B, Stevens CJ (2011) Soil heterogeneity buffers community response to climate change in species-rich grassland. Global Change Biology 17:2002-2011

Funk JL (2013) The physiology of invasive species in low-resource environments. Conservation Physiology 1: 10.1093/conphys/cot026

Galindo-Leal C, Jacobsen TR, Langhammer PF, Olivieri S (2003) State of the hotspots: the dynamics of biodiversity loss. In: Galindo-Leal C and Câmara I de G (ed) The Atlantic Forest of South America: biodiversity status, threats, and outlook. Center for Applied Biodiversity Science and Island Press, Washington, DC, pp 12-23

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley, Chichester

Grime JP, Thompson K, Hunt R et al (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79:259-281

Hopper SD (2009) OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. Plant and Soil 322:49-86

Hopper SD, Brown AP, Marchant NG (1997) Plants of Western Australian granite outcrops. Journal of the Royal Society of Western Australia 80:141-158

Hussey BMJ (1993) Naturalised plants on the southern slopes of the western end of the Helena Valley, Western Australia. The Western Australian Naturalist 19:219-240

Huston MA (1997) Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. Oecologia 110:449-460

INMET (1992) Normais climatológicas (1961-1990). National Institute of Meteorology, Brasília, Brasil

Jacobi CM, do Carmo FF, Vincent RC, Stehmann JR (2007) Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. Biodiversity and Conservation 16:2185-2200

Joly CA, Metzger JP, Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytologist 204:459-473

Leão TC, Fonseca CR, Peres CA, Tabarelli M (2014) Predicting extinction risk of Brazilian Atlantic rorest angiosperms. Conservation Biology 28:1349-1359

Legendre P, Galzin R, HarmelinVivien ML (1997) Relating behavior to habitat: Solutions to the fourth-corner problem. Ecology 78:547-562

Loreau M (1998) Biodiversity and ecosystem functioning: A mechanistic model. Proceedings of the National Academy of Sciences of the United States of America 95:5632-5636

Loreau M (2000) Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3-17

Martinelli G (2007) Mountain biodiversity in Brazil. Brazilian Journal of Botany 30:587-597

Martinelli G, Moraes MA (2013) Red Book of Brazilian Flora. Jardim Botânico do Rio de Janeiro. http://cncflora.jbrj.gov.br. Accessed 26 June 2014

Meirelles ST, Pivello VR, Joly CA (1999) The vegetation of granite rock outcrops in Rio de Janeiro, Brazil, and the need for its protection. Environmental Conservation 26:10-20

Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Westoby M (2005) A brief history of seed size. Science 307:576-580

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858

Negreiros D, Le Stradic S, Fernandes GW, Rennó HC (2014) CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. Plant Ecology 215:379-388

Oliveira TD, Ribeiro MC, Costa ILL, Faria F, Figueira JEC (2004) Estabelecimento de espécies vegetais em um inselberg granítico de Mata Atlântica. Revista Estudos de Biologia 26:17-24

Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica 32:793-810

Ordonez A, Olff H (2013) Do alien plant species profit more from high resource supply than natives? A trait-based analysis. Global Ecology and Biogeography 22:648-658

Pavoine S, Vela E, Gachet S, de Belair G, Bonsall MB (2011) Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. Journal of Ecology 99:165-175

Pérez-Harguindeguy N, Díaz S, Garnier E et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61:167-234

Pierce S, Luzzaro A, Caccianiga M, Ceriani RM, Cerabolini B (2007) Disturbance is the principal α-scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. Journal of Ecology 95:698-706

Pierce S, Brusa G, Vagge I, Cerabolini BEL (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Functional Ecology 27:1002-1010

Pigott JP (2000) Environmental weeds and granite outcrops: possible solutions in the “too hard basket”. Journal of the Royal Society of Western Australia 83:135-137

Pigott JP, Sage LW (1997) Remnant vegetation, priority flora and weed invasions at Yilliminning Rock, Narrogin, Western Australia. Journal of the Royal Society of Western Australia 80:201-208

Porembski S (2000) The invasibility of tropical granite outcrops (‘inselbergs’) by exotic weeds. Journal of the Royal Society of Western Australia 83:131-137

Porembski S (2007) Tropical inselbergs: habitat types, adaptive strategies and diversity patterns. Brazilian Journal of Botany 30:579-586

Porembski S, Barthlott W (2000) Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. Plant Ecology 151:19-28

Porembski S, Seine R, Barthlott W (1997) Inselberg vegetation and the biodiversity of granite outcrops. Journal of the Royal Society of Western Australia 80:193-199

Porembski S, Becker U, Seine R (2000) Islands on islands: habitats on inselbergs. In: Porembski S and Barthlott W (ed) Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions. Ecological Studies, Springer-Verlag, Berlin, pp 49-67

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Reich PB (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102:275-301

Ribeiro KT, Medina BMO (2002) Estrutura, dinâmica e biogeografia das ilhas de vegetação sobre rocha do Planalto do Itatiaia, RJ. Boletim do Parque Nacional do Itatiaia 10:1-82

Ribeiro KT, Medina BMO, Scarano FR (2007) Species composition and biogeographic relations of the rock outcrop flora on the high plateau of Itatiaia, SE-Brazil. Brazilian Journal of Botany 30: 623-639

Safford HD, Martinelli G (2000) Southeast Brazil. In: Porembski S and Barthlott W (ed) Inselbergs – biotic diversity of isolated rock outcrops in tropical and temperate regions. Ecological Studies. Springer-Verlag, Berlin, pp 339-389

Scarano FR (2002) Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Annals of Botany 90:517-524

Seine R, Becker U, Porembksi S, Follman G, Barthlott W (1998) Vegetation of inselbergs in Zimbabwe. Edinburgh Journal of Botany 55:267-293

Silva DM, Batalha MA (2011) Defense syndromes against herbivory in a cerrado plant community. Plant Ecology 212:181-193

Tabarelli M, Silva JMC, Gascon C (2004) Forest fragmentation, synergisms and the impoverishment of neotropical forests. Biodiversity and Conservation 13:1419-1425

Tabarelli M, Pinto LP, Silva JMC, Hirota M, Bedê L (2005) Challenges and opportunities for Biodiversity conservation in the Brazilian Atlantic forest. Conservation Biology 19:695-700

Tecco PA, Díaz S, Cabido M, Urcelay C (2010) Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? Journal of Ecology 98:17-27

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13:235-245

Veloso HP, Rangel Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira, adaptada a um sistema universal. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213-227

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33:125-159

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821-827

Wyatt R (1997) Reproductive ecology of granite outcrop plants from the south-eastern United States. Journal of the Royal Society of Western Australia 80:123-129

Zenni RD, Ziller SR (2011) An overview of invasive plants in Brazil. Brazilian Journal of Botany 34:431-446

Supplementary information:

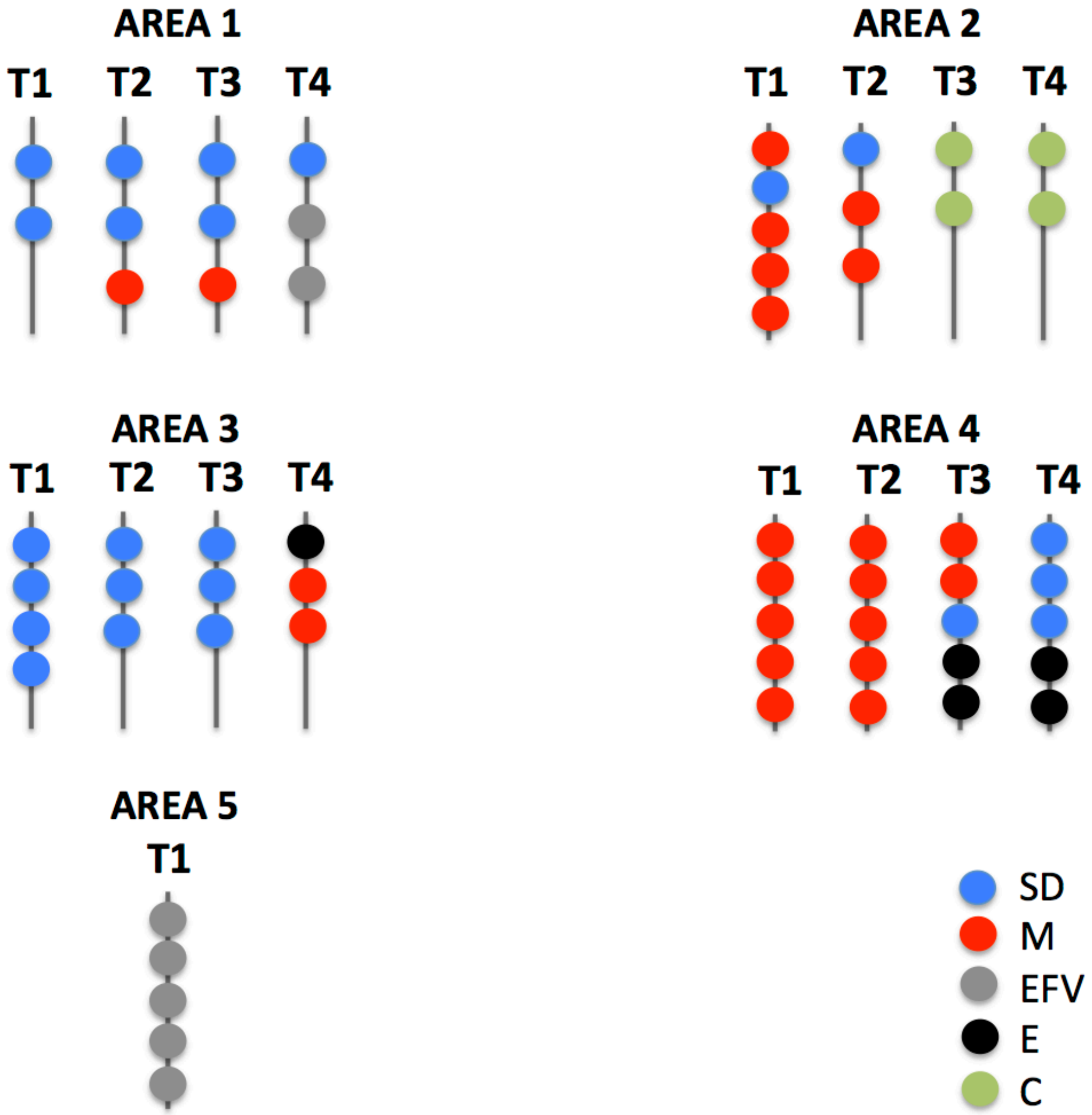
Manuscript: Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic Forest

Journal: Biodiversity and Conservation

Authors: de Paula et al.

Affiliation: Universidade Federal de Minas Gerais

E-mail: luizafap@gmail.com



**Online Resource 1** Schematic representation of the number of transects, vegetation patches and areas sampled on an inselberg in the Atlantic Forest, Minas Gerais, south-eastern Brazil. In each area (1-5), each line represent a transect (T) while the circles with different colors represent the patches surveyed and its predominant microhabitat; SD: shallow depression; M: mat; EFV: ephemeral flush vegetation; E: epilithic; and C: crevice

Supplementary information:

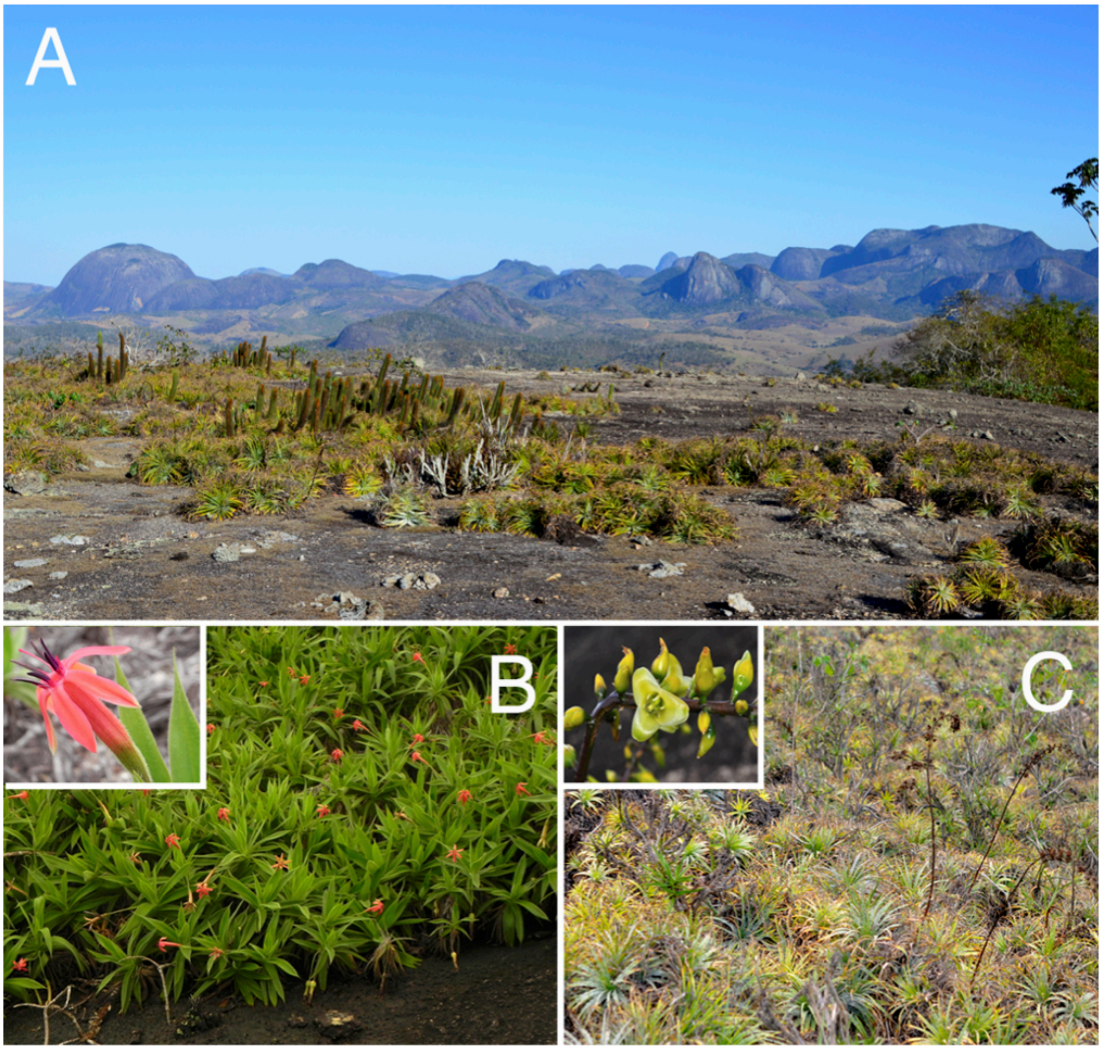
Manuscript: Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic Forest

Journal: Biodiversity and Conservation

Authors: de Paula et al.

Affiliation: Universidade Federal de Minas Gerais

E-mail: luizafap@gmail.com



**Online Resource 2** A general overview of conspicuous and diverse habitat types on inselbergs in the Atlantic Forest, Minas Gerais, south-eastern Brazil. A - Mats composed predominantly by species of monocots forming many patches. B - Monospecific mats of *Barbacenia tomentosa* (Velloziaceae), its flower is detailed (left box). C - Mats of *Encholirium gracile* (Bromeliaceae) with the inflorescence detailed (left box). Photo A by Luiza F. A. de Paula, B by L. O. Azevedo and C by João R. Stehmann

Supplementary information:

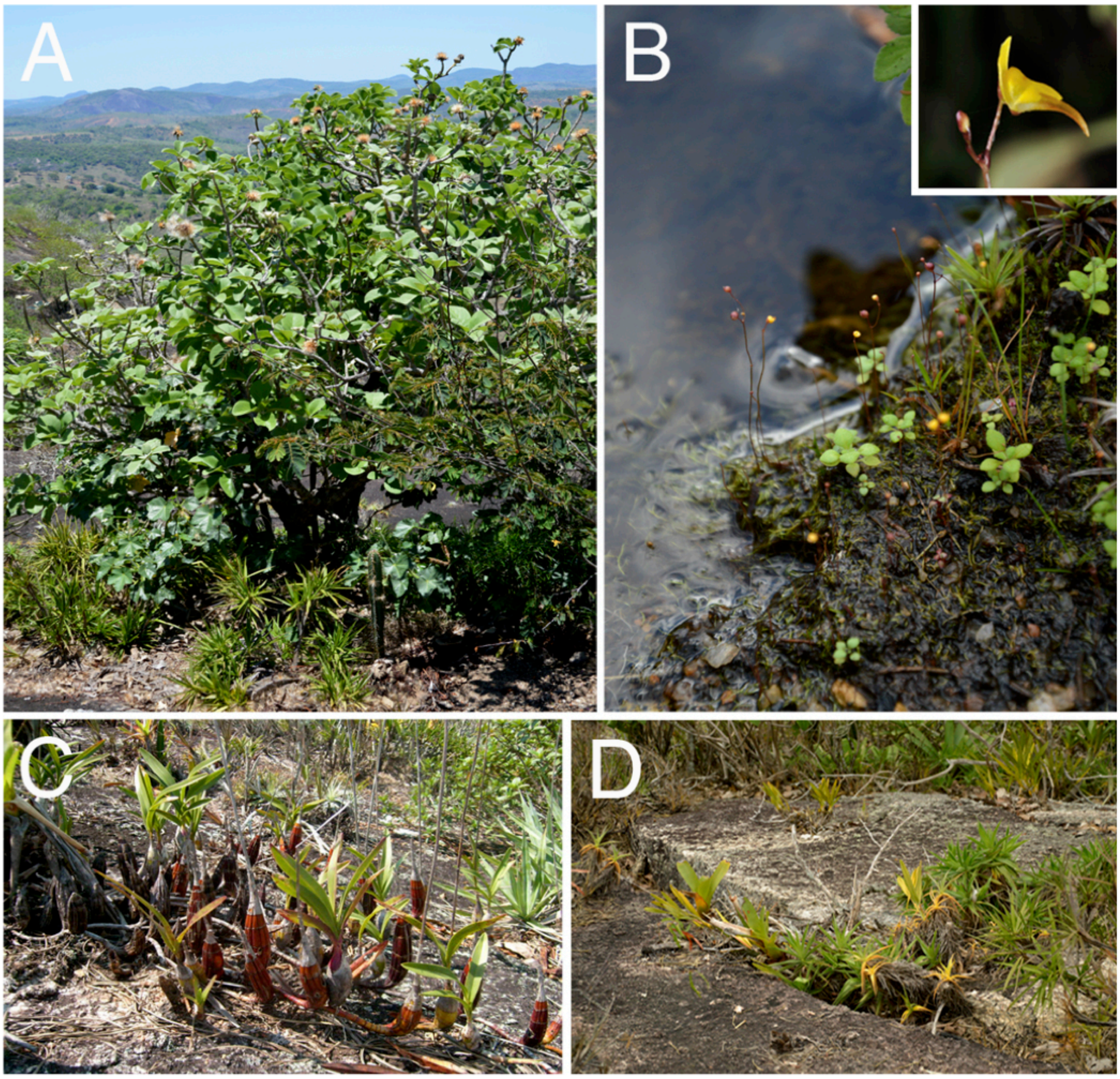
Manuscript: Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic Forest

Journal: Biodiversity and Conservation

Authors: de Paula et al.

Affiliation: Universidade Federal de Minas Gerais

E-mail: luizafap@gmail.com



**Online Resource 3** Habitat types on inselbergs in the Atlantic Forest, Minas Gerais, south-eastern Brazil. A - Shallow depressions composed by shrubs (*Cnidoscolus* aff. *lombardii*, Euphorbiaceae), herbaceous monocots (*Vellozia plicata*, Velloziaceae) and trees (*Wunderlichia azulensis*, Asteraceae). B – Ephemeral flush vegetation with *Utricularia subulata* (Lentibulariaceae), a carnivorous plant typical of this habitat, its flower is detailed (right box). C – Epilithic vegetation showing individuals of *Pseudolaelia geraensis* (Orchidaceae) growing directly on the bare rock. D – Crevices are usually occupied by monocot species and some shrubs. Photos A, C and D by Luiza F. A. de Paula and B by João R. Stehmann

Supplementary information:

Manuscript: Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic Forest

Journal: Biodiversity and Conservation

Authors: de Paula et al.

Affiliation: Universidade Federal de Minas Gerais

E-mail: luizafap@gmail.com

**Online Resource 4** Table 1. Species sampled for functional traits from an inselberg in south-eastern Brazil; Table 2. Functional traits measured

**Table 1**

| **Family** | **Species** | **Life-form** | **Voucher** |
|---|---|---|---|
| Apocynaceae | *Mandevilla grazielae* M.F.Sales et al. | shrub | de Paula, LFA 153 |
| Apocynaceae | *Mandevilla tenuifolia* (J.C.Mikan) Woodson | shrub | de Paula, LFA 606 |
| Apocynaceae | *Marsdenia* sp. | shrub | de Paula, LFA 137 |
| Araceae | *Anthurium* sp. nov. | herb | de Paula, LFA 136 |
| Asteraceae | *Lepidaploa cotoneaster* (Willd. ex Spreng.) H.Rob. | shrub | de Paula, LFA 248 |
| Asteraceae | *Mikania microcephala* DC. | shrub | de Paula, LFA 396 |
| Asteraceae | *Vernonanthura* sp. | shrub | de Paula, LFA 359 |
| Asteraceae | *Wunderlichia azulensis* Maguire & G.M.Barroso | tree | de Paula, LFA 131 |
| Begoniaceae | *Begonia aguiabrancensis* L.Kollmann | shrub | de Paula, LFA 141 |
| Bignoniaceae | *Tabebuia reticulata* A.H. Gentry | tree | de Paula, LFA 401 |
| Bromeliaceae | *Alcantarea simplicisticha* Leme & A.P. Fontana | herb | de Paula, LFA 87 |
| Bromeliaceae | *Encholirium gracile* L. B. Sm. | herb | de Paula, LFA 234 |
| Bromeliaceae | *Orthophytum compactum* L. B. Sm. | herb | de Paula, LFA 86 |
| Bromeliaceae | *Pitcairnia azouryi* Martinelli & Forzza | herb | de Paula, LFA 607 |
| Bromeliaceae | *Portea petropolitana* (Wawra) Mez | herb | de Paula, LFA 331 |
| Bromeliaceae | *Tillandsia stricta* Sol. | herb | de Paula, LFA 326 |
| Bromeliaceae | *Vriesea neoglutinosa* Mez | herb | de Paula, LFA 124 |
| Cyperaceae | *Bulbostylis lagoensis* (Boeckeler) Prata & M.G.López | herb | de Paula, LFA 690 |
| Cyperaceae | *Cyperus coriifolius* Boeckeler | herb | de Paula, LFA 282 |
| Cyperaceae | *Cyperus luzulae* (L.) Retz | herb | de Paula, LFA 637 |
| Cyperaceae | *Fuirena umbellata* Rottb. | herb | de Paula, LFA 806 |
| Cyperaceae | *Scleria* sp. nov. | herb | de Paula, LFA 653 |
| Cyperaceae | *Trilepis lhotzkiana* Nees ex Arn. | herb | de Paula, LFA 134 |

| **Family** | **Species** | **Life-form** | **Voucher** |
|---|---|---|---|
| Erythroxilaceae | *Erythroxylum* cf. *vaccinifolium* Mart. | tree | de Paula, LFA 91 |
| Euphorbiaceae | *Cnidoscolus* aff. *lombardii* Fern.Casas | shrub | de Paula, LFA 130 |
| Euphorbiaceae | *Croton nepetifolius* Baill. | shrub | de Paula, LFA 138 |
| Euphorbiaceae | *Stillingia argutedentata* Jabl. | shrub | de Paula, LFA 132 |
| Gesneriaceae | *Paliavana prasinata* (Ker Gawl.) Benth. | shrub | de Paula, LFA 676 |
| Gesneriaceae | *Sinningia brasiliensis* (Regel & E. Schmidt) Wiehler | shrub | de Paula, LFA 283 |
| Lythraceae | *Cuphea sessilifolia* Mart. | shrub | de Paula, LFA 152 |
| Malvaceae | *Melochia* cf. *morongii* Britton | shrub | de Paula, LFA 677 |
| Malvaceae | *Pseudobombax* cf. *crassipes* Ravenna | tree | de Paula, LFA 378 |
| Melastomataceae | *Tibouchina heteromalla* (D. Don) Cogn. | shrub | de Paula, LFA 168 |
| Melastomataceae | *Tibouchina* sp. | shrub | de Paula, LFA 163 |
| Orchidaceae | *Acianthera prolifera* (Herb. ex Lindl.) Pridgeon & M.W.Chase | herb | de Paula, LFA 346 |
| Orchidaceae | *Cyrtopodium glutiniferum* Raddi | herb | de Paula, LFA 115 |
| Orchidaceae | *Prescottia montana* Barb.Rodr. | herb | de Paula, LFA 338 |
| Orchidaceae | *Pseudolaelia geraensis* Pabst | herb | de Paula, LFA 245 |
| Orchidaceae | *Pseudolaelia vellozicola* (Hoene) C.Porto & Brade | herb | de Paula, LFA 333 |
| Piperaceae | *Peperomia incana* (Haw.) Hook. | herb | de Paula, LFA 139 |
| Plantaginaceae | *Achetaria crenata* (Ronse & Philcox) V.C.Souza | shrub | de Paula, LFA 157 |
| Poaceae | *Andropogon bicornis* L. | herb | de Paula, LFA 298 |
| Poaceae | *Axonopus graniticola* P.L.Viana | herb | de Paula, LFA 145 |
| Poaceae | *Melinis repens (Willd.) Zizka* | herb | de Paula, LFA 395 |
| Poaceae | *Paspalum* sp. | herb | de Paula, LFA 678 |
| Portulaceae | *Portulaca hirsutissima* Cambess. | herb | de Paula, LFA 394 |
| Rubiaceae | *Bradea* sp. nov. | shrub | de Paula, LFA 303 |
| Solanaceae | *Schwenckia* sp. nov. | shrub | de Paula, LFA 239 |
| Velloziaceae | *Barbacenia purpurea* Hook. | herb | de Paula, LFA 640 |
| Velloziaceae | *Barbacenia tomentosa* Mart. | herb | de Paula, LFA 288 |
| Velloziaceae | *Vellozia candida* J.C.Mikan | herb | de Paula, LFA 90 |
| Velloziaceae | *Vellozia plicata* Mart. | herb | de Paula, LFA 287 |
| Verbenaceae | *Stachytarpheta gesnerioides* Cham. | shrub | de Paula, LFA 166 |

Table 2

| Species | Succulent | SLA ($mm^2$ $mg^{-1}$) | LDMC (%) | Leaf area ($mm^2$) | Leaf dry weight (mg) | Leaf fresh weight (mg) | Leaf toughness (KgF $in^{-1}$) | Leaf width (mm) | Plant height (mm) | Seed mass (mg) | C (%) | S (%) | R (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Mandevilla grazielae* | no | 13.46 | 25.05 | 2733.27 | 203.0 | 810.5 | 3.18 | 22.22 | 1046.7 | 2.7173 | 63.95 | 35.65 | 0.41 |
| *Mandevilla tenuifolia* | no | 26.00 | 11.43 | 86.65 | 3.3 | 29.2 | 3.63 | 2.99 | 71.0 | 0.5838 | 5.86 | 0.00 | 94.14 |
| *Marsdenia* sp. | no | 18.26 | 17.43 | 1150.35 | 63.0 | 361.5 | 2.95 | 17.66 | 665.0 | 2.2689 | 60.07 | 15.36 | 24.57 |
| *Anthurium* sp. nov. | yes | 8.29 | 15.74 | 15510.26 | 1870.3 | 11885.5 | 5.93 | 40.65 | 485.0 | 2.4890 | 43.21 | 56.79 | 0.00 |
| *Lepidaploa cotoneaster* | no | 21.02 | 24.01 | 1124.66 | 53.5 | 222.8 | 1.36 | 16.30 | 685.0 | 0.1488 | 43.95 | 29.79 | 26.26 |
| *Mikania microcephala* | no | 20.54 | 16.33 | 8463.48 | 412.0 | 2523.5 | 0.88 | 70.95 | 1577.0 | 0.1345 | 69.93 | 7.33 | 22.74 |
| *Vernonanthura* sp. | no | 14.64 | 14.42 | 5713.25 | 390.2 | 2706.5 | 1.63 | 32.81 | 1104.5 | 0.1427 | 90.35 | 2.79 | 6.86 |
| *Wunderlichia azulensis* | no | 9.54 | 23.36 | 56283.97 | 5899.8 | 25253.2 | 3.33 | 168.43 | 2666.0 | 19.7525 | 79.28 | 20.73 | 0.00 |
| *Begonia aguiabrancensis* | yes | 5.17 | 10.45 | 9927.05 | 1921.5 | 18388.2 | 6.90 | 61.36 | 407.0 | 0.0125 | 41.08 | 58.92 | 0.00 |
| *Tabebuia reticulata* | no | 6.79 | 43.54 | 12845.48 | 1891.0 | 4342.8 | 8.43 | 74.88 | 1988.0 | 21.4505 | 52.78 | 47.22 | 0.00 |
| *Alcantarea simplicisticha* | yes | 8.37 | 17.33 | 46648.62 | 5570.8 | 32143.5 | 15.23 | 101.60 | 457.0 | 1.4251 | 47.86 | 52.14 | 0.00 |
| *Encholirium gracile* | yes | 3.12 | 22.09 | 3322.34 | 1066.2 | 4826.2 | 14.28 | 10.97 | 254.0 | 0.4417 | 35.12 | 64.88 | 0.00 |
| *Orthophytum compactum* | yes | 6.20 | 14.27 | 17603.18 | 2837.0 | 19886.8 | 16.99 | 42.83 | 291.5 | 0.3216 | 43.79 | 56.21 | 0.00 |
| *Pitcairnia azouryi* | no | 11.13 | 18.27 | 4721.51 | 424.3 | 2323.2 | 12.67 | 18.62 | 224.0 | 0.2492 | 82.97 | 17.03 | 0.00 |
| *Portea petropolitana* | yes | 7.84 | 17.77 | 33790.01 | 4312.3 | 24266.3 | 26.17 | 45.36 | 553.5 | 0.2500 | 46.58 | 53.42 | 0.00 |
| *Tillandsia stricta* | no | 10.33 | 18.87 | 120.50 | 11.7 | 61.8 | 7.31 | 1.66 | 60.5 | 0.1130 | 33.31 | 66.69 | 0.00 |
| *Vriesea neoglutinosa* | no | 11.69 | 24.70 | 29617.03 | 2534.0 | 10260.3 | 19.40 | 69.45 | 466.0 | 0.3887 | 75.41 | 24.59 | 0.00 |
| *Bulbostylis lagoensis* | no | 9.19 | 32.57 | 87.31 | 9.5 | 29.2 | 10.42 | 0.36 | 189.0 | 0.0937 | 4.75 | 95.25 | 0.00 |
| *Cyperus coriifolius* | no | 10.97 | 23.93 | 6666.95 | 607.8 | 2540.0 | 6.20 | 17.27 | 337.8 | 0.1811 | 71.11 | 28.89 | 0.00 |
| *Cyperus luzulae* | no | 12.97 | 26.73 | 1439.87 | 111.0 | 415.3 | 10.84 | 5.20 | 431.0 | 0.1502 | 56.54 | 43.46 | 0.00 |
| *Fuirena umbellata* | no | 18.53 | 18.67 | 6299.66 | 340.0 | 1821.5 | 3.77 | 17.94 | 734.0 | 0.0796 | 67.93 | 14.14 | 17.93 |
| *Scleria* sp. nov. | no | 10.11 | 39.71 | 3502.14 | 346.3 | 872.2 | 7.31 | 5.95 | 491.1 | 0.8347 | 48.28 | 51.72 | 0.00 |
| *Trilepis lhotzkiana* | no | 12.09 | 39.02 | 64.50 | 5.3 | 13.7 | 6.77 | 1.78 | 68.5 | 0.1500 | 0.00 | 100.00 | 0.00 |
| *Erythroxylum* cf. *vaccinifolium* | no | 10.71 | 42.41 | 2189.31 | 204.3 | 481.8 | 5.69 | 26.80 | 2725.0 | 33.6514 | 43.08 | 56.93 | 0.00 |
| *Cnidoscolus* aff. *lombardii* | yes | 12.97 | 12.59 | 19334.77 | 1490.5 | 11836.2 | 1.74 | 130.15 | 1007.3 | 42.9491 | 44.21 | 55.79 | 0.00 |
| *Croton nepetifolius* | no | 14.54 | 29.85 | 9137.45 | 628.3 | 2104.8 | 1.51 | 65.38 | 2124.0 | 2.7523 | 61.13 | 35.01 | 3.87 |
| *Stillingia argutedentata* | yes | 12.26 | 12.10 | 4406.68 | 359.5 | 2970.8 | 4.28 | 33.96 | 1398.0 | 9.7163 | 36.77 | 63.23 | 0.00 |
| *Paliavana prasinata* | no | 12.87 | 14.58 | 6523.90 | 506.8 | 3475.3 | 2.07 | 54.08 | 1452.9 | 0.0163 | 96.41 | 3.59 | 0.00 |
| *Sinningia brasiliensis* | no | 25.49 | 11.86 | 6526.30 | 256.0 | 2158.0 | 1.98 | 40.79 | 625.0 | 0.0158 | 65.75 | 0.00 | 34.25 |
| *Cuphea sessilifolia* | no | 13.50 | 32.67 | 148.54 | 11.0 | 33.7 | 3.23 | 8.05 | 397.5 | 0.8047 | 17.70 | 81.43 | 0.86 |
| *Melochia* cf. *morongii* | no | 14.46 | 33.06 | 493.96 | 34.2 | 103.3 | 0.55 | 12.40 | 455.5 | 1.2022 | 35.03 | 59.73 | 5.24 |
| *Pseudobombax* cf. *crassipes* | no | 10.57 | 33.45 | 50018.38 | 4732.3 | 14146.0 | 5.35 | 72.71 | 1475.6 | 45.3072 | 66.51 | 33.49 | 0.00 |
| *Tibouchina heteromalla* | no | 8.57 | 23.77 | 15701.43 | 1832.0 | 7708.0 | 1.80 | 85.72 | 1161.0 | 0.0243 | 74.83 | 25.17 | 0.00 |
| *Tibouchina* sp. | no | 5.10 | 33.07 | 1977.41 | 388.0 | 1173.2 | 3.80 | 22.63 | 1481.0 | 0.0153 | 50.41 | 49.59 | 0.00 |
| *Acianthera prolifera* | yes | 5.34 | 8.48 | 1943.99 | 364.2 | 4296.7 | 10.42 | 31.06 | 70.5 | 0.0072 | 31.73 | 68.27 | 0.00 |

| Species | Succulent | SLA ($mm^2\ mg^{-1}$) | LDMC (%) | Leaf area ($mm^2$) | Leaf dry weight (mg) | Leaf fresh weight (mg) | Leaf toughness ($KgF\ in^{-1}$) | Leaf width (mm) | Plant height (mm) | Seed mass (mg) | C (%) | S (%) | R (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cyrtopodium glutiniferum* | no | 18.93 | 20.92 | 41964.98 | 2216.7 | 10595.7 | 3.95 | 54.38 | 754.4 | 0.0072 | 71.16 | 14.83 | 14.02 |
| *Prescottia montana* | yes | 14.30 | 9.42 | 5976.44 | 418.0 | 4439.0 | 4.35 | 34.63 | 124.3 | 0.0072 | 37.66 | 60.26 | 2.08 |
| *Pseudolaelia geraensis* | no | 6.23 | 28.72 | 3773.06 | 605.3 | 2107.5 | 9.36 | 19.29 | 223.5 | 0.0072 | 60.30 | 39.70 | 0.00 |
| *Pseudolaelia vellozicola* | no | 6.35 | 31.91 | 3224.98 | 508.0 | 1592.0 | 11.08 | 16.16 | 250.0 | 0.0072 | 55.20 | 44.80 | 0.00 |
| *Peperomia incana* | yes | 7.04 | 6.49 | 1142.03 | 162.3 | 2502.7 | 10.15 | 25.62 | 115.0 | 0.3017 | 28.01 | 71.99 | 0.00 |
| *Achetaria crenata* | no | 21.25 | 11.58 | 375.39 | 17.7 | 152.5 | 1.34 | 11.66 | 176.2 | 0.0132 | 49.33 | 0.00 | 50.67 |
| *Andropogon bicornis* | no | 9.45 | 53.72 | 5897.67 | 624.0 | 1161.5 | 8.95 | 4.38 | 577.5 | 0.1260 | 43.10 | 56.90 | 0.00 |
| *Axonopus graniticola* | no | 13.49 | 24.97 | 15775.02 | 1169.2 | 4682.8 | 9.67 | 21.10 | 663.0 | 0.3110 | 72.55 | 27.03 | 0.42 |
| *Melinis repens* | no | 23.05 | 23.98 | 726.11 | 31.5 | 131.33 | 5.07 | 4.55 | 441.5 | 0.2180 | 37.52 | 30.25 | 32.23 |
| *Paspalum* sp. | no | 8.21 | 27.83 | 6023.97 | 734.0 | 2637.7 | 8.27 | 8.63 | 611.3 | 0.3017 | 64.22 | 35.78 | 0.00 |
| *Portulaca hirsutissima* | yes | 15.08 | 5.68 | 75.39 | 5.0 | 88.0 | 2.39 | 3.95 | 58.7 | 0.1397 | 0.14 | 94.03 | 5.83 |
| *Bradea* sp. nov. | no | 11.96 | 26.61 | 715.60 | 59.8 | 224.8 | 1.27 | 10.39 | 585.0 | 0.25 | 50.04 | 49.96 | 0.00 |
| *Schwenckia* sp. nov. | no | 15.81 | 22.67 | 1001.46 | 63.3 | 279.3 | 1.25 | 16.88 | 631.0 | 0.268 | 53.87 | 33.55 | 12.58 |
| *Barbacenia purpurea* | no | 6.99 | 35.54 | 13756.46 | 1967.8 | 5537.2 | 13.24 | 24.47 | 462.0 | 0.2933 | 59.38 | 40.62 | 0.00 |
| *Barbacenia tomentosa* | no | 15.54 | 28.82 | 3851.49 | 247.8 | 859.8 | 4.79 | 19.64 | 255.0 | 0.2933 | 55.66 | 36.67 | 7.68 |
| *Vellozia candida* | no | 6.92 | 35.59 | 4347.69 | 628.2 | 1765.2 | 12.00 | 15.02 | 965.0 | 0.2315 | 53.21 | 46.79 | 0.00 |
| *Vellozia plicata* | no | 5.98 | 41.52 | 3679.65 | 615.2 | 1481.7 | 6.99 | 15.23 | 748.7 | 0.245 | 47.24 | 52.76 | 0.00 |
| *Stachytarpheta gesnerioides* | no | 14.20 | 22.68 | 6008.42 | 423.0 | 1865.2 | 1.59 | 46.50 | 828.5 | 1.8561 | 70.49 | 26.00 | 3.51 |

# CONSIDERAÇÕES FINAIS

Em várias regiões tropicais e subtropicais, ameaças à diversidade biológica dos inselbergs está aumentando de forma acelerada. Além da remoção da vegetação circundante, o que facilita a invasão biológica, inselbergs sofrem crescentes ameaças que incluem a mineração e a extração das espécies atrativas da sua flora (Martinelli 2007; Ferreira *et al.* 2014). Entretanto, para que se possa proteger uma área, são necessárias informações consistentes para o estabelecimento de prioridades que possam conduzir à conservação, à utilização sustentável e à repartição de benefícios da diversidade biológica (MMA 2002).

Os resultados apresentados nessa dissertação revelaram com relação à flora de inselbergs: novas espécies para a ciência, novos registros para o estado de Minas Gerais, elevada riqueza de espécies e alta taxa de endemismos. Esses dados reforçam a necessidade de que sejam intensificados os esforços em pesquisa nesses afloramentos, que ainda apresentam grandes lacunas com relação à sua composição florística e diversos aspectos ecológicos de suas comunidades.

Esse estudo apresenta fortes evidências suportando o papel dos filtros ambientais na estruturação de comunidades de plantas em inselbergs. Além disso, há indicações de que as estratégias ecológicas, aqui apresentadas, foram mais diversas nesses afloramentos graníticos do que o esperado pela teoria. Dessa forma, o conhecimento sobre a diversidade das estratégias ecológicas encontradas nesse trabalho pode ser útil para a restauração de inselbergs após distúrbios. Partindo-se do princípio que as espécies têm diferentes tolerâncias aos estresses abióticos, gestores podem selecionar espécies com base em seu papel funcional.

No que se refere à invasão biológica, um dos fatores que mais ameaçam a flora de inselbergs (Piggot 2000; Porembski 2000; Hopper 2009), reforçamos que esse é realmente um fator que deve ser considerado nos planos de manejo desses afloramentos. Encontramos que, diferente da média da comunidade nativa, espécies invasoras possuem atributos funcionais distintos, que as favorecem em determinados tipos de ambiente. Habitats que apresentam maiores disponibilidades de recurso, e, portanto, condições mais favoráveis, são mais susceptíveis à invasão. Compreender os fatores que favorecem a invasão por plantas exóticas e seu impacto sobre os ecossistemas é complexo e desafiador (Drenovsky *et al.* 2012), todavia, nossos resultados contribuem para uma melhor previsibilidade na dinâmica de invasão biológica em comunidades com recursos limitados.

Argumenta-se, portanto, que estudos que compreendam abordagens diversas, que levam em conta tanto a identidade das espécies quanto seus atributos funcionais, mostram-se fundamentais no contexto dos afloramentos rochosos. A abordagem qualitativa nos possibilita saber quais são as espécies-chave na comunidade, ameaçadas (e que devem entrar nas listas oficiais de ameaça), endêmicas, além de servir de base para estudos de similaridade, biogeografia, filogeografia, entre outros. A abordagem quantitativa funcional contribui para a nossa capacidade de entender como as comunidades vegetais em inselbergs estão estruturadas, além de apresentarem melhor previsibilidade de como essas comunidades respondem às mudanças ambientais. Todas essas informações poderão ser úteis para o desenvolvimento de estratégias de conservação e manejo da vegetação sobre esses afloramentos. Por fim, sugerimos que sejam intensificados os esforços de coleta nos inselbergs, já que sua flora ainda se apresenta pouco explorada, e que sejam feitos mais estudos com uma perspectiva funcional aprofundada, que possa relacionar os filtros ambientais e os traços das plantas em um contexto filogenético e geográfico.

## Referências

Drenovsky, R.E. *et al*. 2012. A functional trait perspective on plant invasion. **Annals of Botany** 110: 141–153.

Ferreira, J. *et al*. 2014. Brazil's environmental leadership at risk. **Science** 346: 706-707.

Hopper, S.D. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. **Plant and Soil** 322: 49-86.

Martinelli, G. 2007. Mountain biodiversity in Brazil. **Brazilian Journal of Botany** 30: 587-597.

MMA. 2002. **Biodiversidade Brasileira: Avaliação e Identificação de Áreas e Ações Prioritárias para Conservação, Utilização Sustentável e Repartição de Benefícios da Biodiversidade Brasileira**. Ministério do Meio Ambiente, Brasília

Pigott, J.P. 2000. Environmental weeds and granite outcrops: possible solutions in the “too hard basket”. **Journal of the Royal Society of Western Australia** 83: 135-137.

Porembski, S. 2000a. The invasibility of tropical granite outcrops (‘inselbergs’) by exotic weeds. **Journal of the Royal Society of Western Australia** 83: 131-137.