



Plant life in *campo rupestre*: New lessons from an ancient biodiversity hotspot[☆]



L. Patrícia C. Morellato^{a,*}, Fernando A.O. Silveira^{b,*}

^a UNESP Universidade Estadual Paulista, Instituto de Biociências, Departamento de Botânica, Laboratório de Fenologia, 13506-900, Rio Claro, São Paulo, Brazil

^b Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, 31270-901, Belo Horizonte, Minas Gerais, Brazil

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ABSTRACT

The years 2011–2020 represent the United Nations Decade of Biodiversity, aiming to inspire worldwide actions to support biodiversity conservation. This Special Issue illustrates the current knowledge of plant life in *campo rupestre*, a megadiverse, highly-endemic vegetation complex, and one under alarming and unprecedented threats. The major research areas grouping the 27 contributions to the Special Issue are: i) plant diversity, ii) species coexistence, regeneration niche and climate change, iii) ecology of species interactions, iv) plant life on *canga*, and v) fire, regeneration ecology, and conservation. We highlight knowledge gaps in plant life in *campo rupestre* and suggest priority avenues of future research and steps forward to understand and preserve ancient ecosystems worldwide. Such efforts include the need to: 1) better assess the ecology of herbaceous species, 2) understand the effects of global change drivers on the vulnerability of endemic species, 3) understand how plant functional diversity and plant–animal interactions shape community structure and function, 4) apply new technologies (cameras, drones and remote sensing proxies) to understand plant phenology in space and time, 5) unravel diversification patterns and distinguish paleoendemism from neoendemism, 6) to disentangle the ecological and evolutionary role of fire, 7) gain insight into the factors that limit ecological restoration in degraded *campo rupestre*, 8) increase awareness and value of ecosystem services, 9) identify essential variables, key measures and areas to conserve *campo rupestre*, 10) promote reviews and research comparing old ecosystems. Therefore, burgeoning literature on *campo rupestre* will benefit from long-term multi- and trans-disciplinary research investigating a wide array of topics, from plant ecology to ecosystem functioning to biodiversity conservation and ecological restoration. All knowledge must reach stakeholders, and it should be translated into an ecosystem services assessment for guiding the rational stewardship of *campo rupestre* and for benefiting local people. A key step forward in the understanding of plant life in *campo rupestre* is the OCBIL Theory (old, climatically-buffered, infertile landscapes), which provides a theoretical framework of testable hypotheses and cross-continental comparisons. We anticipate this Special Issue will foster collaborative research leading to a deeper understanding and appreciation of one of the world's most ancient ecosystems.

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1. Introduction to plant life in *campo rupestre* special issue

The motivation for this Special Issue was a shared desire to illustrate the current knowledge of plant life in *campo rupestre* and invite future research perspectives that both recognize this distinctly Brazilian vegetation complex as megadiverse, highly

endemic, and to communicate its alarming and unprecedented threatened status among globally unique vegetation. We argue that the rapidly expanding research on *campo rupestre* will benefit from long-term multi- and trans-disciplinary projects that coordinate research ranging from plant ecology to ecosystem functioning, and from biodiversity conservation and ecological restoration to the management and stewardship of these precious natural resources. All the knowledge gained from this research must reach stakeholders, including park managers and private companies, and be translated as an ecosystem services assessment for guiding the rational management of *campo rupestre* and for the benefit of local people. We anticipate the present Special Issue will foster collaborative research leading to a deeper understanding of one of the

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* Corresponding authors.

E-mail addresses: pmorella@rc.unesp.br (L.P.C. Morellato), faosilveira@icb.ufmg.br (F.A.O. Silveira).

world's most ancient ecosystems. Preceding our collection of articles, we define *campo rupestre* and explain the importance of a Special Issue on a tropical “grassy” ecosystem.

1.1. Definition of campo rupestre

The term *campo rupestre* has long been used to describe a range of vegetation types, but half a century ago Magalhães (1966) first published this term as a specific name for the spectacular mountaintop vegetation at the Espinhaço Range (Fig. 1). Perhaps owing to heterogeneity at both regional and local spatial scales, i.e. intermingled geographic distribution among surrounding vegetation versus different physiognomies, substrates, and microhabitats, respectively, there has been intense debate often ending in blurred definitions. In the last 50 years, many attempts to redefine, clarify and circumscribe the *campo rupestre* have been offered (Alves et al., 2014 and references therein). Consequently, to describe the same vegetation complex, a variety of terms arose, including altitudinal complex, highland savannas, *cerrado rupestre*, altitudinal rocky fields, and rupestrian grassland, among others, sparking more concerns over the already puzzling terminology (see Mucina, 2018).

The increasing international interest in the complex vegetation and geographic distribution of *campo rupestre* begs a more general definition and unified nomenclature which is beyond the scope of this editorial. Here, we adopt concepts proposed by Silveira et al. (2016), who define *campo rupestre sensu lato*, or simply *campo rupestre*, as a montane, grassy-shrubby, fire-prone vegetation mosaic with rocky outcrops of quartzite, sandstone or ironstone (i.e. banded ironstone formation such as itabirites and cuirasses locally known as *canga*), along with sandy, stony, and waterlogged grasslands. Patches of transitional vegetation such as cerrado, gallery forests, and relictual hilltop forests (forest islands or *capões*) are also within the *campo rupestre sensu lato* (Fig. 2). *Campo rupestre sensu stricto* comprises only the grassland mosaic and associated vegetation on the rocky outcrops, excluding woodlands, and gallery and mountaintop forests (Silveira et al., 2016). The marked differences in geology, pedology, structure, species composition, floristics, and functionality of previously identified quartzitic and ferruginous (ironstone or *canga*) *campo rupestre* may prevent using the term *campo rupestre* for ironstone outcrops (Messias et al., 2013; Carmo and Jacobi, 2016; Carmo et al., 2016; Conceição et al., 2016; Mucina, 2018). Nevertheless, we considered for publications in this special issue papers addressing plant life in *canga* (ironstone) and in granitic and quartzitic outcrops. For more debate about the circumscription of *campo rupestre* and equivalent ecosystems worldwide, please refer to Mucina (2018).

1.2. The tropical “grassy” ecosystems and the special issue on campo rupestre

The years 2011–2020 represent the United Nations' Decade of Biodiversity, which aims to inspire worldwide actions to support biodiversity conservation (CBD, 2010). Achievement of the CBD's strategic goals relies upon the recognition of biodiversity areas, awareness of their values, and the steps needed for their conservation and sustainable use. The present decade also marks the intense debate and acknowledgement of the importance of the once neglected, megadiverse grassy ecosystems and their contrasting fragile conservation status (e.g. Overbeck et al., 2015; Veldman et al., 2015a,b). Increasing awareness of grassy ecosystems concurs with the rapidly growing knowledge about *campo rupestre*, bringing “grassy ecosystems” to the forefront of the ecological literature, uncovering their high species richness and endemism, highlighting the many threats to their persistence, and their relevance for human wellbeing.

The *campo rupestre* is a complex, megadiverse, old-growth vegetation that caught the attention of many explorers and naturalists, including the 19th century Danish botanist, Eugen Warming (Fernandes, 2016). However, it was only in the last century that the collections of plants and discovery of new species resulted in a novel appreciation of *campo rupestre*, leading to several floras, species' descriptions, and taxonomic reviews. However, the recognition of *campo rupestre*'s extraordinary plant species diversity, endemism, and ubiquitous harsh environment, in addition to the acknowledgment of the conservation imperative of this non-forested, grassy biome, emerged only in the last few years. While there are books and special issues dedicated to Neotropical biomes or vegetation domains, for instance, the Atlantic forest: Morellato (1992), Morellato and Haddad (2000), Metzger (2009); Cerrado: Oliveira and Marquis (2002); Caatinga: Leal et al. (2003); dry forests: Sanchez-Azofeifa et al. (2013), and many books and issues for Amazon forest and Neotropical rainforests, this Special Issue is the very first solely devoted to *campo rupestre*.

The review article by Silveira et al. (2016) summarizes up-to-date knowledge and characterizes the *campo rupestre*. The authors postulate the inclusion of the *campo rupestre* vegetation complex as an OCBIL (old, climatically-buffered, infertile landscape) (Hopper, 2009; see Hopper et al., 2016 for further discussion of OCBIL ecology, evolution and conservation). However, all recent research achievements culminate with the seminal work of Geraldo Wilson Fernandes' 2016 book, *Ecology and Conservation of Mountaintop Grasslands in Brazil*, which is the first comprehensive appraisal of the abiotic environmental, fauna and flora, community ecology, functional ecology, conservation, restoration, management, and human dimensions of the *campo rupestre*. Besides representing a landmark for the new ecology of *campo rupestre*, the book's editor embodies the most important contemporary *campo rupestre* researcher and environmentalist who has catalyzed countless students and researchers from Brazil and abroad to work at Serra do Cipó and the *campo rupestre* across the Espinhaço Mountain range in Brazil. The present special issue is both built on and a tribute to his lifelong, relentless, and passionate work on *campo rupestre*.

2. Synthesis and significance of the contributing articles

The papers in this Special Issue embrace diverse ecological scales, from ecophysiology, population ecology and genetics, community and functional ecology, to biogeography and macroecology, all reflecting multiple advances in our knowledge on the structure and functioning of this megadiverse ecosystem. We identified five major areas of contributions to the Special Issue: i) plant diversity, ii) species coexistence, regeneration niche and climate change, iii) ecology of species interactions, iv) plant life on *canga*, and v) fire, regeneration ecology, and conservation.

2.1. Plant diversity

The discussion of *campo rupestre* diversity begins with Mucina (2018) addressing the classification of *campo rupestre* with a global perspective. He suggests that quartzitic *campo rupestre* complex is an azonal and global peino biome, and their analogues outside South America are the South African sourvelds and similar grassland scrub-grassy mosaics on the sandstone plateaus of the Australian Top End. Following the debate on *campo rupestre* diversity, the macroecological study conducted by Neves et al. (2018) addresses the role of isolated patches and floristic from surrounding habitats (including cerrado, Atlantic rainforests, seasonally-dry woodlands and Amazonian rainforests) for the woody flora of *campo rupestre*. Neves et al. (2018) demonstrate an overall lack of compositional identity across the *campo rupestre* woody flora,

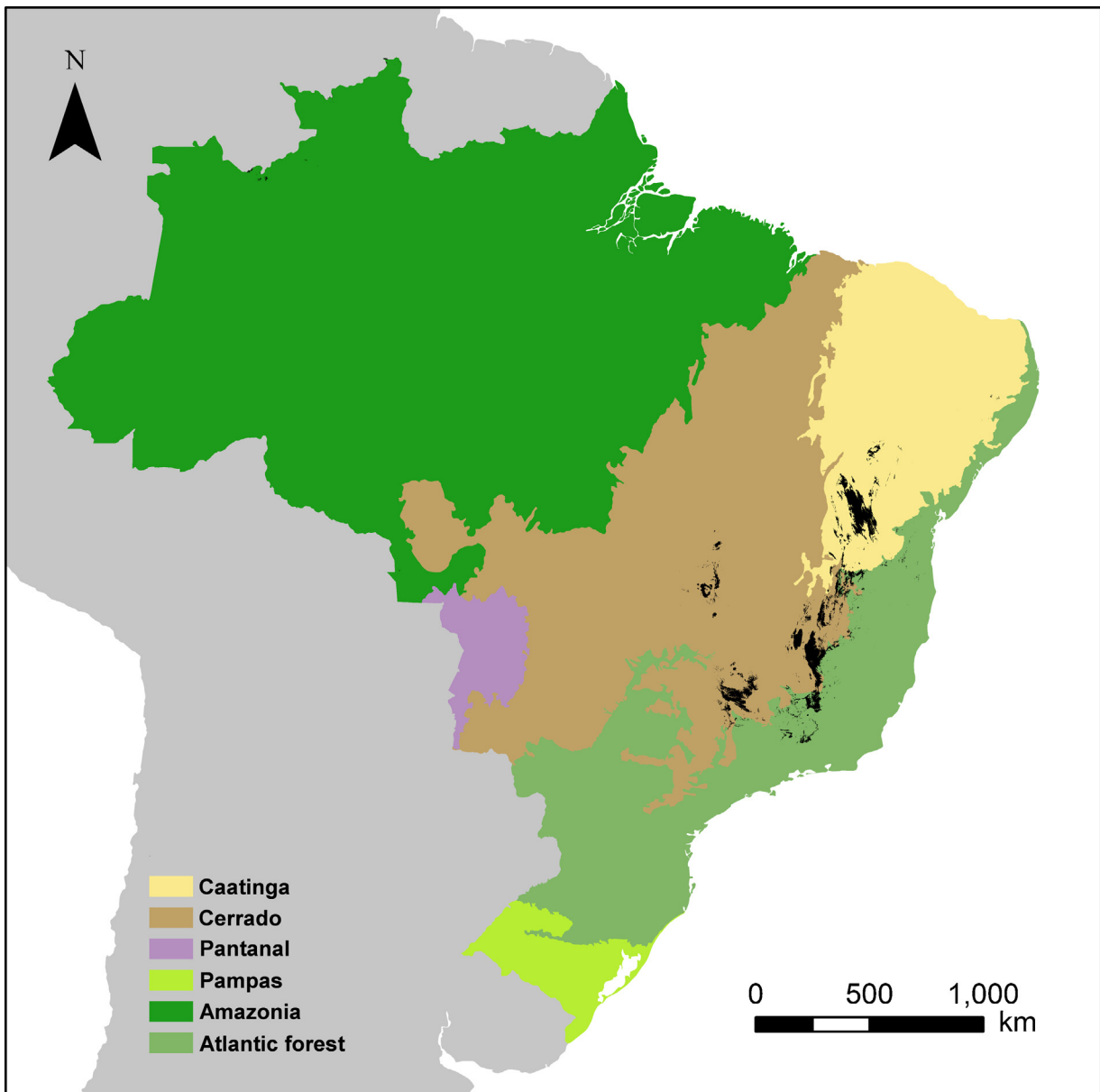


Fig. 1. Map showing the distribution of quartzitic *campo rupestre* in Brazil and associated main vegetation domains according to IBGE (Instituto Brasileiro de Geografia e Estatística).

and a marked similarity between *campo rupestre* and the surrounding lowland cerrado, driven primarily by substrate and climate. Even considering that woody species represent less than 15% of the diversity of *campo rupestre* flora, the huge spatially-structured floristic heterogeneity of woody species has important implications for conservation and management. The community-level article by Mota et al. (2018) discusses changes in floristic composition, structure, and diversity of woody individuals and rosettes across an altitudinal gradient at *Serra do Cipó*. Their key finding is that beta diversity represents 92.7% of the total diversity, with species turnover as the primary mechanism driving beta diversity. Soil is proposed as a key driver of change across the altitudinal gradient. The next community studies take a functional diversity approach to examine two contrasting plant groups, bryophytes and trees. Silva et al. (2018) tested three hypotheses related to organization of moss communities in granitic rocky outcrops, and discovered that despite the convergence in some traits, moss distribution

patterns are not related to annual precipitation and temperature seasonality. Moreover, the random trait organization on some outcrops is not related to dispersal limitation. Unexpectedly, each community has a different functional composition, indicating that moss species may have different trait arrangements to tolerate the environmental severity of rocky outcrops. Coelho et al. (2018a) evaluated the relationship between woody species functional traits and environmental drivers of tree communities in an archipelago of montane forest islands immersed in *campo rupestre*. Strong connections between functional traits and environmental drivers suggest that habitat heterogeneity is also essential in structuring tree communities associated with *campo rupestre*. The authors argue that understanding the connection between environmental parameters and functional traits may help to predict the ecological consequences of anthropogenic or natural impacts to those forests. Finally, from a population genetics point of view, Ribeiro et al. (2018) addressed the taxonomically problematic *Coman-*

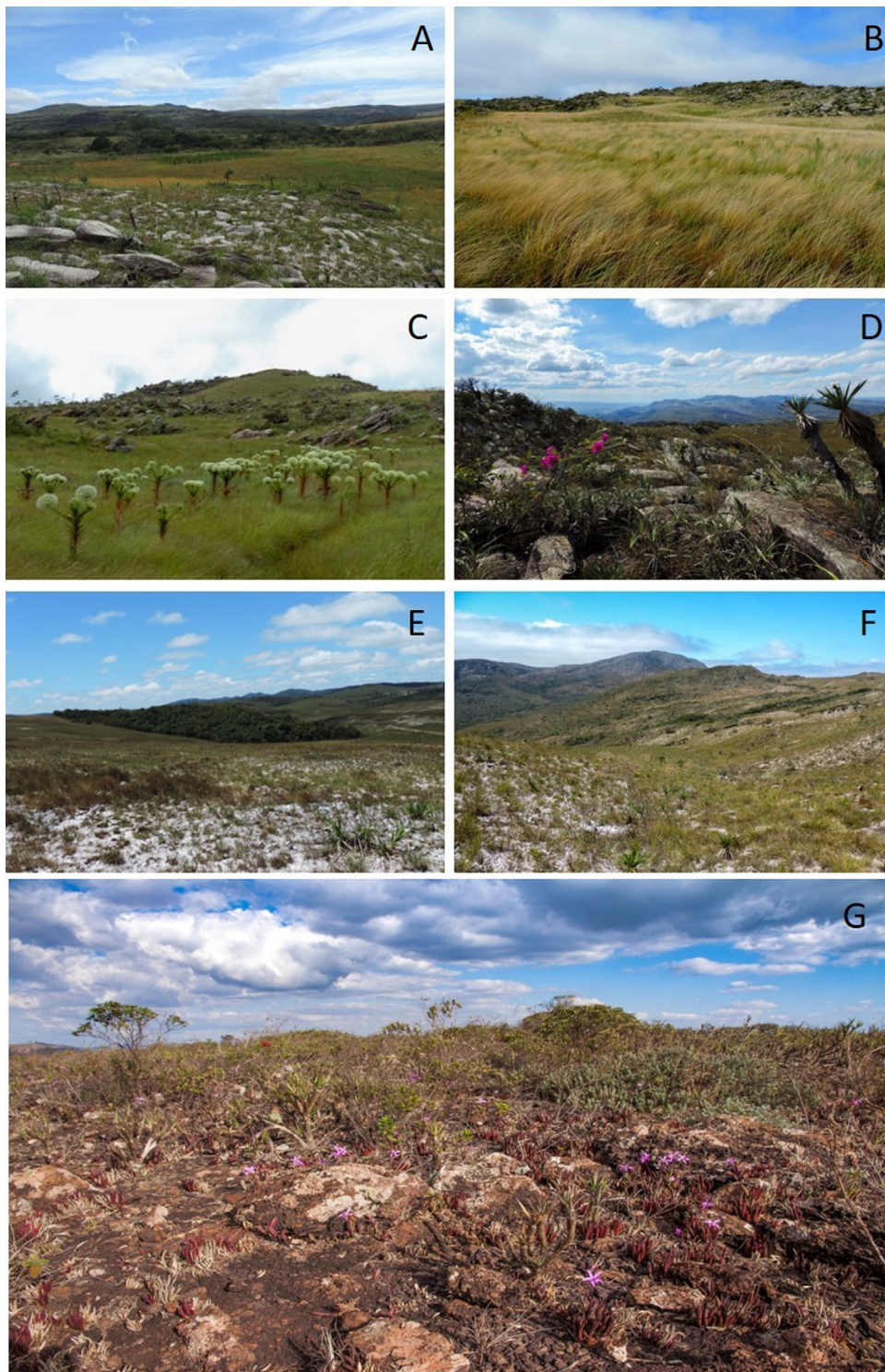


Fig. 2. Images of key vegetation types composing the *campo rupestre lato sensu*: (A) Rocky outcrops with wet grassland and a gallery forest in the back; (B) wet grassland with rocky outcrops in the back; (C) wet and sandy grasslands with a population of *Actinocephalus bongardii*; (D) vegetation growing on rocky outcrop; (E) sandy grassland surrounding the hilltop forest island; (F) stony grassland; (G) ironstone outcrop. Photos: Maria Gabriela G. Camargo (A–F). Augusto Gomes (G).

thera (Eriocaulaceae) species complex, including four sympatric species, all endemic to small areas of *campo rupestre*. Genetic and morphological analyses of 13 natural populations indicate a low intrapopulation genetic and morphological variability and high genetic differentiation among populations, lending support to the re-establishment of *C. hatschbachii* as a valid species instead of a

synonym of *C. curralensis*. Evidence of hybridization and introgression in two populations from individual sites indicates protection is crucial for the maintenance of evolutionary processes in *Comanthera*.

2.2. Species coexistence, regeneration niche and climate change

Covering these Special Issue topics, [Castro et al. \(2018\)](#) investigated the functional mechanisms behind species coexistence through a phylogenetically-controlled assessment of photosynthetic performance and water relations in species of Melastomataceae from xeric vs mesic microhabitats. Owing to consistent differences in water relations, but not in photosynthetic performance among species from these two microhabitats, they argue that differential water-economy strategies support hydrological niche segregation in *campo rupestre*; this species trait may help stabilize species coexistence. Along this line, [Pereira et al. \(2018\)](#) compared photosynthetic and leaf nutrient-use strategies in three phylogenetically-unrelated species with contrasting levels of endemism. The authors ask whether species distribution is linked to ecophysiological parameters, and if so, should widespread species have wider niche breadths compared with endemic ones? The authors found that all species produce highly scleromorphic leaves, but with higher effective quantum yield and electron transport rates in the widespread species compared with endemic ones. To examine whether variation in soil chemical and physical properties drive species distribution and abundance, [Demetrio and Coelho \(2018\)](#) sampled ramets of four clonal *Leiothrix* species (Eriocaulaceae) and found no significant differences in soil conditions in sites with the absence and presence of any species of *Leiothrix*, suggesting dispersal limitation for these species. Another key result is that distinct species colonize soils with different physical and chemical properties, indicating some degree of habitat specialization. Altogether, these studies reinforce the role of microhabitats in determining species coexistence.

The regeneration niche is addressed by [Vieira et al. \(2018\)](#). Investigating light exposure and light quality on seed germination of 11 species of *Vellozia*, they found light exposure time is directly related to R:FR ratio. Species-specific responses suggest different regeneration strategies in sympatric species. In contrast, [Giorni et al. \(2018\)](#) examined the germination requirements of eight species of *Xyris* differing in microhabitat occupancy and geographic distribution. Through controlled laboratory experiments, they found that the effects of temperature on seed germination do not explain the patterns of geographic distribution or endemism. Surprisingly, species occurrence in soils with different water retention capacities cannot be attributed to the capacity of their seeds to germinate under conditions of hypoxia. The effects of increasing temperature on species' geographic ranges and distributions should be especially relevant in *campo rupestre*, where many endemics have dispersal limitations and are specialized on mountaintops where opportunities for upward migration are limited. Along these lines, [Chaves et al. \(2018\)](#) compared heat tolerance between a restricted and widely distributed bromeliad. They found the endemic species, *Vriesea minarum*, has a lower thermal tolerance than the widely distributed species. Further, the low heat tolerance and plasticity of the endemic species suggest greater sensitivity to threats caused by global warming in mountaintop specialized species. [Duarte et al. \(2018\)](#) documented the thermal thresholds for germination in five bromeliads to gain insight into germination responses to predicted climate change scenarios. The bromeliads exhibit differences in their thermal requirements for germination. Under the warming scenarios, the authors detected a reduction in the time required to heat sum units to germinate, but a risk for persistence is identified for *Racinea aerisincola*, the most restricted species. The authors conclude that the determination of thermal thresholds for germination can help identify species vulnerability to climate change and promote strategies for conservation of bromeliads species.

2.3. The ecology of species interaction

In this Special Issue, three papers advance our knowledge on the intricate patterns of species interaction in *campo rupestre*. [Gélvez-Zuñiga et al. \(2018\)](#) examined the reproductive biology and floral visitors of *Collaea cipoensis* (Fabaceae), a hummingbird-pollinated, narrowly-distributed shrub. Among the main results, they found that *C. cipoensis* is self-incompatible and pollen-limited, that *Colibri serrirostris* is the main pollinator, and that illegitimate flower visitors strongly reduce fruit set. [Soares and Morellato \(2018\)](#) revealed the specialized pollination system of the narrow endemic *Trembleya laniflora*, pollinated by large, crepuscular bees. Its buzz-pollinated flowers with poricidal anthers, heterostemony, and pollen as the only reward are dependent on interbreeding; the large, crepuscular bees promote outcrossing within and among patches of naturally-isolated populations on rocky outcrops. [Guerra et al. \(2018\)](#) explore the host range and distribution patterns of the mistletoe *Psittacanthus robustus* (Loranthaceae). Four species of trees (all within Myrtales) comprised 95% of infested individuals, with prevalence increasing with host height for all species and a highly-aggregated distribution in few taller host trees.

2.4. Plant life in ironstone outcrops

The two articles by [Peñaloza-Bojacá et al. \(2018a,b\)](#) explore, in this Special Issue, the ecology of bryophytes, a neglected group of plants in *campo rupestre*. In the first paper they investigate the reproductive strategies of 108 species of bryophytes ([Peñaloza-Bojacá et al., 2018a](#)). Seventy percent of the bryophyte species surveyed were reproductively active, but with contrasting strategies in mosses (mostly asexually) and liverworts (mainly sexually). In the second paper, [Peñaloza-Bojacá et al. \(2018b\)](#) demonstrate deterministic species distributions among microhabitats and anthropogenic disturbances as a key environmental filter. In essence, ironstone outcrops in southeastern Brazil harbor a high bryophyte diversity, highlighting the importance of conserving ironstone outcrops. [Schettini et al. \(2018\)](#) investigate the total and plant-available concentration of heavy elements in soils and their concentration in leaves of 27 sympatric species from an ironstone outcrop. They found values above the toxic limits described in the literature and allowable through environmental legislation. The intraspecific variation in foliar levels of metals suggests different phytoextraction or exclusion potentials. Although most species were not considered hyperaccumulators, [Schettini et al. \(2018\)](#) demonstrate species' potential for phytoremediation, stabilization, phytomining and ecological restoration. Finally, [Bressan et al. \(2018\)](#) describe the genetic structure and divergence among four outcrop mountaintop populations of a wild relative of cultivated rice, *Oryza glumaepatula*, which is typically found in aquatic environments of lowlands surrounded by tropical forests. They compared data on the populations from *canga* outcrops with those occurring in lowlands, and found the outcrop populations exhibit less genetic diversity than lowland populations. This result suggests that outcrop mountain populations experienced a founder effect from their initial establishment. The fixation index was negative for the Carajás lakes populations, and this excess of heterozygotes is unexpected for a traditionally selfing species. The authors discuss the implications of their findings for the conservation of populations threatened by iron mining.

2.5. Fire, regeneration ecology, and conservation of *campo rupestre*

The *campo rupestre* is a fire-prone ecosystem, and studies on regeneration, ecological restoration, and conservation must

Box 1: Priorities for future research in *campo rupestre*: providing the basis for conservation and sustainable use.

Research avenue	Example of approach
1. Diversity and ecology of grasses and other herbaceous species	Species turnover along landscape mosaic and ecological gradients, Pollination ecology, seed ecology
2. Species vulnerability to global warming	The role of intraspecific variation and phenotypic plasticity on species range shifts Fragility of the <i>campo rupestre</i> endemic species to climate change scenarios Plant responses to increasing temperature – phenology, germination, growth
3. Community structure and function	Understanding how species, functional and phylogenetic diversity relate to ecosystem functioning
4. Plant phenology in space-time	Integrate new technologies such as cameras, drones, and remote sensing proxies
5. Diversification patterns	Dated phylogenies and comparative phylogeography in paleo- and neo-endemics, identification of major refugia
6. The role of fire	Addressing the ecology and evolutionary role of fire to support evidence-based fire management policy
7. Ecological restoration	Identify limiting factors to ecological restoration including seed quality, seed dormancy, seedling establishment, species introduction, reintroduction and translocation, and biological invasions
8. Ecosystem services	Identify, characterize, increase awareness and value key ecosystem services
9. Biodiversity conservation	Identify areas for conservation, essential variables and key measures to conserve <i>campo rupestre</i>
10. Theoretical framework for old ecosystems	Comparative reviews and research of old ecosystems framed by OCBIL and other theories

account for this natural or anthropogenic disturbance. In this issue, [Le Stradic et al. \(2018a\)](#) used historical fire records to assess the effects of fire frequency on vegetation recovery and plant composition of the two main *campo rupestre* habitats: the sandy and stony grasslands. They found a rapid biomass recovery of *campo rupestre* vegetation after wildfires, no significant variation in species richness in sandy grasslands according to time after fire, and higher species richness on recently burnt stony grasslands. The high heterogeneity of *campo rupestre* vegetation is the likely explanation for the absence of change in plant composition in response to fire. Moving to strategies, [Joaquim et al. \(2018\)](#) examined the morphology of underground organs and carbohydrate levels and composition in 26 herbaceous species, and argue the storage of a diversity of carbohydrate-based structures may provide tolerance to environmental disturbances (such as fire) and support various phenological strategies. To unravel the effects of fire on seed germination, [Oliveira et al. \(2018\)](#) tested the tolerance to heat shock and desiccation in two species of *Xyris*. They found seeds of both species to be significantly tolerant to heat shock (100 °C for up to five minutes) and germinability decreases only at 180 °C. Together, the results of [Joaquim et al. \(2018\)](#) and [Oliveira et al. \(2018\)](#) suggest that species of *campo rupestre* are indeed highly resilient to fire, concurring with the results of [Le Stradic et al. \(2018a\)](#).

Given that uncontrolled fires and species overharvesting pose significant threats to endemic species of *campo rupestre*, a major challenge is to reconcile the insights of fire ecology, sustainable harvest of native species, and the needs of society. In this issue, [Bedê et al. \(2018\)](#) and [Souza et al. \(2018\)](#) evaluate the combined effects of harvesting and fire on seedling recruitment and population growth, respectively, for two native species harvested for commercial use. [Bedê et al. \(2018\)](#) found that current extractive practices interfere with the recruitment dynamics in *Comanthera elegantula*, an everlasting species: an intermittent fire regime appears to favor seedling establishment and growth, while periodic fire episodes negatively impact the progression of seedling cohorts and the regrowth of the herbaceous cover. [Souza et al. \(2018\)](#) also show that synchronized flowering of *Vellozia sincorana* is triggered by fire; no flowers were recorded in the absence of recent fire. The long-term effects of two common harvesting techniques and different fire intervals indicate that adult survival is the most important life-history variable for population persistence, and recent fires are primarily responsible for increases in reproductive rates. Harvesting may be sustainable, as long as it is low-intensity and fire also occurs periodically.

Finally, [Monteiro et al. \(2018\)](#) offer a conservation plan for the key threatened plant species at risk of extinction on *campo rupestre*, pinpointing priority regions for taking different conservation actions. They found that it is possible to protect, on average, more than 25% of threatened species ranges, while avoiding sites with extensive farming and mining and favoring areas with intensive fire frequency, and while constraining land management to a relatively small area of only 17% of the region. Maps of priority areas with their respective level of protection and conservation strategies can and should be used to support stakeholders and decision makers.

And last, but not least, this Special Issue brings a striking example combining conservation and fire policy – i.e. hilltop forest islands associated with *campo rupestre* grasslands. [Coelho et al. \(2018b\)](#) discuss the dilemma of preserving forest islands in a matrix of fire-prone grasslands. They highlight the need for improved conservation policy owing to well-recognized ecosystem services (mainly water recharge and support for specific fauna), and call for increased conservation efforts in this singular natural forest island mosaic.

3. New paths for an ancient ecosystem

Our Special Issue leads inevitably to the conclusion that there is still much to understand about the *campo rupestre* (Box 1). Plant ecological studies are still spatially, functionally, and phylogenetically biased. There is a high concentration in studies at *Serra do Cipó* but several other sites are still unexplored, even in the basic aspects of floristic studies (e.g., [Viana et al., 2016](#); [Staudt et al., 2017](#); [Valente et al., 2017](#)). Research in some of those understudied sites will fill knowledge gaps and reduce geographic biases. Unfortunately, the dynamics and changes on species distributions and conservation issues of *campo rupestre* still rely on the survey and analyses of the most abundant families, such as Poaceae and Cyperaceae, along with the iconic Eriocaulaceae, Xyridaceae, Velloziaceae, among others (see Fig. 3). The *campo rupestre* is extremely heterogeneous on both a large- ([Silveira et al., 2016](#)) and micro-scale ([Alves and Kolbek, 2010](#)), and these multiple scales provide strong opportunities for research on niche segregation and species coexistence, and the role of habitat heterogeneity on niche divergence in *campo rupestre* (e.g., [Marques et al., 2014](#); [Brum et al., 2017](#)), among other topics. The studies on the comparative eco-physiology and biochemistry of *campo rupestre* species are essential to understand factors driving species distribution across different scales ([Castro et al., 2016](#); [Boaneres et al., 2018](#); [Brum et al.,](#)



Fig. 3. The diversity of flowering plants from *campo rupestre* at Serra do Cipó. (A) Velloziaceae – *Barbacenia* cf. *flava*; (B) Melastomataceae – *Marcetia* *taxifolia*; (C) Orobanchaceae – *Esterhazyia* *splendida*; (D) Velloziaceae – *Vellozia* *albiflora*; (E) Melastomataceae – *Cambessedesia* *semidecandra*; (F) Ericaceae – *Agarista* cf. *duartei*; (G) Asteraceae – *Lychnophora* cf. *humillima*; (H) Amaranthaceae – *Xerosiphon* *aphyllus*; (I) Cyperaceae – *Bulbostylis* cf. *paradoxa*; (J) Iridaceae – *Sisyrinchium* *vaginatum*; (K) Eriocaulaceae – *Paepalanthus* *argenteus*; (L) Cyperaceae – *Bulbostylis* *eleocharioides*; (M) Poaceae – *Tatianyx* *arnacites*; (N) Xyridaceae – *Xyris* *pterygoblephara*; (O) Poaceae – *Axonopus* sp.; (P) Cyperaceae – *Rhynchospora* *consanguinea*; (Q) Gentianaceae – *Schultesia* *gracilis*; (R) Droseraceae – *Drosera* *chrysolepis*; (S) Polygalaceae – *Polygala* *celosioides*; (T) Asteraceae – *Dasyphyllum* *reticulatum*; (U) Melastomataceae – *Microlicia* *graveolens*; (V) Cyperaceae – *Rhynchospora* *recurvata*; (W) Eriocaulaceae – *Actinocephalus* *polyanthus*; (X) Fabaceae – *Lupinus* *coriaceus*. Photos: Maria Gabriela G. Camargo.

2017). Dramatic reductions in habitat and species diversity are predicted by species distribution models in some areas of *campo rupestre* as a consequence of global warming (Bitencourt et al., 2016), and assessing plant species response to high temperatures requires more in situ and ex situ experiments and valuations of ecophysiological responses. Two papers in this SI support the idea that endemic species are likely the most vulnerable to population decline and loss due to increasing temperatures (Chaves et al., 2018; Duarte et al., 2018).

Functional ecology of *campo rupestre* is at its infancy. *Campo rupestre* communities establish on shallow, extremely nutrient-impoverished soils, where plants are exposed to high irradiance, strong winds, seasonal droughts and fires. The combination of such strong abiotic filters has shaped the functional ecology of its native species and communities (Miazaki et al., 2015). However, there is still a long path to understand the functional ecology of *campo rupestre* species, including assessing the role of phylogeny in driving the evolution of species traits (e.g. Dayrell et al., 2017; Brito et al., 2017). For instance, leaf structural components, leaf construction costs, and photosynthetic carbon assimilation are fundamental to understand plant ecological strategies (Wright et al., 2004) and can be assessed by remote sensing (Ustin and Gamon, 2010). The preliminary studies of Streher et al. (2017a) on *campo rupestre* highlight the potential use of remote sensing to identify *campo rupestre* species and functional responses across different biological levels.

Species interactions became central in ecology due to their relevance in maintaining ecosystem functioning. With the incorporation of network theory, the field of species interactions has flourished and recently, the *campo rupestre* has been the stage for the development of novel and exciting theories on the complex between mistletoes–host (Mourão et al., 2017), ant–plants (Costa et al., 2016; Fagundes et al., 2017), plant–pollinator (Carstensen et al., 2016, 2017), fruit–frugivore (Guerra et al., 2017), plant–mycorrhizae (Coutinho et al., 2015), and plant–gall (Coelho et al., 2017) interactions. Such studies are important to determine ecosystem resilience following different kinds of disturbance.

Phenological studies, which are key for linking plant–animal interactions and to support biological conservation (Morellato et al., 2016) are poorly understood in *campo rupestre*. For instance, studies addressing temporal changes in plants from the vegetation complex of *Serra do Cipó* are still rare and primarily focus on plant reproduction (Rocha et al., 2016; Le Stradic et al., 2018b). However soils, as recognized for ancient systems, play a key role on species phenology and also distribution and diversification in *campo rupestre* (Le Stradic et al., 2018b). There is still a lack of understanding of leaf exchange dynamics in the *campo rupestre* (but see Garcia et al., 2017), and the resilience and recovery response of different habitats and vegetation types from fire events also remain poorly documented and understood. Large-scale climatic and leafing patterns at the Espinhaço Range indicate differences among forests, grasslands and savannas that need to be further explored (Streher et al., 2017b). However, direct measurements of leaf mineral content and phenological strategies of communities and individual plants are lacking. The application of digital cameras in embedded networks to monitor phenology across the *campo rupestre* using repeated photography is on its way forward, and will allow us to understand the seasonality on leafing patterns and fire recovering across the landscape in the near future (see Alberton et al., 2017, for description of the technique and applications). We also recommend other technologies to investigate the complex *campo rupestre* landscape as the combined use of UAVs (unmanned aerial vehicles) and cameras to survey and monitor *campo rupestre* in the e-phenology project (<http://www.recod.ic.unicamp.br/ephenology/client/index.html#/>; Box 1).

The *campo rupestre* is a fire-prone ecosystem, but surprisingly, the effects of fire on plant populations and on vegetation are poorly

understood (Figueira et al., 2016; Martins and Paiva, 2016). A recent reconstruction of historical fire occurrence data has shown that annual rainfall volume is weakly and negatively correlated with burned area, with drought during the ignition season being the strongest predictor of burned area (Alvarado et al., 2017). Such results suggest a moisture-dependent fire regime in contrast to the fuel-dependent fire regimes described for African savannas. Our Special Issue points out the importance of fire, from regeneration to conservation issues, but there is still much to learn about fire resilience. Experimental work is needed to establish effective, science-based management policies and minimize threats from anthropogenic changes in natural fire regimes (Batista et al., 2018).

The primary threats to biodiversity and ecosystem services include farming, overharvesting of endemic species, uncontrolled fires, mining, non-sustainable tourism, biological invasions, and climate change (Silveira et al., 2016; Ribeiro et al., 2017; Monteiro et al., 2018). We are just beginning to conduct the science supporting sustainability and restoration, especially in ironstone outcrops (Nunes et al., 2015; Giannini et al., 2017). New data and insights to support the valuation of ecosystem services provided by endemic plants is a promising way forward (Ferreira et al., 2017).

The *campo rupestre* opens countless new venues for research in this ancient ecosystem (Box 1). In particular, ecological restoration is extremely challenging and should be addressed in future research. The endeavor needs long-term research programs at diverse levels, from individuals to populations and communities to ecosystems and at multiple spatial and temporal scales.

4. The next step – OCBIL theory and worldwide comparisons

Finally, we contend that a major step forward in the understanding of plant life in *campo rupestre* is the OCBIL theoretical framework (Hopper, 2009). OCBIL theory has the merit of providing testable hypotheses that have been partially or totally corroborated in *campo rupestre* (Silveira et al., 2016). Present evidence on diversification dates of *campo rupestre* species is ambiguous (Loeuille et al., 2015; Rando et al., 2016), and we call for population genetics and comparative phylogeographic studies aiming to unveil diversification patterns in *campo rupestre*. Despite recent claims against the fundamentals of OCBIL theory (Mucina, 2018), its principles and predictions have been widely supported across continents in both southern and northern hemispheres (e.g., Hopper et al., 2016; Onstein and Linder, 2016; Rundel et al., 2016; Copenhaver-Parry et al., 2017; Feng et al., 2017; Pillon et al., 2017; Rull and Montoya, 2017); therefore, it is proving useful for understanding plant ecology and evolution worldwide.

Thanks to OCBIL theory, lessons learned from similar vegetation types on other continents can foster our knowledge on plant life in *campo rupestre*, and we hope the scientific community is ready to recognize the *campo rupestre* as a vegetation analogue of the famous Cape Floristic Region in South Africa and the Southwestern Australia Floristic Region (Fiedler, 2015). More importantly, we argue that incorporating long-term geological, pedological, and climatic aspects of vegetation, as proposed by OCBIL theory, opens fresh perspectives that will increase awareness of megadiverse ecosystems, promote cross-continental scientific collaboration, supporting conservation and sustainable use of *campo rupestre* and other ancient landscapes.

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