

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

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Abstract The Atlantic forest is among the hottest hotspots for biodiversity conservation. Within this biome, 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 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 driver, 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

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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 (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 conditions 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 et al. 1997; Porembski and Barthlott 2000), 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. These rocky outcrops 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 (Tecco et al. 2010; 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). This set of traits would include attributes associated with resource acquisition and fast growth (Tecco et al. 2010).

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 to check whether the invasive and resident species show converging or diverging functional traits in resource-limited communities. We expected invasive species to have particular ecological strategies, which could give them some advantage over native species, and also to display microhabitat preference leading to heterogeneity in invasion.

Materials and methods

Study area and sampled species

This study was performed on an inselberg inserted into an Atlantic forest matrix, in Teófilo Otoni, 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°15'439''W) with altitudes ranging from 306 to 676 m a. s. l. The climate 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 microhabitats on the inselberg. We placed four transects in areas 1–4, plus an additional transect in area five (Supplementary Material 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 (Supplementary Material 2 and 3). Patch sampling reflected patch occurrence in the study area, therefore we sampled different numbers of patch per category (Supplementary Material 1). Patch area ranged from 0.03 to 79.12 m² (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) (Supplementary Material 4), but we sampled functional traits for only 53 species, because 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 drivers and functional trait measurements

For each patch, we determined species richness and measured the following environmental drivers: 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 drivers were chosen because they were used in different studies as the basis for the classification of microhabitats 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 (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] (Pérez-Harguindeguy et al. 2013) (Supplementary Material 4) 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, packed in plastic bags and kept in a cooler until placed in a refrigerator for minimum periods of 12 h at 4 °C. Measurements were taken from two undamaged, full-grown leaves (including the petiole) per individual.

Leaf area was obtained by measuring scanned leaves in the software leaf area measurement (www.nucleodiversus.org/uploads/file/leafarea.zip). Leaf area was calibrated using graph-paper squares of known area. Leaf fresh weight was obtained from 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 with a digital penetrometer (Chatillon® model DFE-010, Florida, USA) coupled to a cone-shaped tip (model SPK-FMG-009A) (Silva and Batalha 2011). Leaf toughness values 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.

CSR classification

The CSR (C: competitive; S: stress-tolerant; R: ruderal; Grime 2001) plant ecological strategy scheme 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 dm² 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 the invasive species and the

native plant community of invaded patches. At patch-level, a PCA was also run to identify the main axes of variation and to seek trends in correlation between environmental drivers 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 species richness, soil depth, patch area, CM ruderalism and seed mass; for CM 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 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 data (Quinn and Keough 2002). To conduct the RLQ analysis, a correspondence analysis was used for the community presence/absence (L) matrix, while a 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).

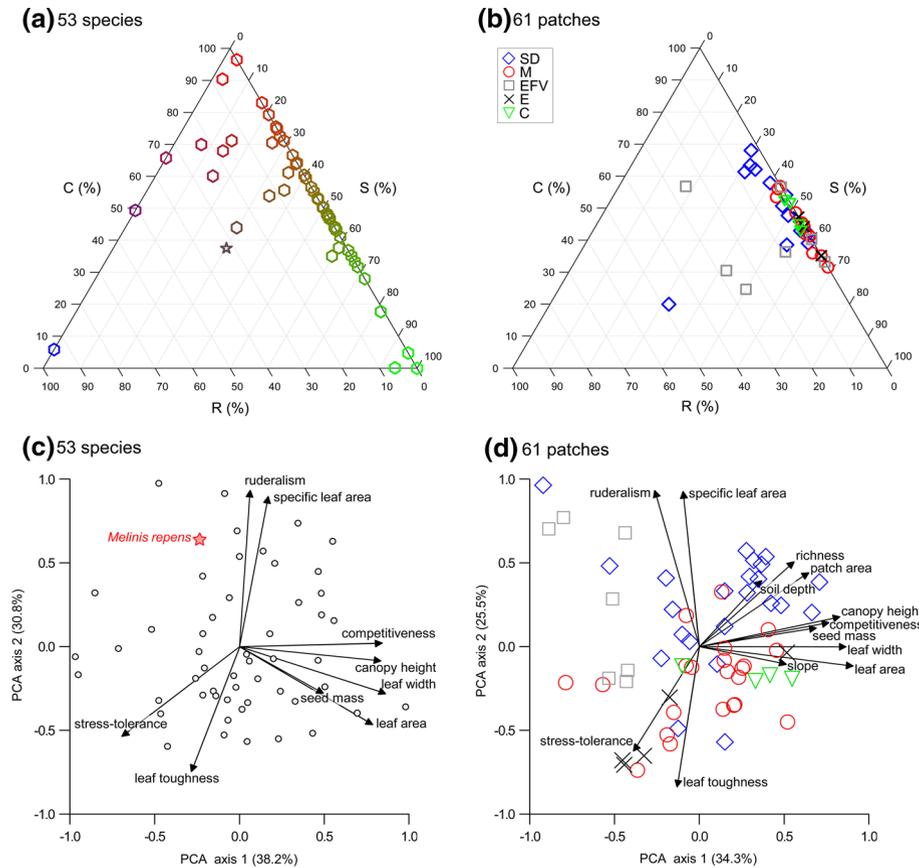


Fig. 1 CSR classification showing the relative importance of the C (competitiveness), S (stress-tolerance) and R (ruderalism) axes in plant species (a) and in vegetation patches (b) from inselberg communities at Minas Gerais, south-eastern Brazil. Principal component analyses of species (c) and patches (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

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).

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

Table 1 Comparison between native plant community of invaded patches (mean \pm 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	<i>M. repens</i>	One-sample <i>t</i> test
Ruderalism (%)	4.4 \pm 1.7	32.2	−13.792**
Specific leaf area (mm ² mg ^{−1})	11.9 \pm 0.7	23.1	−10.512**
Leaf width (mm)	38.7 \pm 6.3	4.6	8.052**
Leaf area (cm ²)	110.7 \pm 25.3	7.3	5.835**
Competitiveness (%)	51.6 \pm 3.8	37.5	3.744*
Stress-tolerance (%)	44.0 \pm 4.2	30.3	3.291*
Seed mass (mg)	5.2 \pm 2.0	0.2	3.170*
Canopy height (mm)	824.3 \pm 111.8	441.5	2.368
Leaf toughness (KgF)	5.8 \pm 0.8	5.1	−1.043

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

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).

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).

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 axis 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).

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

Fig. 2 Results of the fourth corner test showing the connection between environmental drivers 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. (Color figure online)

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

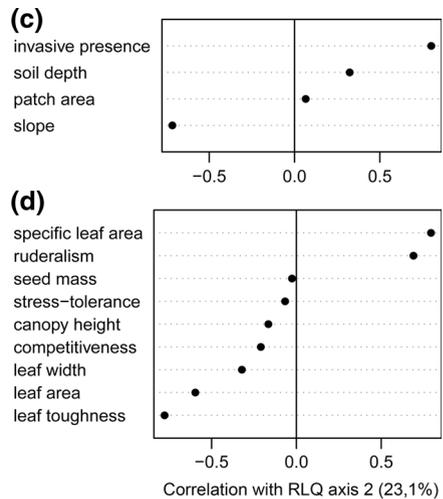
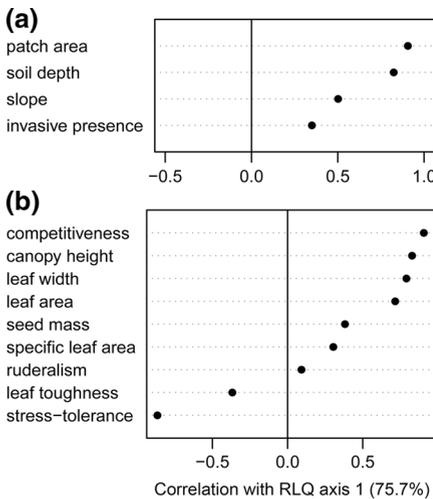


Fig. 3 Results of the first two axes of RLQ analysis showing the relationship between environmental drivers of vegetation patches and functional traits from inselberg plant communities at Minas Gerais, south-eastern Brazil: Pearson’s correlation between environmental drivers (a), functional traits (b)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

which have narrower, smaller and tougher leaves. Patch 5 represents the vulnerability of inselbergs to biological invasions: *M. repens* (brownish colour, with intermediate CSR strategy) usually coexists with more ruderal native species in patches set in flatter areas.

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 showed species with higher

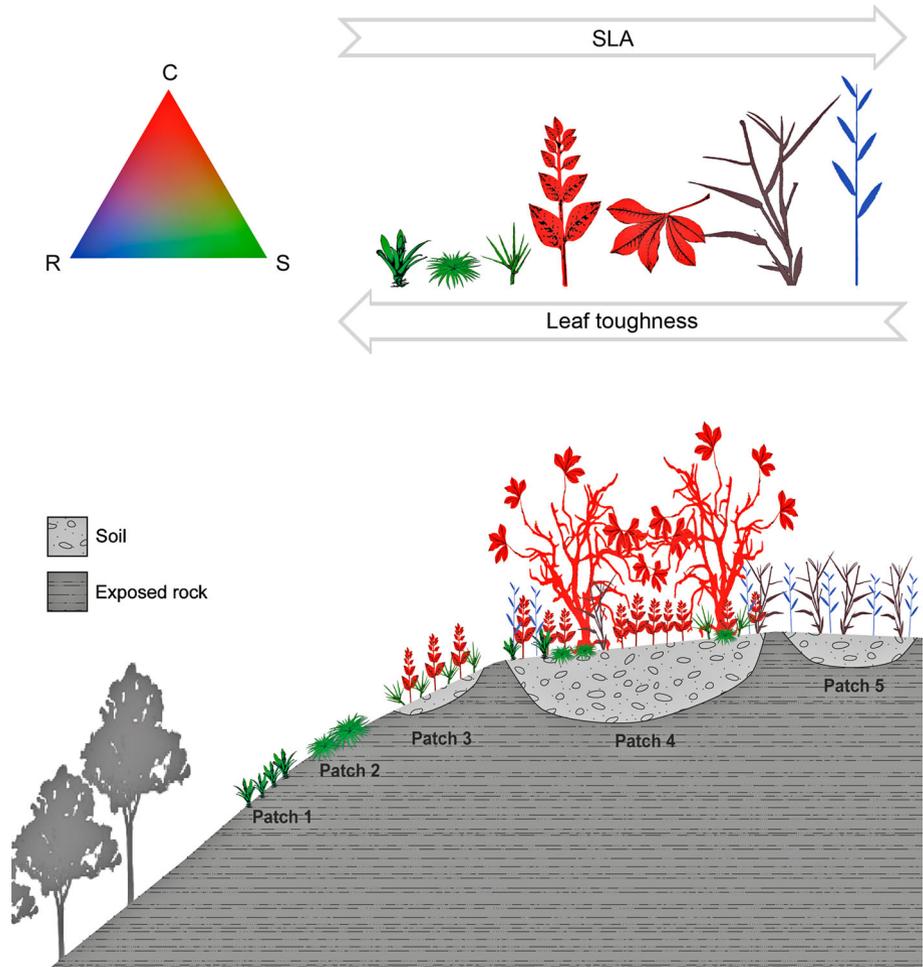


Fig. 4 Schematic representation of the relationship between patch structure and functional traits of plants from inselberg communities. The *triangle* represents Grime's (2001) scheme of plant strategies: competitiveness (*red*), stress-tolerance (*green*) and ruderalism (*blue*). Soil depth and patch 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 resident 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. (Color figure online)

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 be related 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 understanding 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 acquisitive 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 Olf 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 toughness 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 argue that more studies focussed 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.

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Conflict of interest The authors declare that they have no conflict of interest.

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