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Research Article

Non-native plant species on inselbergs of Brazilian tropical forests: checklist and insights for biodiversity management and conservation

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Abstract

The invasion of non-native species into spatially restricted habitats with unique plant communities poses a major challenge to biodiversity conservation. Inselbergs, granitic and/or gneissic outcrops with distinct abiotic conditions, host highly specialised plant species, but are increasingly threatened by the colonisation of exotic plants. This study aimed to: (1) compile the first comprehensive checklist of non-native plant species on inselbergs in two Brazilian phytogeographic domains: Atlantic Forest (AF) and Caatinga (CA), with a focus on identifying the invasive species; (2) analyse domain-specific associations of non-native species; (3) evaluate whether specific life forms of non-native species are associated with a particular domain; and (4) propose future research directions and management strategies. We documented 99 non-native species across AF (71 spp.) and CA (54 spp.) inselbergs using data from public online databases and published literature, of which 33 (33.3%) were classified as invasive. Therophytes were significantly associated with CA inselbergs and chamaephytes with AF inselbergs, reinforcing that certain life forms amongst non-native species exhibit domain-specific affinities, likely reflecting adaptations to contrasting environmental conditions. The findings of this study reveal that non-native species are widespread across inselbergs in both analysed domains, with many of them being invasives, underscoring the urgent need for early intervention. Future studies should concentrate on linking functional traits to invasion patterns in inselbergs, as well as integrating biogeographic and phylogenetic information, which will be crucial to anticipating and mitigating the spread of invasive species in these vulnerable environments.

Key words: Atlantic Forest, Caatinga, disturbance, exotic species, granites, inventory, rock outcrops, weeds

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Introduction

Human-mediated species dispersal, though not exclusive to modern times, has been a constant process throughout human history, intensifying alongside the expansion of civilizations and their interactions with the environment (Seebens et al. 2018). In recent centuries, however, anthropogenic activities have exponentially accelerated the introduction of non-native species, whether accidentally, through the

transport of goods, or deliberately, through agriculture, horticulture and landscaping (Vitule and Prodocimo 2012; Pyšek et al. 2020). This ongoing influx has become a major driver of ecological change on a global scale, disrupting ecosystems and threatening native biodiversity (Pyšek et al. 2020; Seebens et al. 2021). While many non-native species remain benign in their new environments, those that become invasive are widely recognised as significant agents of ecological imbalance and biodiversity loss, often contributing directly to species extinctions (Bellard et al. 2016). The success of such invasions is influenced by various factors, including the susceptibility of recipient communities, especially those with low species diversity or fragmented habitats, favourable abiotic conditions and the intensity of ongoing human disturbances (Stohlgren et al. 1999; Turner et al. 2021).

Ecosystems that are highly specialised and spatially restricted, such as islands and rock outcrops, are particularly prone to the impacts of biological invasions (Hopper 2009). Amongst these rock outcrops, inselbergs — residual rocky formations whose name is derived from the German words *insel* (island) and *berg* (mountain) — stand out as "terrestrial islands" embedded in continental landscapes (Bornhardt 1900). Predominantly composed of granitic and/or gneissic rocks, inselbergs rise abruptly from the surrounding plains, especially in tropical and subtropical regions (Porembski and Barthlott 2000). They harbour unique plant communities that have evolved under extreme abiotic stressors, such as high solar radiation, shallow impermeable soils and pronounced water scarcity (Porembski et al. 1998; Bremer and Sander 2000).

These formations not only support distinctive evolutionary and ecological processes, but also foster unusual and often endemic lineages across diverse taxonomic groups (Porembski and Barthlott 2000; Porembski et al. 2021; Vanschoenwinkel et al. 2024). Inselbergs act as refugia for biota with both recent and ancient phylogenetic histories (Vanschoenwinkel et al. 2024) and are typically characterised by species assemblages that are rarely found in the surrounding matrix (Porembski 2007). Numerous studies from tropical and subtropical regions, ranging from Australia (Yates et al. 2019; Hopper et al. 2021) to Madagascar (Rabarimanarivo et al. 2019), West Africa (Parmentier et al. 2005), Brazil (Couto et al. 2017; de Paula et al. 2020) and French Guiana (Sarthou et al. 2017), have documented the remarkable botanical diversity of inselbergs. Despite this resilience, increasing human disturbances are now compounding threats to these ecosystems (Porembski et al. 2016).

For instance, human activities, such as road construction and agriculture, often introduce propagules from disturbed areas like roadside margins and pastures, further facilitating the establishment and spread of invasive organisms to inselbergs (Porembski 2000; Hopper 2002; Barbosa et al. 2010; Porembski et al. 2016). Once established, invasive species can outcompete native flora for scarce resources, alter essential ecological processes and complicate natural regeneration (Hopper 2009; de Paula et al. 2015). This vulnerability is critical given that many inselberg species exhibit slow growth, limited dispersal capacity and a high dependence on specialised microhabitats, conditions that are easily disrupted by prolonged droughts or altered disturbance regimes (Porembski 2007; Hopper 2009; de Paula et al. 2017; Vanschoenwinkel et al. 2024).

Conservation efforts for inselberg biodiversity face additional challenges due to a lack of comprehensive mapping and surveys, a shortfall that has exacerbated the rapid escalation of various threats worldwide (Porembski et al. 2016; Van-

schoenwinkel et al. 2024). The pressures on these unique outcrops are multifaceted, not only do invasive species pose a threat, but so do commercial quarrying, uncontrolled fires, unplanned urbanisation and unsustainable tourism (Porembski et al. 2016). Recreational activities, such as off-road driving, can eradicate slow-growing vegetation and disturb fragile, shallow soil patches, thereby increasing erosion (Couto et al. 2022). Furthermore, the degradation of the surrounding matrix can impair essential ecological interactions (e.g. those involving pollinators and seed dispersers like bats and hummingbirds), which are crucial for the maintenance of these ecosystems (Vanschoenwinkel et al. 2024). Such threats ultimately undermine the vital ecosystem services provided by inselbergs, for example, in certain regions, these formations serve as key water catchments, functioning as vital sources of freshwater for nearby human settlements (Lehmann et al. 2021).

Brazil, for instance, hosts one of the world's largest concentrations of inselbergs, predominantly distributed within the phytogeographic domains of the Atlantic Forest and Caatinga, both tropical forest ecosystems (Porembski 2007; de Paula et al. 2016, 2020; da Silveira et al. 2022; Azevedo et al. 2024). Yet, these domains have suffered long-term degradation due to pervasive human activities (Giulietti et al. 2004; Tabarelli et al. 2006; Vancine et al. 2024) and, over recent decades, such degradation has significantly transformed the landscapes, leading to the growing dominance of non-native species (Cardoso et al. 2004; Fabricante 2013; Vitule et al. 2021). Increasing evidence points to non-native species invasions as a mounting threat to the biodiversity of inselbergs in these domains (de Paula et al. 2015, 2020; Pereira et al. 2018; Pinto Junior et al. 2021). However, despite these alarming trends, there is currently no comprehensive inventory of invasive species affecting these rock outcrops and little is known about the ecological patterns that govern their establishment and spread (but see de Paula et al. 2015).

To address this knowledge gap, this study aims to: (1) compile the first comprehensive checklist of non-native plant species occurring in Atlantic Forest inselbergs (AFI) and Caatinga inselbergs (CAI) by synthesising data from public online databases and the literature, with a particular focus on identifying invasive species; (2) analyse domain-specific associations of non-native species; (3) evaluate whether specific life forms of non-native species are associated with a particular domain; and (4) propose future research directions and management strategies to mitigate the impact of non-native species in inselberg ecosystems. Ultimately, the conservation and management of inselberg vegetation demand urgent attention to preserve these unique natural laboratories and the critical ecosystem services they provide.

Material and methods

Notes on the conceptualisation of terms

In scientific literature, the term "inselberg" is well established as the designation for granite and/or gneiss outcrops (inselberg *sensu stricto*) (Porembski and Barthlott 2000). However, in ecological studies, the term is often used more broadly, encompassing ancient, isolated rock outcrops of various lithologies within the landscape (inselberg *sensu lato*) (Vanschoenwinkel et al. 2024). In this study, we considered only inselbergs *sensu stricto*.

For the definition of non-native species, we followed the framework established by Soto et al. (2024). We classified the species into two groups: non-native species, those transported beyond their natural biogeographic range; and invasive non-native species (hereafter, "invasive species"), which refer to established non-native species that have recently spread or are rapidly expanding within the invaded area, with or without human mediation.

Study area

The Atlantic Forest, along Brazil's eastern coast, is a global biodiversity hotspot (Myers et al. 2000), comprising heterogeneous forest ecosystems with diverse phytophysiognomies across tropical and subtropical climates (Oliveira-Filho and Fontes 2000). Within this domain, inselbergs occur in both lowland and highland regions (Azevedo et al. 2024). In the lowlands, they form the distinct "Sugarloaf Land" (de Paula et al. 2016, 2020), home to the iconic Sugarloaf Mountain, while in the highlands, they are known as "Campos de Altitude" (Safford 1999).

In contrast, the Caatinga is a dryland domain characterised by xerophytic vegetation, with short-statured trees and shrubs adapted to arid conditions (Prado 2003; Giulietti et al. 2004). It contains the largest fragment of Seasonally Dry Tropical Forests (SDTF) in the Neotropics, recognised for its high species richness and endemism (Pennington et al. 2000; Dryflor et al. 2016). Inselbergs are widespread across the Caatinga (Azevedo et al. 2024), where extensive "typical inselberg fields" are found (Ab'Sáber 2003).

Following Ab'Sáber (2003), we refer to the Atlantic Forest and the Caatinga as phytogeographic domains (hereafter, "domains"). This study includes non-native species from both Atlantic Forest highland and lowland inselbergs (AFI) and from Caatinga typical inselberg fields (CAI).

GBIF and SpeciesLink compilation

Occurrence records from herbaria collections within the Atlantic Forest and Caatinga domains were compiled using the databases of the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/pt/) and SpeciesLink (http://www.specieslink.net/). These records were georeferenced and filtered using domain shapefiles provided by the Instituto Brasileiro de Geografia e Estatística (IBGE; http://www.ibge.gov.br/geociencias/downloads-geociencias.html). To identify potential records from inselbergs, we further filtered the dataset by selecting entries that included specific keywords in the fields "locality", "occurrence remarks" or "field notes", such as "inselberg", "granito", "granítica", "granítico", "gneiss", "gnáissicos", "gnaisses", "inselbergue", "incelberg", "incelbergue", "pão de açúcar", "afloramento", "afloramentos", "lagedo", "lagedos", "lajedo" and "lajedos".

From this refined dataset, we generated a comprehensive list of species occurring on AFI and CAI. To determine their native or non-native status, we cross-referenced this list with the Flora e Funga do Brasil platform (under construction 2024), which categorises species as "Native", "Cultivated" or "Naturalised". For this study, we reclassified species listed as "Cultivated" and "Naturalised" as non-native. The analysis was performed using the FLORA package (Carvalho 2020; updated in January 2024) within the R software environment (R Core Team 2021). Records not identified to the species level and infraspecific taxa (e.g. subspecies, varieties)

were excluded or consolidated at the species level. Additional databases, including Plants of the World Online (https://powo.science.kew.org/) from Kew Gardens, World Flora Online (http://www.wfoplantlist.org/) and Tropicos (http://www.tropicos.org), were used for taxonomic verification and corrections.

Literature review

A comprehensive literature review was conducted to compile previously published floristic lists and taxonomic revisions relevant for the study regions. From the compiled list, the same procedure was applied to filter only the species classified as non-native. For this purpose, species identified as cultivated, naturalised or exotic in literature were uniformly categorised as non-native. Botanical nomenclature was verified and updated according to the taxonomic databases mentioned above. All procedures were carried out with the assistance of BRAHMS software (http://www.herbaria.plants.ox.ac.uk/bol) and Excel (Microsoft Office 365 2019).

Review of invasive species notifications

We compiled the non-native species coming from online herbaria collections and literature review, excluding duplicates. To determine whether the listed non-native species had previously been reported as invasive within the two analysed domains, a review of specific databases was conducted. In addition to the Flora e Funga do Brasil platform, the following sources were consulted: the list of invasive species in Brazil proposed by Zenni et al. (2024), the National Database of Invasive Exotic Species – Horus (http://www.institutohorus.org.br), the Global Register of Introduced and Invasive Species – Brazil (GRIIS; http://www.gbif.org/dataset/21cf83b3-fec6-4c42-95bc-b8555a991bc3#) and the list of invasive species in protected areas from ICMBio (http://www.gov.br/icmbio/pt-br/assuntos/biodiversidade/manejo-de-especies-exoticas-invasoras/listas-de-eei-em-ucs). It is important to highlight that GRIIS includes both introduced and invasive species in a single dataset, without distinguishing between these categories. In contrast, the Horus database, the list proposed by Zenni et al. (2024) and the ICMBio list consist exclusively of species recognised as invasive. Additionally, specific lists of non-native species relevant to the Atlantic Forest and Caatinga were consulted, including those by Cavalcante and Major (2006), Gonçalves et al. (2011), Fabricante (2013), Fabricante and Andrade (2014), Moro et al. (2012), Almeida et al. (2015), Araújo et al. (2017), Carmo et al. (2023) and Silva et al. (2023).

Classification of life forms, biomes and continents of origin

The life forms of non-native species found on AFI and CAI were classified using Raunkiaer's system (1934), which categorises plants, based on their responses to different climatic conditions, focusing on the position and protection of growth organs (buds and shoots) in relation to seasonal variations (Veloso et al. 1991). The species were grouped into the following life forms: phanerophytes, woody plants whose buds or tips of persistent branches are located in shoots projecting above the ground; chamaephytes, with vegetative buds close to the soil surface; hemicryptophytes, with buds at soil level and often protected by scales, leaves or sheaths; cryptophytes, with growth organs buried in

the soil, including geophytes, which have buds in subterranean structures; and therophytes, annual plants that complete their life cycle during favourable seasons, with seeds surviving unfavourable periods in the substrate (Raunkiaer 1934; Veloso et al. 1991). Life-form classifications were established, based on scientific articles with detailed species descriptions, complemented by data from Plants of the World Online database (2024).

Growth forms (herb, liana, shrub, tree) were categorised, based on the classification described for each species in the Flora e Funga do Brasil (2024). Additionally, the biomes (Wet Tropical Forest, Subtropical, Desert or Dry Shrubland, Temperate, SDTF) and the continents of origin of the non-native species (Africa, Asia, Europe, North America, South America, Oceania) were identified through the Plants of the World Online database (2024) or, when necessary, information from the literature (references in Suppl. material 1).

Analysis

To analyse domain-specific associations of non-native species, we employed a multi-step approach. First, to assess the association between individual non-native species and each domain (AFI and CAI), we applied Fisher's exact test using 2 × 2 contingency tables. The presence and absence of each species were cross-tabulated against the two domains and the resulting odds ratios (ORs) were used to interpret domain-specific associations. In our analysis, CAI was set as the reference group. Thus, OR values greater than 1 indicate that a species is more likely to occur in CAI compared to AFI, while OR values less than 1 suggest a stronger association with AFI. An OR equal to 0 implies that the species is completely absent from CAI and present only in AFI, whereas an infinite OR (Inf) denotes exclusive occurrence in CAI, with no records in AFI. These OR values were used to infer domain-specific ecological preferences amongst non-native species.

Next, to complement the association analysis, we used the IndVal method, which combines species frequency and specificity within each domain to identify ecological indicator species. Unlike Fisher's exact test, which only considers presence or absence between groups, IndVal detects species that occur in a consistent and preferential manner in a particular domain, even if they are not exclusive to it. This analysis was conducted using floristic data compiled from 58 CAI and 59 AFI, sourced from published literature and online herbaria collections (Suppl. material 2).

We also compared the overall composition of non-native species between CAI and AFI using PERMANOVA, implemented via the adonis function. Finally, to analyse the frequency of non-native species in each domain, we adapted the rank-abundance approach by converting presence-absence data into frequency, quantifying the number of inselbergs in which each species was present within each domain. From here on, we refer to this method as rank-frequency analysis.

To assess whether specific life forms of non-native species are associated with a particular domain, we applied Fisher's exact test (CAI was set as the reference group). This analysis allowed us to determine whether the distribution of life forms significantly differed between CAI and AFI. By evaluating the association between life forms and domains, we aimed to identify potential ecological patterns that may influence the establishment and spread of non-native species across inselbergs in these distinct environments.

Results

A total of 99 non-native species were recorded for AFI and CAI, including 95 angiosperms, two ferns, one lycophyte and one bryophyte (see Suppl. material 1). Amongst them, 33 species (33.33%) were classified as invasive, based on all the four analysed databases (Zenni et al. (2024), Horus, GRIIS and ICMBio), with 27 already recorded as invasive in Brazilian protected areas (ICMBio 2024) (Suppl. material 1). Of the invasive species identified on inselbergs in this study, 26 were listed as invasive in Brazil by both Zenni et al. (2024) and the Horus database — with complete overlap between the two sources for this subset. The remaining six species were not included in these lists, but were reported as invasive in the ICMBio survey of protected areas (*Bidens pilosa* L., *Cenchrus pedicellatus* (Trin.) Morrone, *Chloris gayana* Kunth, *Digitaria insularis* (L.) Fedde, *Oeceoclades maculata* (Lindl.) Lindl. and *Persea americana* Mill.). Examples of non-native species occurring on inselbergs are illustrated in Fig. 1.

Records of non-native plants compiled from both scientific literature and online databases across 118 inselbergs (comprising 58 inselbergs in the Atlantic Forest and 60 in the Caatinga) are presented in Fig. 2. The distribution

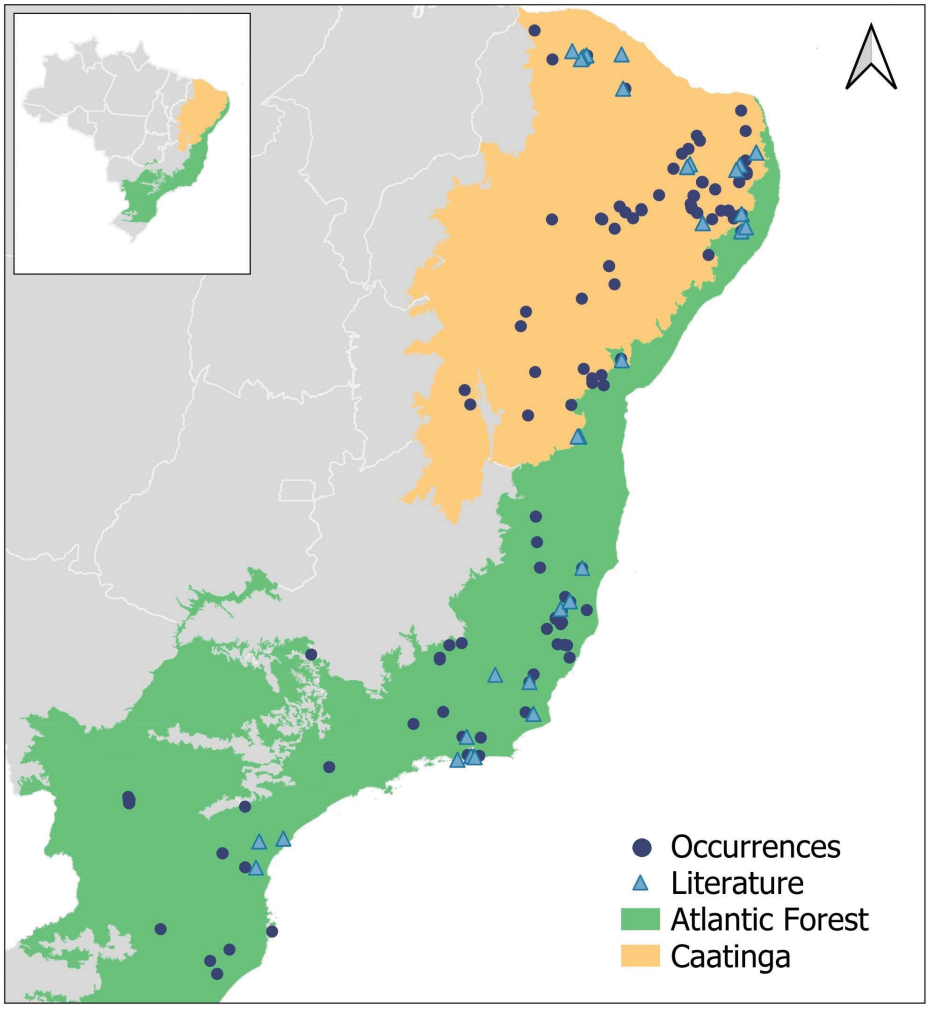

Figure 1. Records of non-native plants on inselbergs retrieved from scientific literature (blue triangles) and online databases (blue circles), covering two Brazilian phytogeographic domains: Atlantic Forest (green area) and Caatinga (orange area).

Figure 2. Non-native species occurring on inselbergs of the Brazilian Atlantic Forest: **A.** *Furcraea foetida* (L.) Haw. (Asparagaceae), primarily used as an ornamental plant; **B.** The non-native *F. foetida* (blue arrow) alongside the native *Alcantarea glaziouana* (Leme) J.R.Grant (Bromeliaceae) (red arrow), highlighting the functional convergence of the rosette form between native and non-native species; **C.** *Melinis repens* (Willd.) Zizka (**D**) (Poaceae), a widespread invasive on Brazilian inselbergs; **D.** *Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs (Poaceae), widely used as forage. Various non-native species on Arpoador inselberg in Rio de Janeiro City, an area known for its high tourist visitation: *Opuntia dillenii* (Ker Gawl.) Haw. (blue arrow) (Cactaceae), *Kalanchoe* sp. (yellow arrow) (Crassulaceae), *Agave* cf. *americana* (red arrow) and *F. foetida* (purple arrow) (**E**).

of non-native species showed distinct patterns: 45 species were found only in the AFI, 28 species were exclusive to the CAI and 26 occurred in both domains. In the AFI, 71 non-native plant species were found, including 67 angiosperms (from 38 families), two ferns (*Christella dentata* (Forssk.) Brownsey & Jermy and *Macrothelypteris torresiana* (Gaudich.) Ching), one lycophyte (*Lycopodiella caroliniana* (L.) Pic.Serm.) and one moss (*Campylopus introflexus* (Hedw.) Brid.). In

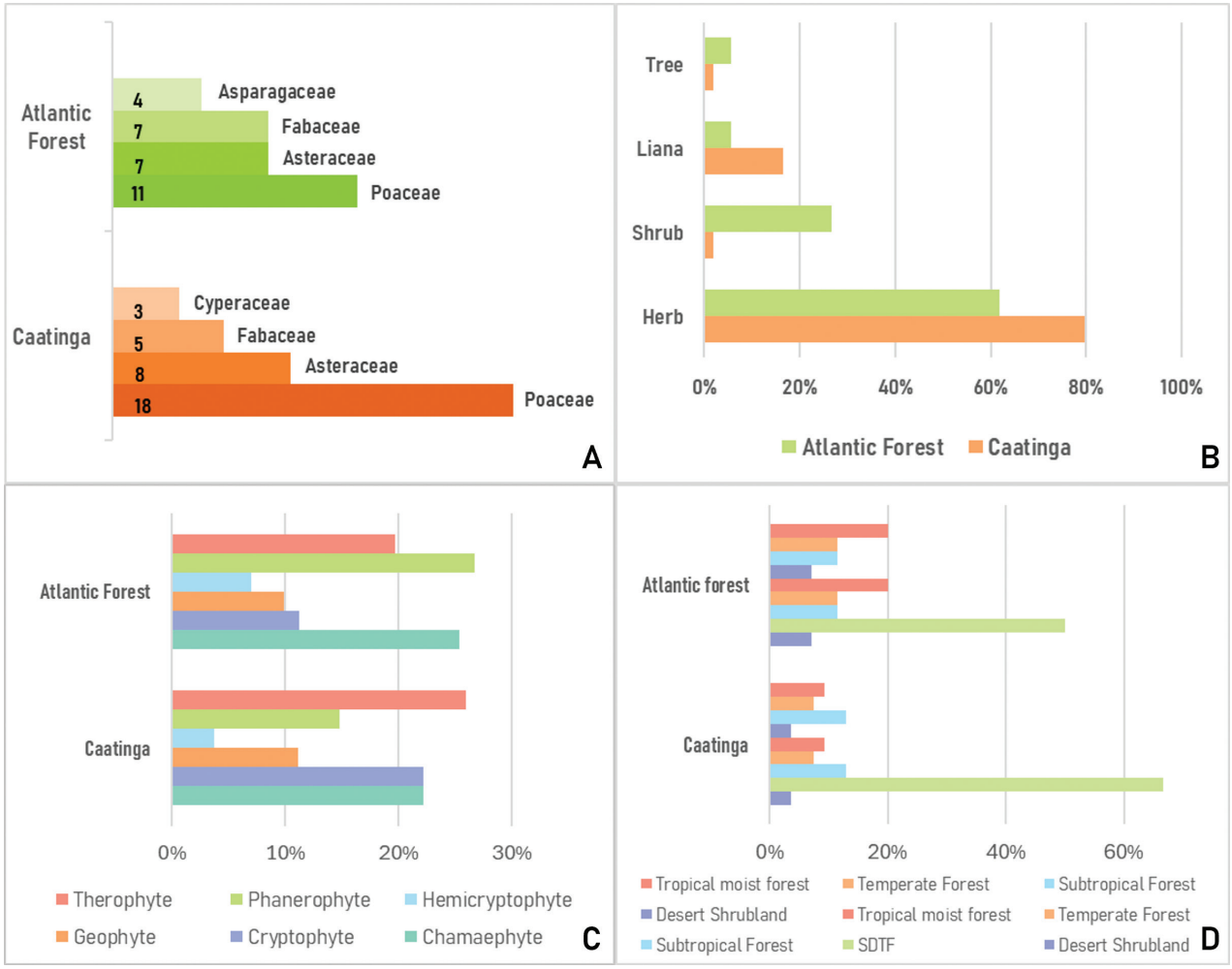

Figure 3. Non-native species on inselbergs of the Caatinga and Atlantic Forest phytogeographic domains in Brazil: **A.** Most representative families; **B.** Growth forms; **C.** Life forms; **D.** Biome of origin.

the AFI, dominant families included Poaceae (11 spp.), Asteraceae (seven spp.), Fabaceae (seven spp.) and Asparagaceae (four spp.) (Fig. 3A). In CAI, 54 species were distributed across 20 angiosperm families, with Poaceae (18 spp.), Asteraceae (eight spp.), Fabaceae (five spp.) and Cyperaceae (three spp.) being the most prominent. Although listed as a non-native species in the Flora e Funga do Brasil database and not classified as invasive by any of the consulted sources (GRISS; Horus, ICMBio; Zenni et al. 2024), the moss *C. introflexus* has already been recorded on inselbergs in the States of Paraná and Rio de Janeiro (GBIF IDs: 1931777436 and 1987023310). These records represent new regional occurrences and expand the known distribution of the species within Brazil.

Fisher's exact test revealed significant associations ($p < 0.05$) between five non-native species and the two domains, highlighting domain-specific ecological preferences. Although the recorded *Melinis* species were present in both domains, *Melinis minutiflora* ($p = 0.001$; OR = 0.07) was significantly associated with AFI, while *Melinis repens* ($p = 0.015$; OR = 3.16) was significantly associated with CAI. *Urochloa mollis* ($p = 0.01$; OR = Inf) and *Boerhavia diffusa* ($p = 0.03$; OR = Inf) were recorded exclusively in CAI, while *Desmodium incanum* ($p = 0.04$; OR = 0) was exclusive to AFI — all showing significant associations with the domain where they occurred. Complementing these results, the IndVal analysis

Figure 4. A. Indicator non-native species of the Atlantic Forest (green bar) and Caatinga (orange bar) phytogeographic domains in Brazil, identified by the Indicator Value Index (IndVal). The X-axis represents the values of the IndVal, which reflects the association of each species with a specific domain. The coloured bars represent species significantly associated ($p < 0.05$) with each domain, with p-values indicated inside the bars; **B.** Rank-frequency curves of non-native species recorded in the inselbergs of the Atlantic Forest and Caatinga. The X-axis represents the species rank, based on their frequency of occurrence, while the Y-axis indicates the number of inselbergs where each species was recorded. The points represent the species and the labels highlight the three most frequent species in each domain, along with their respective occurrence values.

also revealed domain-specific associations amongst non-native species. In AFI, only *M. minutiflora* was identified as a significant indicator species ($p = 0.012$). In CAI, three species were considered indicators: *M. repens* ($p = 0.009$), *U. mollis* ($p = 0.01$) and *Dactyloctenium aegyptium* ($p = 0.04$) (Fig. 4A).

The PERMANOVA analysis, which assessed differences in non-native species composition between the two domains, revealed a statistically significant difference ($F = 2.61$, $p = 0.002$; $R^2 = 0.022$). However, the low explanatory power (R^2) indicates that the domain alone accounts for only a small fraction of the variation. In addition, non-native species exhibited distinct frequency patterns

between AFI and CAI (Fig. 4B). In AFI, *M. minutiflora* was the most frequently recorded species, occurring in nine inselbergs, followed by *Lantana camara* L. (seven inselbergs) and *M. repens* (six inselbergs). In contrast, in CAI, *M. repens* had the highest frequency, being recorded in 17 inselbergs, while *L. camara* and *Bidens pilosa* L. were recorded in 10 and eight inselbergs, respectively.

Regarding life forms, we identified 24 species as phanerophytes, 21 as therophytes, 21 as chamaephytes, 12 as geophytes, 15 as cryptophytes and six as hemicryptophytes (Fig. 3C and Suppl. material 1). In the AFI, the most dominant life forms were phanerophytes (19 species; 26.76%) and chamaephytes (18 species; 25.35%), followed by therophytes (14 species; 19.72%), cryptophytes (8 species; 11.27%), geophytes (7 species; 9.86%) and hemicryptophytes (5 species; 7.04%). In contrast, in the CAI, therophytes (14 species; 25.93%) were predominant, followed by chamaephytes and cryptophytes (both with 12 species; 22.22%), phanerophytes (8 species; 14.81%), geophytes (6 species; 11.11%) and hemicryptophytes (2 species; 3.70%). Additionally, some species were recorded in both domains, in which chamaephytes (nine species) and therophytes (seven species) were the most representative life forms within this group. Fisher's exact test revealed that only chamaephytes ($p = 0.043$; OR = 0.54) were significantly associated with AFI, while therophytes ($p = 0.030$; OR = 1.93) showed a significant association with CAI.

With respect to the growth forms, most exhibited an herbaceous habit in both domains, accounting for 61.97% (44 species) in the AFI and 77.78% (42 species) in the CAI (Fig. 3B). In the AFI, shrubs also stood out (26.76%), followed by lianas (5.63%) and trees (5.63%) in lower proportions. In contrast, in the CAI, the pattern was more restricted, with a clear predominance of herbaceous species, while the other habits were poorly represented (nine lianas, one shrub and one tree).

Based on their biomes of origin, most non-native species originated from Seasonally Dry Tropical Forests, both in the AFI (35 species; 50%) and in the CAI (36 species; 66.67%) (Fig. 3D). In the AFI, other important sources included tropical moist forests (14 species; 20%) and subtropical or temperate forests (8 species each; 11.43%). In contrast, in the CAI, the contribution of moist environments was lower, with a notable presence of species from subtropical forests (7 species; 12.96%) and tropical moist forests (5 species; 9.26%), as well as a smaller representation of species originating from arid regions, such as desert shrublands.

Discussion

Non-native species on inselbergs

This study provides the first comprehensive checklist of non-native plant species, highlighting invasive taxa, specifically compiled for inselbergs in the Atlantic Forest and Caatinga, two biodiversity-rich domains with a high concentration of granitic outcrops (de Paula et al. 2020; da Silveira et al. 2022; Azevedo et al. 2024). This checklist offers a critical baseline for advancing ecological research and guiding targeted conservation strategies in these vulnerable and understudied ecosystems.

Despite the ecological significance of these isolated ancient granitic outcrops (Vanschoenwinkel et al. 2024), information on non-native species in inselbergs remains limited. Our literature review revealed only one publication focused on the non-native flora of AFI (Machado et al. 2020) and none addressing the CAI.

Most available studies either omit non-native species or explicitly limit their surveys to native flora. Such under-reporting is concerning, as the introduction and spread of non-native species can drive local extinctions and result in substantial ecological, economic and social impacts (Johnson et al. 2020). Given the ecological importance and vulnerability of inselbergs (de Paula et al. 2015; Vanschoenwinkel et al. 2024), identifying and assessing the invasive potential of non-native species should be considered a pressing conservation priority.

In this context, herbarium collections have traditionally played a key role in tracking the introduction and spread of non-native species (Crawford and Hoagland 2009). However, they also present a major limitation: non-native plants are often overlooked by botanists during fieldwork and rarely collected (Zenni and Ziller 2011; Moro et al. 2012). As a result, these species are under-represented in herbaria, creating gaps in distribution data and limiting our ability to reconstruct invasion histories or evaluate ecological impacts (Zenni and Ziller 2011).

Therefore, the list of non-native and invasive species compiled in this study must be interpreted considering these limitations. The absence of certain taxa may be attributed primarily to two factors: (1) the scarcity of detailed metadata in herbarium records, as many collections do not specify habitat information such as “inselberg”, thus complicating targeted searches; and (2) a persistent research bias favouring native species, which results in the systematic under-collection of non-native plants during floristic surveys and, consequently, their under-representation in herbarium records.

The recent update of the Brazilian invasive species list (Zenni et al. 2024) highlights the urgent need for targeted assessments of non-native species across diverse ecosystems. Most of the species we identified as invasive are also included in Zenni et al. (2024), with the exception of seven species that appear only in the ICMBio national database (ICMBio 2025). These discrepancies may stem from differences in the inclusion criteria, with the ICMBio list emphasising species of concern in protected areas or specific domains, whereas Zenni et al. (2024) adopts a broader ecological risk framework. They may also reflect lags in data integration across agencies, regional variability in species behaviour or gaps in documentation and expert validation. Ultimately, addressing these inconsistencies and knowledge gaps will require coordinated efforts to integrate herbarium data, field surveys and expert-driven assessments, while also overcoming historical biases that have minimised the importance of non-native species in botanical research. Expanding monitoring and collection efforts to include all components of the flora, regardless of origin, is an essential step towards understanding and mitigating the impacts of biological invasions in inselbergs and beyond.

The PERMANOVA analysis revealed a significant difference in the composition of non-native species between the two domains, although the domain itself explained only a small portion of the overall variation. This suggests that local factors, such as anthropogenic disturbance, microhabitat conditions and propagule pressure, may play a more prominent role in shaping invasion patterns on inselbergs (Porembski 2000; de Paula et al. 2015). Subsequent analyses supported domain-specific associations for a few species. *Melinis minutiflora* was consistently associated with the AFI, while *M. repens* and *U. mollis* showed stronger associations with the CAI, as indicated by both Fisher’s exact test and the IndVal analysis. The overlap of these results across methods highlights recurring patterns of domain affinity. Yet, the small number of significantly

associated species highlights the challenge of detecting clear biogeographic patterns amongst non-native taxa, many of which may exhibit broad ecological tolerances, low frequencies or early invasion stages (Williamson and Fitter 1996; Pyšek et al. 2020). Frequency analysis further supported these patterns, with *M. minutiflora* and *M. repens* emerging as the most widespread species in AFI and CAI, respectively. The shape of the rank-frequency curves also revealed contrasting structures: in CAI, a few species dominate broadly, suggesting potential vulnerability to aggressive invaders, whereas in AFI, species frequencies are more evenly distributed, indicating a more diverse, but less dominated non-native flora. Altogether, these findings suggest that, while domain-specific environmental filters do influence some non-native species distributions (de Paula et al. 2015; Machado et al. 2020), invasion patterns in inselbergs are also shaped by more localised, complex and species-specific dynamics (Vanschoenwinkel et al. 2024).

Although only a few species exhibited statistically significant associations with a specific domain, several taxa occurred consistently across multiple sites, indicating successful establishment and suggesting the potential for broad ecological influence. Many of these species possess traits commonly associated with invasiveness — such as clonal reproduction, high drought tolerance and widespread use in ornamental horticulture — and have well-documented invasion histories in other ecosystems. In the sections below, we highlight some of the most frequently recorded non-native species and additional taxa that, while less common in our dataset, are recognised as invasive on inselbergs in other tropical and subtropical regions. Together, these examples help illuminate the ecological strategies, potential introduction pathways and broader conservation concerns associated with non-native plant establishment on inselbergs.

Notably, the African grass *M. repens* emerged as one of the most frequently recorded species across both domains. This species has been documented as an invader of inselbergs in south-eastern Brazil (Porembski et al. 1998; de Paula et al. 2015, 2017), where it colonises ephemeral vegetation and shallow depressions, microhabitats with comparatively higher resource availability (de Paula et al. 2015). In contrast, it is typically absent from more extreme microhabitats, such as epilithic vegetation and monocot mats, reinforcing the idea that invasibility in inselbergs is strongly mediated by fine-scale habitat heterogeneity (de Paula et al. 2015). Similarly, *M. minutiflora*, another African grass significantly associated with AFI, is notorious for its impact in Cerrado ecosystems, where it alters fire regimes, increases fine fuel loads and promotes positive feedbacks that facilitate its persistence, while displacing native herbaceous flora (Rossi et al. 2014). Its occurrence on inselbergs, ecosystems already prone to intense drought and poor soils (Vanschoenwinkel et al. 2024), raises concerns that similar dynamics may be developing in rock outcrops, especially in microhabitats where flammable biomass can accumulate.

Amongst shrub species, *Lantana camara* was the second most frequently recorded non-native across both phytogeographic domains. Although it is native to tropical America and widely distributed in Brazil (Sinha and Sharma 1984; Cardoso et al. 2018), *L. camara* is listed as introduced in both the Flora do Brasil database and GRISS, which was considered in its inclusion in this study. Globally recognised as one of the most problematic invasive species, *L. camara* is known for its broad environmental tolerance, allelopathic effects and the formation of dense thickets that suppress native vegetation and alter disturbance

regimes, including fire (Shackleton et al. 2017; Alemayehu et al. 2024). Its ornamental use and repeated escape from cultivation likely contribute to its frequent detection on inselbergs worldwide (e.g. Hopper 2002; Araújo et al. 2017).

Although *Furcraea foetida* (L.) Haw. was not amongst the most frequently recorded species in our sampling, its occurrence in both CAI and AFI (e.g. Meirelles et al. 1999; Cordeiro et al. 2018; Machado et al. 2020), as well as on inselbergs in other parts of the world, is noteworthy. Widely cultivated for ornamental use and fibre production, *F. foetida* has escaped cultivation and established naturalised populations in a variety of environments. It is considered invasive in several regions, including coastal ecosystems in Brazil (Barbosa et al. 2017), as well as inselbergs in South Africa (Crouch and Smith 2011) and other regions of tropical Africa (Biedinger et al. 2000). Its invasive potential is mainly attributed to vegetative reproduction via bulbils, high drought tolerance and human-mediated dispersal through landscaping and informal plantings in peri-urban areas (Barbosa et al. 2017).

The presence of *F. foetida* and other ornamental succulents with traits that promote invasiveness in arid and rocky environments, such as drought tolerance, clonal propagation via foliar plantlets and efficient dispersal, like species of the genus *Kalanchoe* (Smith et al. 2022), on inselbergs near tourist hubs (e.g. the metropolitan region of Rio de Janeiro; Meirelles et al. 1999), as shown in Fig. 1, points to a recurring invasion pattern shaped by life-history traits and human-mediated introductions. This highlights the need for systematic monitoring of ornamental escapes, especially in urban landscapes bordering rocky outcrops and within or adjacent to protected areas, where early detection and targeted management are essential to preventing further spread.

Remarkably, the moss *Campylopus introflexus* (Hedw.) Brid. recorded in AFI, although often overlooked due to its diminutive size, is recognised as a highly invasive species in Europe (Honrado et al. 2008). It is typically associated with anthropogenically disturbed environments, where it readily colonises open, moist soils, especially in degraded forest communities subjected to fires, trampling or trail formation (Honrado et al. 2008). Its ability to spread rapidly and form dense mats allows it to outcompete native bryophytes, thereby altering community composition and ecosystem processes. Although this species is not listed as invasive in the consulted databases, its occurrence on Brazilian inselbergs and its invasive status on rock outcrops in other regions highlight that even inconspicuous taxa like mosses can pose substantial ecological risks to the fragile inselberg systems.

Biomes and continents of origin

Our results indicate that SDTF is the primary source biome for non-native species established on inselbergs. The prominence of SDTF species in both domains likely reflects ecological similarities between these source habitats (Dryflor et al. 2016) and inselbergs (Porembski 2007), namely, high solar radiation, shallow soils and strong seasonality. Malcicka et al. (2015) state that ecological compatibility, rather than shared evolutionary history, may better explain the success of biological invasions, especially when the invaded habitats offer conditions like those in the species' native range.

A significant proportion of the non-native species originated from Africa and Asia, reflecting the historical introduction of economically and ornamentally valuable plants brought to Brazil through Portuguese colonial networks (Zenni 2014).

Such botanical transfers were a crucial component of the "conquest of cultures", in which colonial powers deliberately selected and disseminated specific cultural elements to sustain and exert control over colonial societies (Dean 2001). While many of these introductions were facilitated by colonial routes, it is likely that other species arrived through alternative pathways (Zenni 2014; Pyšek et al. 2020). It is remarkable that the biogeographic origin of non-native species revealed contrasting patterns between domains. While Asia and Africa were the main continental sources overall, Asian species were more prevalent in the AFI, whereas African species dominated in the CAI. This contrast may be linked to historical plant introductions associated with agricultural and ornamental uses, particularly from regions with climatic regimes similar to those of the recipient domains. For instance, many African species introduced into north-eastern Brazil are associated with forage, erosion control or ornamental purposes and may find conditions in the Caatinga more similar to their native ranges, such as *Cenchrus ciliaris* (Alves et al. 2018) and *Dactyloctenium aegyptium* (Alves and Fabricante 2019; Carvalho et al. 2022). Likewise, the dominance of Asian species in the AFI may reflect introductions from tropical Asia for medicinal, ornamental or silvicultural purposes, aligning with the domain's wetter and more stable conditions, such as *Alpinia zerumbet* (Tribess et al. 2015) and *Artocarpus heterophyllus* (Abreu and Rodrigues 2010).

Together, these findings suggest that both ecological pre-adaptation to rocky environments and biogeographic-historical factors (such as source pool composition and introduction pathways) contribute to shaping the current assemblage of non-native species on inselbergs across Brazil's biogeographic domains.

Life forms

Therophytes were significantly associated with CA inselbergs and chamaephytes with AF inselbergs, reinforcing that certain life forms amongst non-native species exhibit domain-specific affinities, likely reflecting adaptations to contrasting environmental conditions. While other life forms showed no significant association, their frequency patterns remain ecologically meaningful.

The life-form spectra of non-native species in both CAI and AFI closely mirror patterns observed in native rock outcrop floras in these domains. In CAI, non-native therophytes dominate, followed by chamaephytes and cryptophytes, similar to native inselberg flora where therophytes are consistently prevalent (Araújo et al. 2008; Pereira et al. 2018). In AFI, non-native phanerophytes are the most common, followed by chamaephytes, reflecting native flora compositions (de Paula et al. 2017; Pena and Alves-Araújo 2017; Pinto Junior et al. 2020).

These parallels suggest that environmental filtering, favouring traits adapted to local conditions, influences both native and non-native floras (Carlucci et al. 2014; de Paula et al. 2015, 2020; Neri et al. 2017). In the arid CAI, annuals like therophytes are favoured by extreme seasonality, shallow soils and high irradiance (Araújo et al. 2008). In contrast, AFI's more humid and stable conditions promote perennial forms such as woody phanerophytes and chamaephytes (de Paula et al. 2017).

Despite these overarching similarities, our data point to potential deviations in life-form representation between native and non-native species, particularly with the increased prominence of certain life forms in the non-native flora. For example, cryptophytes were more frequent amongst non-native species in the CAI than previously recorded for native species, where they were either rare

or absent (Araújo et al. 2008; Pereira et al. 2018). This may reflect the greater ruderal capacity of some non-native cryptophytes, which possess underground storage organs allowing rapid regeneration after disturbance — traits that may be advantageous in inselberg microhabitats prone to episodic environmental stress or anthropogenic disturbance. Likewise, in the AFI, therophytes ranked third amongst non-native life forms, while they are amongst the least represented in the native flora (Meirelles et al. 1999; de Paula et al. 2017; Pena and Alves-Araújo 2017). This suggests that some non-native annuals may capitalise on disturbed microsites or marginal zones within the AFI, where competition from dominant native phanerophytes is reduced. In both domains, these subtle shifts may indicate that, within the broader framework of environmental filtering, ruderal strategies, particularly traits linked to colonisation and disturbance tolerance, play a significant role in shaping the composition of non-native floras.

Future research topics

Our checklist of non-native species on Brazilian inselbergs provides a foundation for conservation management and future studies. By identifying the distribution of non-native taxa across biogeographic domains, it supports the detection of invasion hotspots, the selection of priority species for monitoring and control and the development of early detection strategies, especially in protected areas and near urban centres. Future research could address non-native species interactions with native communities (e.g. Gillerot et al. 2021), assess invasion potential under changing land use and climate (e.g. Bradley et al. 2010) and examine how landscape features affect invasion dynamics. This integrated approach can provide information for policy, guide the sustainable use of ornamentals and strengthen biosecurity in these unique ecosystems.

While connectivity can benefit native biodiversity, it may also facilitate the entry of invasive species, which is particularly concerning in inselbergs (Hopper et al. 2009, 2016). Natural and anthropogenic corridors, such as trails and roads, can promote the movement of non-native propagules into inselbergs, while also enabling inselberg-adapted species to colonise disturbed habitats in the surrounding matrix, where they may become invasive weeds (Porembski 2000; Proches et al. 2005). Future studies should assess how dispersal mode, landscape configuration and disturbance influence these dynamics, guiding connectivity management to reduce invasion risks.

Another key priority is understanding the genetic and phylogeographic consequences of invasions in insular systems. Inselberg plant populations often show high local genetic diversity and strong differentiation amongst outcrops (Barbará et al. 2007; Palma-Silva et al. 2011; Hmeljevski et al. 2015, 2017; Nazareno et al. 2020), reflected in high beta diversity (Sarthou et al. 2017; de Paula et al. 2020; Yates et al. 2019; Pinto Junior et al. 2023). Generalist invaders may drive biotic homogenisation (McKinney and Lockwood 1999), threatening endemism and evolutionary legacies. Assessing the extent to which invasions erode genetic and floristic uniqueness across spatial scales is essential, particularly in the context of inselbergs.

Investigating the functional traits associated with invasion success in resource-limited environments is also crucial. Inselbergs are marked by shallow soils and seasonal drought (Vanschoenwinkel et al. 2024), yet some invasive

species thrive there. Traits such as rapid growth, short life cycles and efficient resource acquisition are commonly associated with invasive success in harsh conditions (Grime 2001; Drenovsky et al. 2012; Reich 2014). For instance, *M. repens* exemplifies how ruderal traits facilitate colonisation in microhabitats with greater resource availability (de Paula et al. 2015). Trait-based approaches can be used to compare the functional strategies of invasive and native species, helping to identify inselberg microhabitats that are especially susceptible to colonisation at broader spatial scales.

Finally, our dataset offers a starting point for developing invasion risk assessment frameworks specific to rocky outcrop ecosystems. These tools could help environmental managers and policy-makers to prioritise species and areas for monitoring and restoration. Linking functional traits to invasion patterns in inselbergs, as well as integrating biogeographic and phylogenetic information, will be crucial for anticipating and mitigating the spread of invasive species in these fragile environments (Daehler 2003; Funk 2013; Seabloom et al. 2015). Such efforts should also emphasise the restoration of vulnerable microhabitats and the maintenance of healthy surrounding matrix vegetation to increase ecosystem resilience and long-term conservation effectiveness.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Use of AI

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

List of non-native plant species recorded on inselbergs in the Atlantic Forest and Caatinga of Brazil

Authors: Fernanda G. L. Moreira, Fernanda A. Carvalho, Luiza F. A. de Paula

Data type: xlsx

Explanation note: List of non-native plant species recorded on inselbergs in the Atlantic Forest and Caatinga of Brazil. The table provides detailed information on each species, including the phytogeographic domain of occurrence, botanical family (according to POWO), data source (literature, GBIF, Reflora, or SpeciesLink), scientific name, presence in lists of introduced or invasive species (GRISS, Zenni et al. 2024, ICMBio, and Horus), as well as specific references for each record. Additional data include the continent and biome of origin, growth form, Raunkiaer life form, and the sources used for this classification.

Link: https://doi.org/10.3897/neotropical.20.e156777.suppl1

Supplementary material 2

List of non-native species occurrences in inselbergs of the Brazilian Atlantic Forest and Caatinga domains

Authors: Fernanda G. L. Moreira, Fernanda A. Carvalho, Luiza F. A. de Paula

Data type: xlsx

Explanation note: List of non-native species occurrences in inselbergs of the Atlantic Forest and Caatinga domains in Brazil, based on online herbarium records and published literature. The table includes information such as the domain and name of the inselberg, botanical family, scientific name of the species, life form according to Raunkiaer, specimen data (herbarium code, catalog number, and record number), collector, locality, state, municipality, geographic coordinates, elevation (when available), source of the record, and GBIF ID.

Link: https://doi.org/10.3897/neotropical.20.e156777.suppl2