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Review

Review

Biogeography and evolution of the vertebrate fauna in *campo rupestre*, a megadiverse Neotropical montane open ecosystem

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ABSTRACT

Mountains are hotspots of biodiversity and endemism, but biogeography and diversification in tropical montane grasslands remain poorly understood. We reviewed hypotheses explaining the origin of vertebrate fauna ranging from phylogeography to community-scale patterns, while also considering historical biogeography and macroevolutionary dynamics in *campo rupestre* in the Espinhaço Range. We conducted a systematic review of papers published in 1945–2023 on vertebrate ecology, biogeography, and diversification in *campo rupestre*. The vertebrate fauna of *campo rupestre* is characterized by high levels of biodiversity and endemism relative to area extent across most taxa. Unfortunately, such diversity is increasingly threatened, with ~20% of endemic species listed on the IUCN Red List. Hummingbirds are key pollinators, whereas seed dispersal

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is performed primarily by generalist birds, small mammals, and lizards. A combination of isolation, range shifts, and species persistence played key roles in shaping diversification dynamics in these ancient mountains. High levels of diversity, endemism, and the occurrence of threatened species underscore the pressing need for funding conservation of the outstanding biodiversity in the Espinhaço Range. We propose a research agenda to fill knowledge gaps and promote research needed to provide a more complete understanding of the biogeographical scenario and accelerate protection strategies.

Keywords: Central Brazilian Plateau; Espinhaço Range; Serra da Canastra; tropical mountains; fishes; amphibians; reptiles; birds; mammals

INTRODUCTION

Mountains compress climates and vegetation types into relatively short-distance gradients, providing unique habitats and opportunities for evolution, adaptation, and provision of ecosystem services (Immerzeel *et al.* 2020, Perrigo *et al.* 2020). Although covering only 13%–25% of land surface, mountains host more species richness and endemic species than any other terrestrial ecosystem (Rahbek *et al.* 2019). They are megadiverse considering their restricted area, low productivity levels, and often relatively young geological age compared to surrounding lowlands, challenging well-known ecological paradigms that predict species richness to increase positively with area, geological age, and energy (Tenorio *et al.* 2023). Geodiversity frequently shapes endemism and species trait diversity and determines, to a large extent, opportunities for dispersal over time (Azevedo *et al.* 2020a, Guedes *et al.* 2020). The dynamics of mountain biodiversity are susceptible to rapid changes in climate, with the current climate crisis representing a major threat to these ecosystems.

Although there is a growing interest in mountain ecology and biogeography, most studies are focused on young mountains, alpine, and forest montane biota. As a result, there is little integrative understanding of taxa origin, diversification, biogeography, and ecology in ancient, snow-free, tropical montane open ecosystems, despite their highly diverse, endemic, and endangered biota (Guedes *et al.* 2020). Available syntheses focus on plants (Silveira *et al.* 2016, Colli-Silva *et al.* 2019, Vasconcelos *et al.* 2020, Barros-Souza and Borges 2023), but similar efforts for vertebrates are limited both taxonomically and geographically (but see Oswald *et al.* 2024). Here, we focus on the vertebrate fauna of *campo rupestre*, a megadiverse, tropical montane, grassy–shrubby, fire-prone vegetation mosaic established on extremely nutrient-impoverished quartzite, sandstone, or ironstone outcrops along with white sands, stony soils, and peatlands (Miola *et al.* 2021; Fig. 1; Supporting Information, Figs S1, S2).

The *campo rupestre* physiognomy is highly heterogeneous, dominated by open grasslands and shrublands, but also with natural patches of shrubby savanna and forest islands scattered throughout the landscape. Like other mountaintop ecosystems, *campo rupestre* comprises naturally fragmented montane open-canopy patches (sky islands; McCormack *et al.* 2009, Flantua *et al.* 2020, Love *et al.* 2023) immersed in a lowland matrix of forests or savannas. The *campo rupestre* occurs mostly as large, naturally fragmented blocks along the Espinhaço Range in eastern Brazil, but also as isolated sky islands in central Brazil, southeastern Amazonia, in the iconic Tepuis in the Guiana Shield, among others (Rull *et al.* 2019, Guedes *et al.* 2020, Miola *et al.* 2021).

We conducted a systematic review of papers published in the Web of Science, Scopus, and Scielo from 1945–2023 on *campo rupestre* vertebrates (Supporting Information, Figs S1, S2) to provide a synthesis of knowledge about current hypotheses explaining diversity patterns, focusing on the Espinhaço Range, the most studied *campo rupestre* region, for which more data are available. We reviewed specific predictions that can be used to test contrasting hypotheses at the population and species levels, while also considering historical biogeography, trait-based diversification, and macroevolutionary dynamics. We also reviewed the ecology of vertebrate–plant interactions and provided suggestions of future research to fill knowledge gaps identified here.

BIOGEOGRAPHICAL PATTERNS

Vertebrate diversity, endemism, and conservation

Campo rupestre corresponds to <1% of Brazilian territory but harbours >15% of the plant diversity in the country, of which >40% are endemic (Miola *et al.* 2021). Early attempts to quantify diversity and endemism in *campo rupestre* arrived at 25% bird and mammal, 14% amphibian, and 8% freshwater fish diversity in Brazil (Alves *et al.* 2008, Leite *et al.* 2008, Lessa *et al.* 2008, Vasconcelos *et al.* 2008). However, these numbers are underestimated given that some groups are poorly known and that many vertebrate species continue to be described (Fernandes *et al.* 2018).

The central Brazilian and Guiana shields harbour relatively few species of fish, probably attributable to high extinction rates during the Neogene and Quaternary periods (Albert *et al.* 2020), but contain numerous ancient, endemic lineages (Ribeiro 2006). At the Espinhaço Range, fish diversity encompasses 49 species (ICMBio 2024) in 26 genera and nine families. Endemic genera include *Copionodon* (four species) and *Glaphyropoma* (one species; Table 1). Both genera belong to Copionodontinae, which, along with Trichogeninae, is sister to all remaining lineages of the widespread Trichomycteridae (Datovo and Bockmann 2010, Ochoa *et al.* 2020). Trichomycteridae and Loricariidae are the most diverse fish families in the *campo rupestre*, with 15 species each.

The diversity of anuran amphibians at the Espinhaço Range corresponds to ~9% of all Brazilian species (Leite *et al.* 2008, Segalla *et al.* 2021; Table 1). However, these numbers are underestimates, because new endemic species are being reported continuously. Recent inventories at the Espinhaço Range, Central Plateau, Veadeiros Plateau, and Serra da Serra da Canastra (Azevedo *et al.* 2016, Oswald *et al.* 2024) identified ≥50 endemic anurans in 18 genera and seven families. The high richness of anurans endemic to the *campo rupestre* compared with other vertebrates (Table 1; Supporting Information, Table S1) might be related to the limited dispersal ability of most species (Smith and Green 2005), which is more accentuated in mountaintops. Most *campo rupestre* endemics occur in the Espinhaço Range, the core geographical locality of *campo rupestre* (Fig. 1). The Hylidae tribes Cophomantini (12 species) and Scinaxini (eight

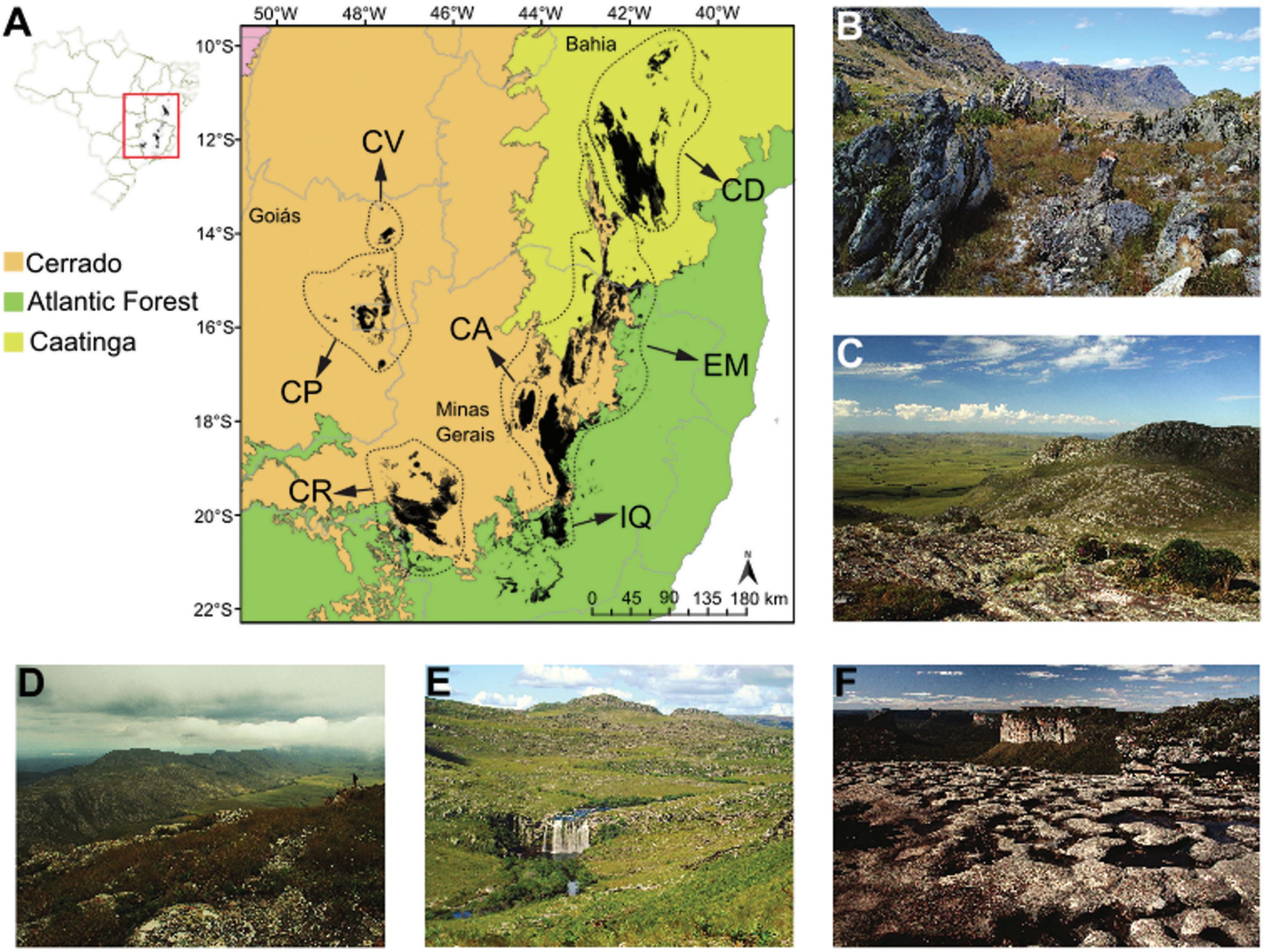


Figure 1. Geographic distribution of the core areas of *campo rupestre* (depicted in black) showing the highlands of the Espinhaço Range in Bahia and Minas Gerais states at the ecotone of the Cerrado to the west (orange), Atlantic Forest to the east (green) and the Caatinga to the north (yellow). Common landscapes on mountaintops at the Espinhaço Range, including *campo rupestre* grasslands with rocky outcrops, natural forest islands, grasslands, and small rivers. CD–Chapada Diamantina, CA–Cabral Range, CP–Central Plateau, CV–Veadeiros Range, CR–Canastra Range, EM–Espinhaço Mineiro, IQ–Iron Quadrangle. Together, CD, CA, EM, and IQ form the Espinhaço Range. Maps are shown in EPSG 4326; source of the layers follow Silveira *et al.* (2016). Photo Credits: B- Tadeu Guerra; C and D- Guilherme Freitas; E- Tadeu Guerra; F- Guilherme Freitas.

Table 1. Diversity, endemism, and conservation status for vertebrates in the *campo rupestre*.

	Total species [*N* (%)]	Endemic species [*N* (%)]	Endemic Threatened species (*N*)	Threatened species (*N*)
Fishes	49 (1.3)	16 (32.6)	2	3
Amphibians (Anura)	105 (9)	~50 (48)	13	6
Reptiles	242 (28.3)	21 (8.7)	3	15
Birds	220 (11.1)	7 (3.1)	2	16
Mammals (Rodentia)	52 (19.5)	2 (3.8)	1	2
Mammals (Chiroptera)	43 (23.4)	1 (2.3)	0	1

species) have the highest levels of endemism. Finally, *Rupirana* is the only genus endemic to *campo rupestre* (Santos *et al.* 2020, but see Mângia *et al.* 2025).

For reptiles, distribution data (Azevedo *et al.* 2016, Colli *et al.* 2016, Nogueira *et al.* 2019, Uchôa *et al.* 2022) indicate a total of 242 species in 94 genera and 22 families for *campo rupestre*, the highest richness and percentage of Brazilian species among vertebrates assessed here (Supporting Information, Table S1; Guedes *et al.* 2023). Most Squamata species are in Dipsadidae (114 species) and Gymnophthalmidae (19 species), respectively, the most species-rich families of snakes and lizards in Brazil. Testudines are represented only by *Hydromedusa maximiliani*

(Chelidae), and no crocodilians are native to *campo rupestre*. Endemics to the *campo rupestre* include 16 lizards, three snakes, and two worm lizards (Amphisbaenidae) (Guedes *et al.* 2023). No reptile genus is endemic to the *campo rupestre*. The main regions with high reptile endemism are the Chapada Diamantina and the Espinhaço Mineiro. For snakes, areas containing high levels of phylogenetic endemism were identified scattered along a few mountaintops of central Brazil, some of them coinciding with Espinhaço Range limits, corroborated by some species that also occur (restricted) in *campo rupestre* (Azevedo *et al.* 2020b).

A bird checklist of 205 species (~10% of Brazilian birds) occurring in *campo rupestre* of the Espinhaço Range (Vasconcelos and Rodrigues 2010) has been updated with new records published over the last decade (D. Hoffmann and M. F. Vasconcelos, unpublished work). The revised checklist includes 220 species across 42 families and 18 avian orders (Table 1). The main species-rich families are Thraupidae (31 species) and Trochilidae (23 species). As for other vertebrates, *campo rupestre* sites outside the Espinhaço lack comprehensive ornithological surveys. However, notable records include the mountaintop endemic *Polystictus superciliaris* (Tyrannidae) in the Serra da Canastra (Vasconcelos *et al.* 2003) and *Embernagra longicauda* (Thraupidae) in an isolated *campo rupestre* area within the Rio Doce basin (Lopes *et al.* 2016). Currently, seven endemic species are reported, all restricted to the Espinhaço Range. *Augastes* (Throchilidae, two species) is the only bird genus endemic to the *campo rupestre* (Chaves *et al.* 2014, 2020).

Most mammal surveys in the Espinhaço Range lack specific sampling site details, but available data suggest that *campo rupestre* mammal fauna is similar to the surrounding lowland Cerrado fauna (Andrade *et al.* 2017). A total of 115 species of small mammals are recorded in the *campo rupestre,* including 20 marsupials, 43 bats, and 52 rodents, with one bat and two rodents restricted to the Espinhaço Range (Table 1; Abreu *et al.* 2023, Norões *et al.* 2023). The only genus endemic to the *campo rupestre* is the monospecific *Calassomys* (*Calassomys apicalis*; Supporting Information, Table S1) (Pardiñas *et al.* 2014). Medium-to-large mammals include widespread herbivores, such as the genus *Mazama* (Cervidae), *Dicotyles* (Tayassuidae), and *Tapirus* (Tapiridae), whereas examples of carnivores include common species such as *Leopardus wiedii*, *Puma concolor*, and *Chrysocyon brachyurus* (Lessa *et al.* 2008).

Because of high endemism and increasing threats posed by mining, silviculture, intensive agriculture, ongoing urbanization, and climate change, many *campo rupestre* vertebrates, particularly endemics, are now threatened (Table 1; Supporting Information, Tables S1 and S2). Because *campo rupestre* occurs as naturally fragmented areas, it is relatively resilient to habitat fragmentation. Among endemic vertebrates, approximately one-fifth are included on the International Union for Conservation of Nature (IUCN) Red List, i.e approximately 13% of fishes, 26% of amphibians, 14% of reptiles, 29% of birds, and 33% of mammals (IUCN 2023; Supporting Information, Table S1). Unfortunately, many endemics, mainly fish (~44%), lack assessments of conservation status (IUCN 2023). Although downgrading, downsizing, or degazettement of protected areas are not particularly concerning in *campo rupestre* (Bernard *et al.* 2014), current protected area networks are insufficient to protect its megadiversity (Silveira *et al.* 2016).

Sky islands and barriers

Most available phylogeographical studies show that structuring patterns of sky islands (Love *et al.* 2023) in anurans (Nascimento *et al.* 2018) imply the existence of several barriers acting as filters among mountaintops. The lowlands between the Espinhaço Mineiro and Chapada Diamantina are the major barrier (Leite *et al.* 2008), consistent with plant biogeography (Colli-Silva *et al.* 2019). Endemic species composition in Chapada Diamantina is unique, with 13 exclusive species, including the endemic frog genus *Rupirana*. Only four anuran species occur in both northern and southern portions of the Espinhaço Range (Oswald *et al.* 2024), indicating that the mountain range is a strong filter for amphibians. The Couto de Magalhães depression between Diamantina plateau and Grão Mogol at the core Espinhaço Mineiro is recognized as a phylogeographical break for at least five frog species (Oswald *et al.* 2022). Moreover, the anurofauna at Serra do Cabral is characterized by the absence of widespread species from the core Espinhaço, the presence of restricted endemics, and a deeply differentiated lineage of *Bokermannohyla saxicola* (Oswald *et al.* 2022, 2024). This suggests another putative barrier between Serra do Cabral and the Espinhaço Mineiro. For anurans and squamates, Azevedo *et al.* (2016) identified 13 areas of endemism in the Cerrado, with at least four areas coinciding within *campo rupestre* (Central Plateau, Espinhaço Mineiro, Chapada dos Veadeiros Plateau, and Serra da Canastra), with the Espinhaço ranking first in endemism. Neotropical amphibians from lowlands exhibit higher phylogeographical diffusion rates in comparison to endemic species from *campo rupestre* (Magalhães *et al.* 2024). These reduced rates also account for the island-like genetic structure in *campo rupestre* anurans.

For birds, 26 lowland regions have been identified as potential barriers to dispersal in eastern Brazil highlands (Chaves *et al.* 2014). Those barriers are between Chapada Diamantina and Espinhaço Mineiro and between other mountain systems (e.g. Canastra, Mantiqueira, and Serra do Mar ranges). Similar to patterns observed for anurans, the main barrier that probably promotes bird speciation along the Espinhaço Range is represented by areas covered by Cerrado and Caatinga vegetation in southern Bahia (Vasconcelos *et al.* 2012, Chaves *et al.* 2014). Based on the distribution of endemic *campo rupestre* birds, two centres of endemism along the Espinhaço Range have been proposed: the south-central portion (including northernmost Minas Gerais) and the Northern portion (Chapada Diamantina and adjacent mountains; Vasconcelos 2008). Considering the description of a new species (Freitas *et al.* 2012), range extension of *Augastes scutatus* (Vasconcelos *et al.* 2012), and the split of another hummingbird species previously treated as a subspecies (Lopes *et al.* 2017), the south-central portion extends into southern Bahia, comprising the following species: *Campylopterus diamantinensis*, *Augastes scutatus*, *Cinclodes espinhacensis*, and *Asthenes luizae*. The northern area is delimited by the ranges of *Augastes lumachella* and *Formicivora grantsaui* (Vasconcelos 2008, Chaves *et al.* 2014). This division is consistent with studies on the flora (Colli-Silva *et al.* 2019) and amphibians (see above).

As stated above, the recognition of areas of endemism for amphibians and birds, the presence of endemic genera (e.g. *Rupirana* and *Augastes*) and species, and the identification of unique lineages through phylogeographical studies highlight the biogeographical, evolutionary, and conservation relevance of the *campo rupestre* mountaintops along the Espinhaço range. Additionally, the shared history among plants, amphibians, and birds corroborates the break between Espinhaço Mineiro and Chapada Diamantina (including areas of Caatinga/Cerrado vegetation) as common biogeographical barriers. However, this overview is based on data for only a few taxa (especially if considering macroevolutionary data), which makes our knowledge about the biogeographical history of the *campo rupestre* still incomplete.

MULTI-SCALE EVOLUTIONARY PROCESSES IN *CAMPO RUPESTRE*

Geomorphological, biogeographical, and ecological drivers interact to shape evolutionary processes across time and space, making the understanding of diversification in mountains a challenging task (Antonelli *et al.* 2018, Flantua *et al.* 2020). Multiple hypotheses have been proposed to explain mountain diversification dynamics, from intraspecific to community scales (Flantua and Hooghiemstra 2018, Rapini *et al.* 2021) and considering both historical biogeography and macroevolutionary perspectives (Perrigo *et al.* 2020, García-Rodríguez *et al.* 2021), with few examples for *campo rupestre* (Rapini *et al.* 2021, Guillory *et al.* 2024). The evolutionary and biogeographical processes that shaped the biodiversity of *campo rupestre* can be fitted into one of two non-mutually exclusive types: phylogeographical-level hypotheses and population- and community-level hypotheses.

Phylogeographical-level hypotheses

The Pleistocene refugia hypothesis (PRH; Haffer 1969) is frequently evoked to explain demographic processes and speciation in *campo rupestre* biota (Guillory *et al.* 2024). Extant mountaintop endemics that tolerate relatively colder conditions would represent relict populations of taxa widely distributed during glacial periods that became fragmented during interglacials, forming montane sky island refugia (McCormack *et al.* 2009) (Fig. 2A). This expansion–contraction (EC) model (Provan and Bennett 2008) predicts that effective population sizes (N_e) decrease (Fig. 2A) and a more pronounced population structure is established during interglacial contractions. On the contrary, during glacial expansions, N_e is expected to increase (Fig. 2A), and populations might either lose the accumulated differentiation owing to secondary contact or speciate under reproductive incompatibility scenarios; the so-called species pump hypothesis (Fig. 2A; Haffer 1969, McCormack *et al.* 2009). However, it is possible that interglacial cycles were shorter than expected for allopatric speciation, hindering the evolution of reproductive isolation between fragmented populations through neutral evolution, except for ecological speciation (Hendry *et al.* 2007). Furthermore, because gene flow during expansion phases of the Pleistocene tends to erase the neutral differentiation accumulated during the contraction phases, the species pump hypothesis seems to be unlikely in many cases (Jansson and Dynesius 2002). Additionally, another critique to the PRH considers overall stability in plant distribution at the Espinhaço Range throughout the Pleistocene (Rapini *et al.* 2021) and challenges the idea of EC cycles. Hence, the EC model is usually deemed overly simplistic and overlooks a range of population-level processes that might have occurred during the Pleistocene climatic cycles.

The vanishing refuge model (VRM; Vanzolini and Williams 1981), although rarely tested in mountains (Damasceno *et al.* 2014), provides a stronger theoretical foundation to explain phylogeographical and species-level divergence. The VRM posits that the vicariant effect of EC cycles can influence speciation through divergent selection of pre-adapted phenotypes when populations are trapped in their relictual habitats that would eventually vanish. The VRM can be tested using functional information and test scenarios of climatic divergence of those involving functional traits associated with both lowland and mountaintop lineages. Below, we review other hypotheses that can still apply to population-level divergence, while also expanding to other ecological and evolutionary scales.

Population- and community-level hypotheses

The flickering connectivity system (FCS) hypothesis (Flantua and Hooghiemstra 2018, Flantua *et al.* 2019) provides an expanded perspective on the PRH, postulating that EC cycles influence diversity patterns in mountaintops, from population to community scales, through: (i) fragmentation of geographical distributions during interglacial cycles and subsequent isolation in mountaintops; (ii) slope colonization in glacial cycles owing to elevational changes during climatic optima; (iii) hybridization between previously isolated allopatric populations or species (Fig. 2A, B); and (iv) biota intermixing owing to landscape connection and movements of multiple species among areas (Fig. 2B). Species responses to EC cycles depend on vagility and physiological tolerance, while the level of isolation of each sky island depends on the distance to other mountaintops, environmental differences between high-elevation ecosystems and their surrounding slopes and lowlands, and the temporal variability of isolation (Flantua *et al.* 2020). Consequently, biota in each site has its unique 'mountain fingerprint' driven by the relative importance of each process through time (Flantua *et al.* 2019).

An alternative species-level model, the 'escape-to-radiate' (Rapini *et al.* 2021), postulates that the mechanisms behind the disjunctions and diversity of *campo rupestre* endemic lineages could be associated with adaptive niche expansion rather than climate-mediated fluctuations in range sizes. This model proposes that populations of endemics with marginal distributions could experience an alleviation of selective pressures owing to environmental disturbances, which allows for expanded niche breadths, increased genetic variability, and lowland colonization. Consequently, they would be able to overcome barriers and colonize adjacent islands of *campo rupestre* (Fig. 2C). Rapini *et al.* (2021) also proposed the 'colonization-to-specialization' model, which predicts that allochthonous lineages from adjacent biomes might have colonized the *campo rupestre* and subsequently specialized owing to distinct environmental filters (Fig. 2D).

Evidence supporting population-level hypotheses

Most evidence on population-level responses to the Pleistocene climatic cycles comes for anurans, including *Bokermannohyla oxente* and *Bokermannohyla alvarengai* (Anura: Hylidae), EC occurring for both species, and gene flow after fragmentation occurring between populations of the latter (Oliveira *et al.* 2021). Two non-sister species have been demonstrated to result from both population expansion and introgression between *Pithecopus ayeaye* and *Pithecopus*

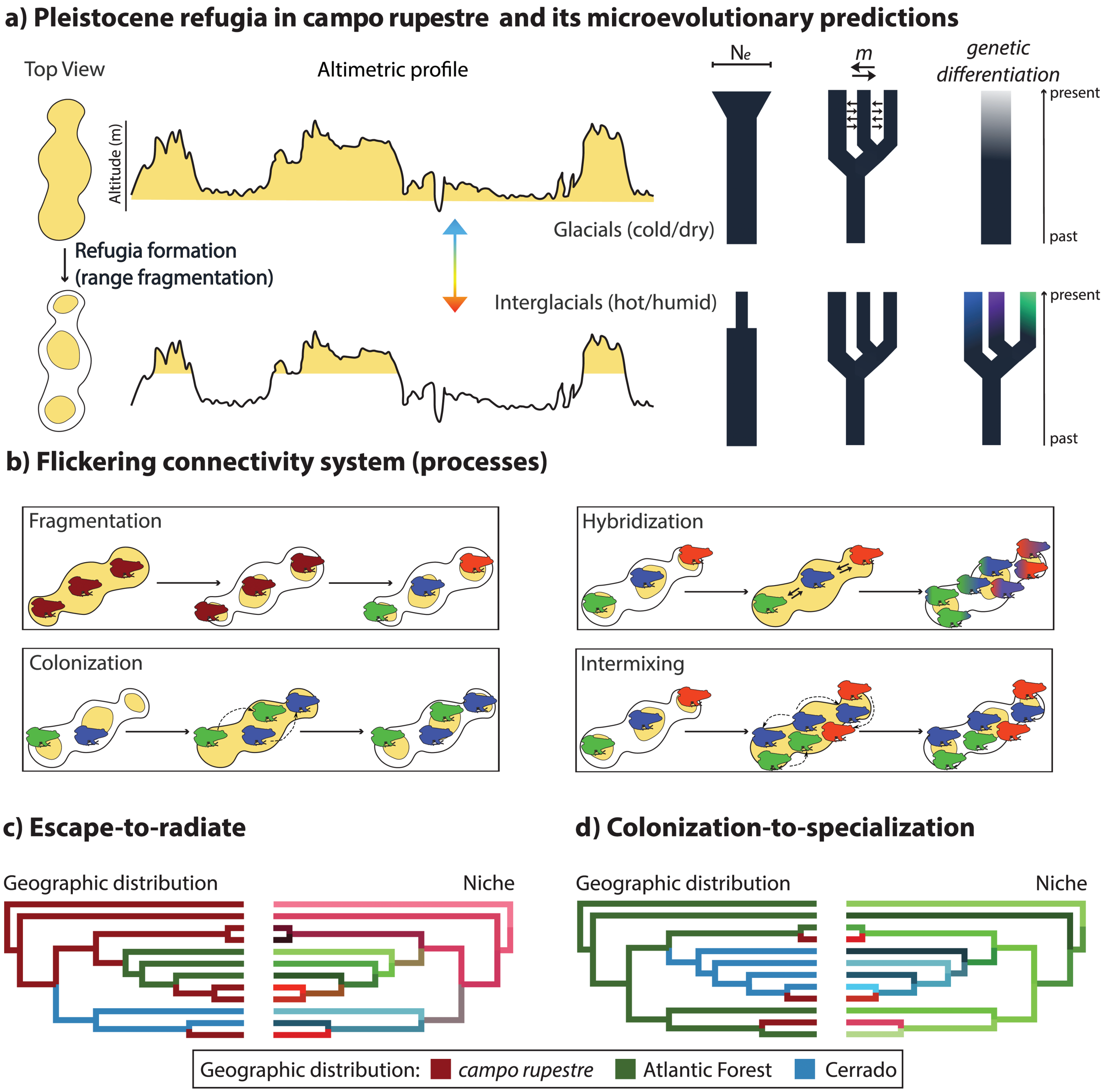


Figure 2. Conceptual hypotheses, models, and theories depicting four hypotheses explaining biogeography and diversification in *campo rupestre*. A, mountain profile depicting expected elevational shifts in geographical distributions (beige) between glacial and interglacial periods and expected population contractions during interglacials (red arrowhead) and expansions during glacials (blue arrowhead). B, geographical implications of processes associated with the flickering connectivity system model. Different coloured frogs represent distinct species, while gradient colours indicate admixture. Although the result of fragmentation is consistent with the 'species pump' model in the illustration, this process does not always result in speciation. C, D, relationship between changes in geographical distribution and niche evolution under 'escape-to-radiate' and 'colonization-to-specialization' models, respectively. Note that niches with similar hues are more alike. Blue and green hues represent broader niches compared with red ones. A and C were adapted from Flantua and Hooghiemstra (2018).

megacephalus (Anura: Hylidae) during the Middle Pleistocene (Magalhães *et al.* 2021), and the population structure patterns and geographical distribution of *Bokermannohyla saxicola* resulted from colonization (Oswald *et al.* 2022), corroborating the FCS. Although intraspecific lineages of *Scinax curicica* (Anura: Hylidae) diverged in the Pleistocene, there is no evidence of demographic changes for its different populations (Santana *et al.* 2024). Although not strictly tested, hybridization between non-sister species of *Tropidurus* lizards at Serra da Moeda (Domingos *et al.* 2017) might support the FCS, because *Tropidurus itambere* is a strictly saxicolous species mostly distributed in *campo rupestre*, whereas *Tropidurus torquatus* is widespread in open formations in eastern South America.

Diversification in the *campo rupestre*: historical biogeography and macroevolutionary dynamics

Although the above-mentioned models can mostly be tested using population-level data (either phylogeographical or addressing communities of closely related lineages), diversification hypotheses also need to be tested above the species level. The old, climatically buffered, infertile landscapes (OCBIL) theory comprises a series of hypotheses addressing different evolutionary and ecological scales, including diversification and trait evolution in OCBILs (Hopper *et al.* 2021). The accentuated persistence hypothesis predicts that the lack of strong climatic changes since at least the Permian has resulted in low extinction rates and allowed the persistence of ancient lineages (Fig. 3), older than 10 Mya. This period coincided with the expansion of fire-prone savannas across central South America, between the late Miocene (~10 Mya) and early Pliocene (~4 Mya) (Simon *et al.* 2009, Azevedo *et al.* 2020a). It is hypothesized that ancient lineages originated before this event and underwent diversification during the fragmentation of the predominant ecosystem owing to the expansion of lowland savannas (Rapini *et al.* 2021). The resulting newly formed sky islands of *campo rupestre* probably served as OCBIL refugia for lineages sensitive to climatic seasonality and the recurrent fires that established in the lowlands thereafter (Rapini *et al.* 2021). Furthermore, the reduced hybridization hypothesis proposes that typically small, fragmented populations in OCBILs might have evolved mechanisms that maintain heterozygosity, mitigating the negative impacts of inbreeding and consequently developing strong post-mating barriers as an incidental outcome (Hopper *et al.* 2021).

Most population-level hypotheses (PRH, VRM, and FCS) focus on the effects of Pleistocene glacial cycles on biodiversity, whereas OCBIL theory assumes long-term climatic buffering. Hence, these hypotheses can be tested based on their temporal premises using estimated or expected species divergence times. In contrast, the 'escape-to-radiate' and the 'colonization-to-specialization' models refer to diversification processes without strict temporal premises, providing complementary explanations for *campo rupestre* diversification both during and before the Pleistocene. Reduction in gene flow is expected by the OCBIL theory and is an implicit assumption of the pump speciation hypothesis (McCormack *et al.* 2009), whereas the FCS recognizes it as a mechanism generating genetic diversity (Flantua *et al.* 2020; Fig. 2B).

All discussed models contribute to explaining the diversification of *campo rupestre* vertebrates to some extent, as in the case for plants (Vasconcelos *et al.* 2020, Rapini *et al.* 2021). All these hypotheses are also applicable to mountains (especially those dominated by erosive processes) at the global scale and do not exclude the effects of regional and local events, such as neotectonic and climatic changes on the Brazilian Plateau during the Miocene and Pliocene, on the diversification of *campo rupestre* vertebrates (Chaves *et al.* 2020).

Evidence from historical biogeography

The evolutionary history of subfamilies and genera of vertebrates endemic to the *campo rupestre* seems to align with the accentuated persistence hypothesis. Copiodontinae (Teleostei: Siluriformes), an autochthonous fish radiation from Chapada Diamantina, diverged from the Trichogeninae ~56 Mya, with the endemic genera *Glaphyropoma* and *Copionodon* diverging during the Oligocene (~30 Mya) and *Copionodon* diversifying in the Miocene (~11 Mya) (Fig. 4; Ochoa *et al.* 2017). Likewise, the frog *Rupirana cardosoi* (Anura: Leptodactylidae) diverged from the remaining Paratelmatobiinae 41 Mya (Fig. 4; Santos *et al.* 2020). For reptiles, the lizard *Rhachisaurus brachylepis* (single member of Rhachisaurinae), mostly distributed along the Espinhaço Range, diverged from its sister taxon, Gymnophthalminae (which is widespread in South America) during the Eocene, ~50 Mya (Fig. 4; Recoder *et al.* 2020). For birds, *Augastes* (Trochilidae) diverged from *Schistes* (Trochilidae) 7 Mya (Chaves *et al.* 2020). The timing of the origin of the endemic rodent *Calassomys* (Mammalia: Cricetidae) is uncertain, but it revolves around 6.5

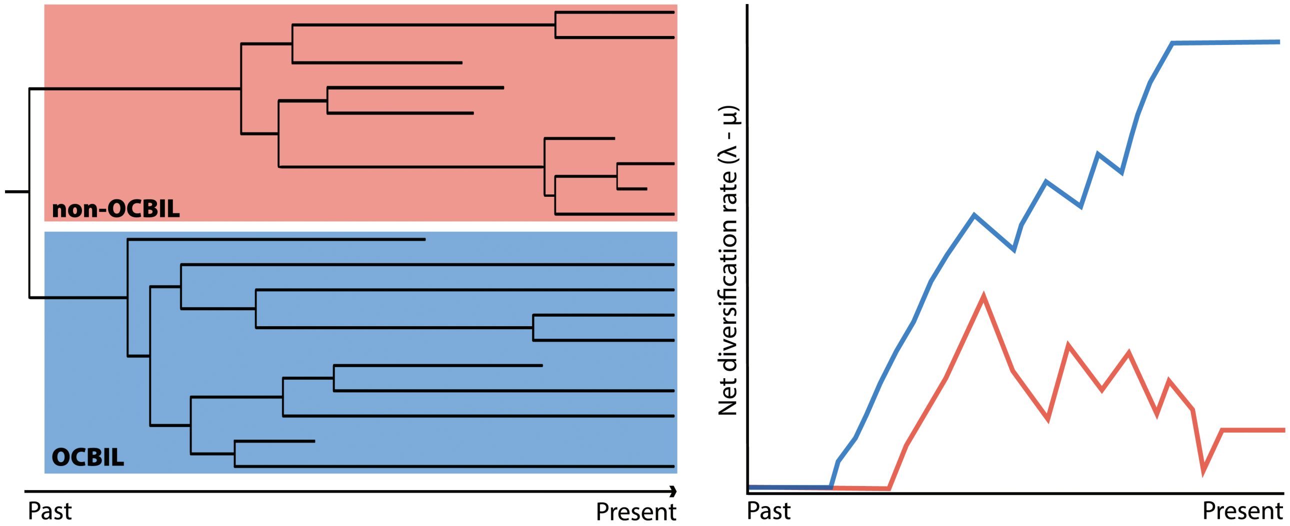


Figure 3. Expectations based on the old, climatically buffered, infertile landscapes (OCBIL) theory. OCBIL landscapes harbour ancient and recent lineages, with a low extinction rate and high persistence of ancient lineages. In contrast, in non-OCBIL landscapes, the extinction rate is higher, resulting in the predominance of more recent lineages. Blue represents OCBIL and red non-OCBIL diversifications. Abbreviations: λ, speciation rate; μ, extinction rate.

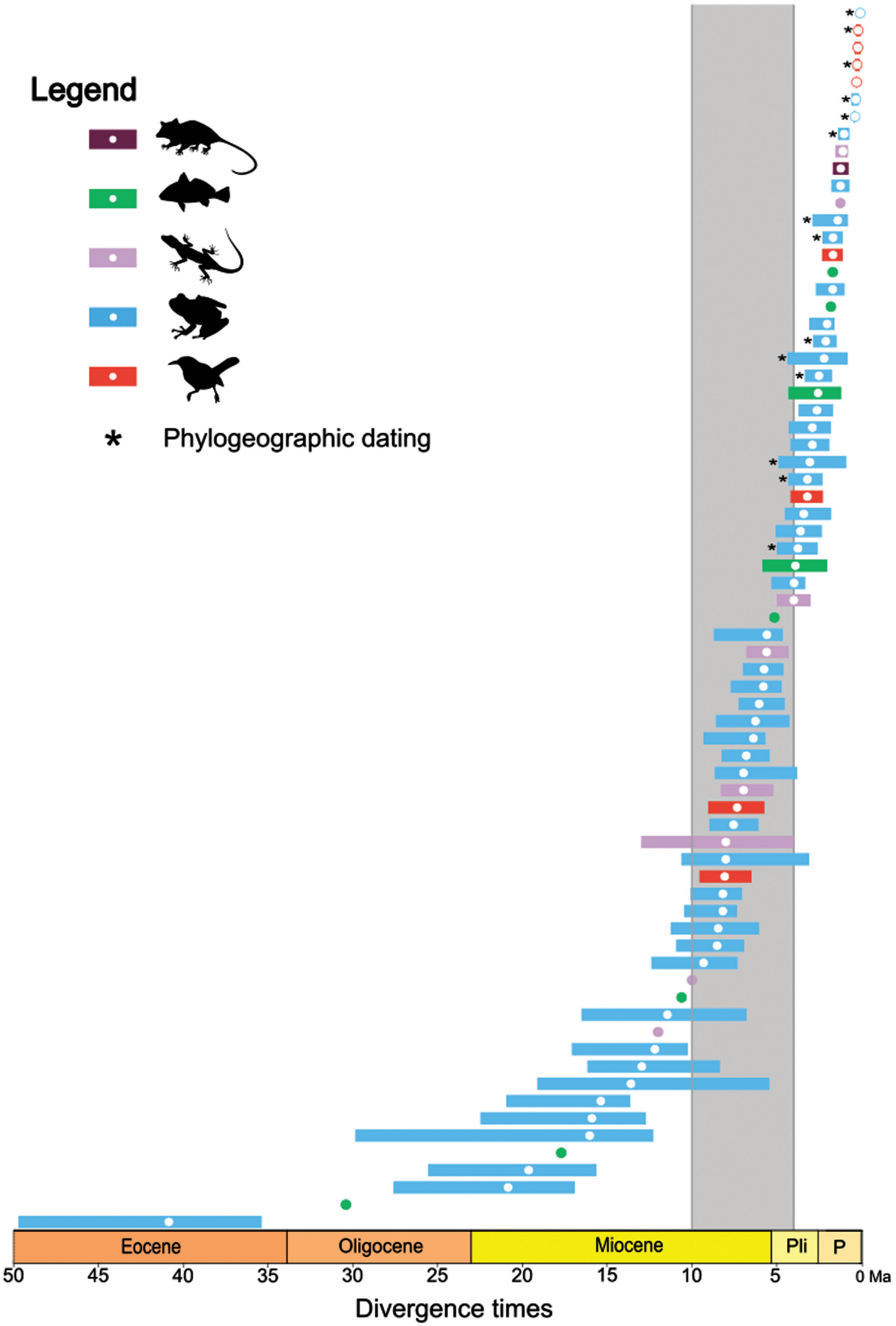


Figure 4. Mean (circles) and range (bars) times of divergence for endemic vertebrates from *campo rupestre* are depicted. Filled circles without bars represent data where only means were reported. Phylogeographical dating (bars with asterisks) includes both species crown dating and intraspecific divergences, whereas lines without asterisks represent stem dating. The vertical grey bar denotes the time frame of origin and expansion of fire-prone savannas across central South America, ranging from the late Miocene (~10 Mya) to the early Pliocene (~4 Mya). On the geological scale, P represents Pleistocene and Pli, Pliocene. All times falling within or preceding this interval are considered ancient, aligning with the OCBIL theory. Raw data and references are provided in Supporting Information, Table S1. The silhouette images were obtained from https://www.phylopic.org/.

Mya, the age established for the earliest divergence within the tribe Phyllotini (Fig. 4; Gonçalves *et al* 2020). It is important to note that Heyer (1999) suggested that the current geographical distribution of *Rupirana* might be the result of extinctions within the genus in regions adjacent to Chapada Diamantina, suggesting *Rupirana cardosoi* to be a biogeographical relict. The same hypothesis could apply to all the aforementioned species. Reliable fossil records are needed to validate this hypothesis and to test the accentuated persistence hypothesis more consistently.

Recently, a new species of *Rupirana* (*Rupirana kaatinga*) was described from Serra do Assuruá, a region characterized by rocky outcrops embedded within the Caatinga that might resemble the *campo rupestre* functionally (Mângia *et al.* 2025). This finding raises the possibility that *Rupirana* might have originated in the *campo rupestre* and later dispersed into the Caatinga or vice versa. Nevertheless, *R. kaatinga* exhibits a broader distribution, with most occurrences in typical *campo rupestre* ecosystems (M. T. T. Santos, pers. comm.). Serra do Assuruá is situated at the westernmost limit of the Chapada Diamantina, where the Caatinga biome exerts strong influence on the landscape. Given this, the type locality of *R. kaatinga* is likely to represent a marginal habitat for the species rather than its core ecological niche. In summary, current evidence suggests that the genus *Rupirana* remains endemic to the *campo rupestre*, although further research is necessary to confirm this biogeographical pattern.

Most endemisms in *campo rupestre* are at the species level, with a few known endemic radiations. Heyer (1999) first proposed that *campo rupestre* anurans resulted from colonization from adjacent biomes, mainly from the Atlantic Forest. Indeed, most endemic anurans are part of typical Atlantic Forest clades and, to a lesser extent, from the Cerrado (Oswald *et al.* 2024), suggesting that 'colonization-to-specialization' might be an important diversification process. On the contrary, *campo rupestre* is the ancestral area of a clade of *Leptodactylus* frogs that shows its greatest diversity at the Espinhaço Range (Carvalho *et al.* 2021). The origin of this clade dates from the Miocene, ~6.4 Mya, probably in the Espinhaço Range, which aligns with OCBIL theory. Another example of ancient radiation is a *Bokermannohyla* clade that originated and diversified in the Miocene, nearly 8.46 Mya (Brunes *et al.* 2023).

The diversification of Espinhaço Range lizards has attracted attention since Vanzolini (1982) suggested that some mountaintop endemic taxa could be relics of past events of colder and drier climates. Ancient radiation also occurs among worm lizards (Amphisbaenia). A small clade composed of four species (*Amphisbaena bahiana*, *Amphisbaena longinqua*, *Amphisbaena mongoyo*, and *Amphisbaena uroxena*), occurring mostly at Chapada Diamantina, originated in the Miocene, ~15 Mya (Graboski *et al.* 2022), probably from dispersal events from adjacent open ecosystems in the Cerrado and Caatinga. A recent phylogenetic analysis also showed that lizard populations in *campo rupestre* attributed to *Tropidurus etheridgei* should be a new species sister to a clade of species native to an area from the western Cerrado to the Bolivian montane dry forests, in the Andes foothills (Carvalho *et al.* 2018).

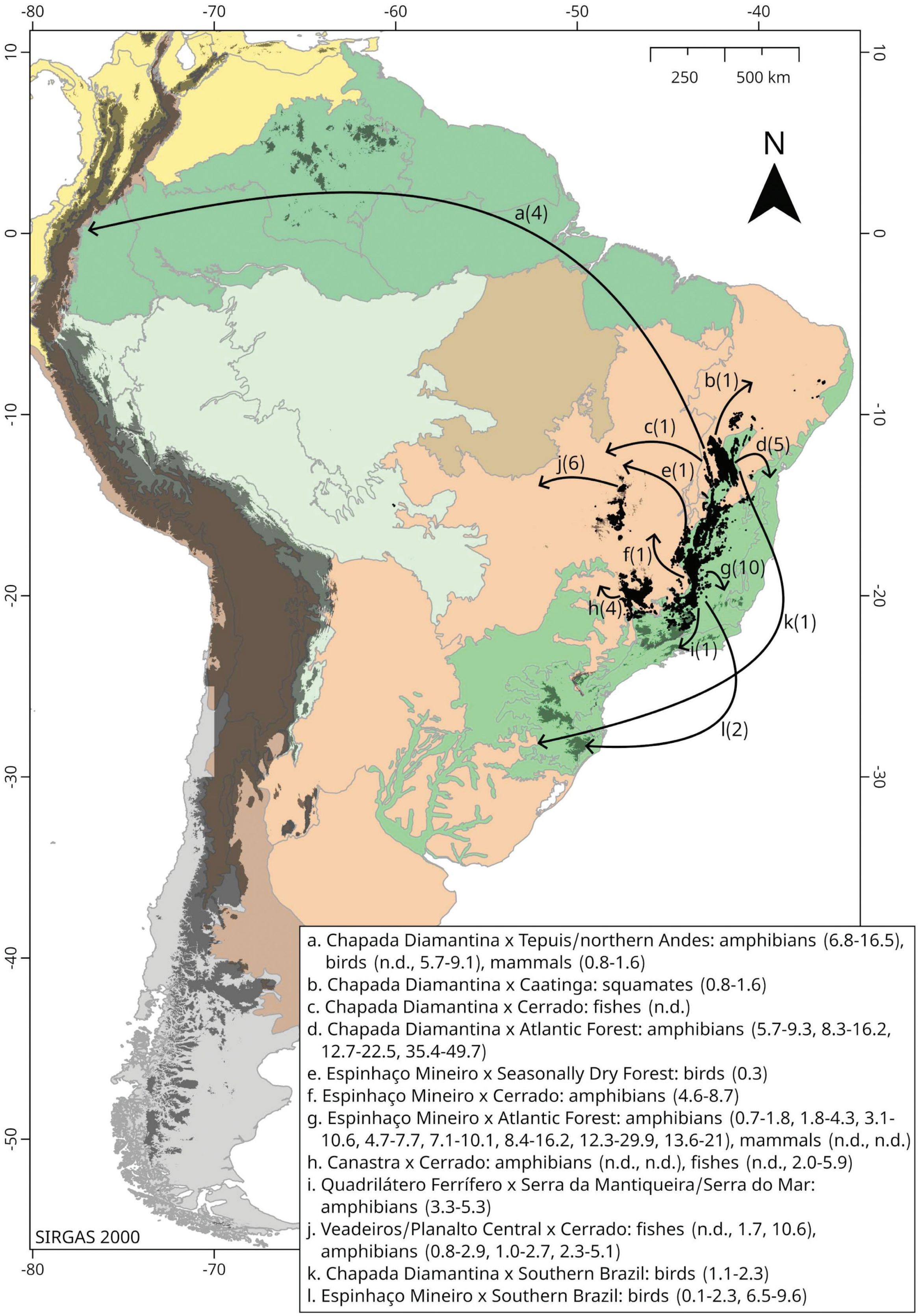
For birds, phylogenetic analyses of endemic species indicate biogeographical affinities with the Andes or southern South America (Derruberry *et al.* 2011, Freitas *et al.* 2012, Chaves *et al.* 2020; Fig. 5). The hummingbirds *Augastes lumachella* and *A. scutatus* form a clade with *Doryfera*, *Colibri*, and *Schistes*, all predominantly distributed in Tropical Andes or Tepuis (Chaves *et al.* 2020). The divergence between the Andean *Schistes* and *Augastes* in the Late Miocene suggests a vicariant event associated with geoclimatic changes in South America (Chaves *et al.* 2020). However, it cannot be ruled out that the colonization-to-speciation model, as an alternative to vicariance, might explain the endemism of *Augastes*. Nevertheless, the connection through the southern cone of South America is demonstrated by the ovenbird (Furnariidae) endemics *Cinclodes espinhacensis* and *Asthenes luizae* (Fig. 5). The latter species split from a clade containing species restricted to the Andes and Patagonia at ~8.1 Mya (Derryberry *et al.* 2011).

Small non-volant mammals, however, show more ambiguous biogeographical patterns. Endemism is rare, with only two species recognized, *Oligoryzomys rupestris*, belonging to a widespread genus (Weksler and Bonvicino 2005), and *Calassomys apicalis*, an endemic genus (Pardiñas *et al.* 2014). *Calassomys apicalis* is a sister group to the rest of the tribe Phyllotini, including *Calomys*, common in open formations throughout South America, and a clade including species closely associated with the Andes, Patagonia, and Chaco (Pardiñas *et al.* 2014). These phylogenetic relationships can be interpreted under different biogeographical scenarios, both in terms of close species from the *campo rupestre* with affinities with Andean groups, as in birds, or as the persistence of a relictual group adapted to colder and drier climates, as postulated for some groups of reptiles.

The endemic vertebrate species of the *campo rupestre* have phylogenetic affinities with sister lineages that inhabit mainly adjacent biomes (Fig. 5) and few from distant cold and dry environments. Each species has a unique evolutionary history, with different patterns of biogeographical connections at different geographical and time scales (Figs 4, 5), with different processes of origin (Fig. 2). The diversification patterns in *campo rupestre*, encompassing both ancient, persistent lineages and more recently diverged ones, suggest that a combination of both OCBIL theory and Pleistocene climatic models is required to explain the evolutionary processes shaping its biota comprehensively (Fig. 4). Estimating extinction rates in *campo rupestre* is essential to elucidate the role of environmental stability in maintaining ancient lineages (Fig. 3), which would provide further evidence supporting or refuting the OCBIL theory. Additionally, all observed intraspecific divergence events occurred in the Plio-Pleistocene, after the establishment of the lowland fire-prone lowland savannas (Fig. 4). This indicates that the climatic cycles of these epochs are likely to have influenced the population structure of *campo rupestre* species (Supporting Information, Fig. S3). Such patterns suggest a combination of isolation, cladogenesis, and species persistence in shaping diversification dynamics in South American mountains (Rosauer and Jetz 2015, Azevedo *et al.* 2020a). Model-based biogeographical methods (Matzke 2013), coupled with functional traits and inferences of species niche evolution, will further elucidate the origins and diversification of endemic vertebrates in *campo rupestre*.

TRAIT-BASED DIVERSIFICATION AND MACROEVOLUTIONARY DYNAMICS

Trait-based approaches have had a remarkable impact in ecology and evolution across levels of organization, allowing for



a. Chapada Diamantina x Tepuis/northern Andes: amphibians (6.8-16.5), birds (n.d., 5.7-9.1), mammals (0.8-1.6)
b. Chapada Diamantina x Caatinga: squamates (0.8-1.6)
c. Chapada Diamantina x Cerrado: fishes (n.d.)
d. Chapada Diamantina x Atlantic Forest: amphibians (5.7-9.3, 8.3-16.2, 12.7-22.5, 35.4-49.7)
e. Espinhaço Mineiro x Seasonally Dry Forest: birds (0.3)
f. Espinhaço Mineiro x Cerrado: amphibians (4.6-8.7)
g. Espinhaço Mineiro x Atlantic Forest: amphibians (0.7-1.8, 1.8-4.3, 3.1-10.6, 4.7-7.7, 7.1-10.1, 8.4-16.2, 12.3-29.9, 13.6-21), mammals (n.d., n.d.)
h. Canastra x Cerrado: amphibians (n.d., n.d.), fishes (n.d., 2.0-5.9)
i. Quadrilátero Ferrífero x Serra da Mantiqueira/Serra do Mar: amphibians (3.3-5.3)
j. Veadeiros/Planalto Central x Cerrado: fishes (n.d., 1.7, 10.6), amphibians (0.8-2.9, 1.0-2.7, 2.3-5.1)
k. Chapada Diamantina x Southern Brazil: birds (1.1-2.3)
l. Espinhaço Mineiro x Southern Brazil: birds (0.1-2.3, 6.5-9.6)

Figure 5. Biogeographical connections between endemic *campo rupestre* lineages and its sister lineages, according to the phylogenetics hypothesis available in the literature (see Supporting Information, Table S2, which provides the list of taxa associated with each arrow). Colours represent distinct biogeographical provinces of the Neotropical region following Morrone *et al.* (2022). For each arrow, in parentheses is indicated in the map the number of lineages/hypotheses, and the key indicates the interval (in millions of years) of the split, or n.d. when there is no dating.

inferences on community assembly, comparative diversification, and understanding of trait–environmental relationships, adaptive radiations, and niche evolution (Foote 1997, Wagner and Estabrook 2014, Stroud and Losos 2016). Unfortunately, the functional ecology of *campo rupestre* vertebrates is largely overlooked, suggesting several opportunities for future research.

For fishes and anurans, most research has focused on traits allowing species to thrive in fast-running, nutrient-poor, acidic waters in streams and rivulets (Zanata and Primitivo 2013). Such traits include an opercular apparatus with external teeth (odontodes) used for substrate attachment in Loricariidae and Trichomycteridae fishes (Lujan and Conway 2015). Odontodes may also be used primarily as an attachment organ to assist with station holding and locomotion, as in Copionodontinae fishes, a hypothesized plesiomorphic trait for living in fast-water habitats (de Pinna 2018).

Tadpoles of *Bokermannohyla pseudopseudis* and *Bokermannohyla martinsi* species groups (Hylidae: Cophomantini; Faivovich *et al.* 2005) and *Corythomantis botoque* (Lophiohylini; Marques *et al.* 2021) show depressed bodies, enlarged oral discs with additional rows of denticles, absence of gaps on marginal papillae (Lins *et al.* 2018, Marques *et al.* 2021, Pezzutti *et al.* 2021), and robust, muscular tails (Eterovick *et al.* 2001), which are thought to perform similar functions to the odontodes of fishes. Functionally, the oral discs anchor tadpoles to the rocky substrate, allowing them to scrape food without being carried away by strong currents (Altig and McDiarmid 1999). In addition, tadpoles of *B. pseudopseudis* and *B. martinsi* species groups show unusually long periods of larval development and reach great length during the larval stage, suggesting delayed development in comparison to congeneric counterparts from adjacent biomes (Pezzuti *et al.* 2015), thus providing one of the few available lines of evidence of niche evolution in *campo rupestre* vertebrates (see also Bandeira *et al.* 2021). Differences include a higher degree of ossification at the initial stages of development, suggesting a heterochronic developmental pattern in these endemic lineages (Eterovick and Brandão 2001, Leite and Eterovick 2010, Lins *et al.* 2018).

Trait–environmental relationships in the harsh environmental conditions of *campo rupestre*, including high solar radiation levels and extreme heat and cold, are little explored. Adults of *Bokermannohyla alvarengai* and congeneric species are frequently observed basking in sunlight for extended periods (Brandão *et al.* 2012, Centeno *et al.* 2015). The morphology and biochemical aspects of lipid secretions from the skin of *B. alvarengai* might aid in thermoregulation and involve changes in skin colour for light reflectance (Centeno *et al.* 2015). Additionally, its body presents an extra-epidermal lipid layer on the dorsal surface, well-developed ventral skin folds, and an extensive hypervascularization, potentially assisting in water conservation (Centeno *et al.* 2015). Finally, the role of ecophysiological traits such as thermal tolerance has been explored only for populations of the lizard *Coleodactylus meridionalis*, showing specific thermal trait variation, probably related to the temperature oscillations experienced through different seasons (Damasceno *et al.* 2014). However, it has yet to be determined whether these traits represent adaptations to mountaintop habitats and/or have an impact on diversification rates.

VERTEBRATE–PLANT INTERACTIONS

Vertebrates are key mobile links connecting habitats in space and time through pollination and seed dispersal, transporting individuals and genes, driving ecological and evolutionary dynamics of plant populations and ecosystem functioning (Lundberg and Moberg 2003). Nectar, fruits, and seeds are important resources for vertebrates engaging in facultative mutualisms in *campo rupestre* (Guerra *et al.* 2016). Little is known, however, about how changes in soil properties propagate in pollination and seed dispersal. For example, it is well established that soil abiotic and biotic characteristics regulate plant physiology and affect the spatial abundance and diversity of flowers and fruits, such that fertile soils have a higher percentage of fleshy-fruit species and infertile soils are more likely to have a community of plants that develop elaiosomes and arils (Carvalheiro *et al.* 2021). Below, we discuss pollination and seed dispersal in *campo rupestre*, focusing on specific hypotheses aiming to stimulate further research that will be able to test whether mutualisms influence speciation, extinction, and immigration.

Pollination ecology

Hummingbirds are remarkable pollinators in *campo rupestre*, visiting flowers of phylogenetically unrelated endemic and widespread species (Machado *et al.* 2007, Carstensen *et al.* 2014, Monteiro *et al.* 2021, Maianne *et al.* 2022). Across individual sites, interactions between 6 and 16 resident hummingbirds and plants in 25 families (mostly Asteraceae, Bromeliaceae, Cactaceae, Gesneriaceae, and Velloziacae) occur year-round, owing to continuous flowering phenology (Rodrigues *et al.* 2011, Rodrigues and Rodrigues 2014, Maianne *et al.* 2022). Although most endemic hummingbirds are somewhat geographically restricted, common species (*Colibri serrirostris*, *Chlorostilbon lucidus*, and *Eupetomena macroura*) are often dominant, playing central roles as pollinators. However, *Augastes scutatus* is one of the most abundant birds and might play special roles in pollination in some places (Costa and Rodrigues 2012, Rodrigues and Rodrigues 2014).

Many *campo rupestre* plant species show ornithophilous flowers pollinated by hummingbirds (Monteiro *et al.* 2021). However, hummingbird pollination in typically entomophilous flowers (i.e. small, fragrant, non-red flowers) is common (Amorim *et al.* 2022). Hence, plant–hummingbird interactions in the *campo rupestre* mirror patterns found in open Neotropical ecosystems, where interactions involving higher degrees of phenotypic generalization are important for maintenance of these pollinators (Maruyama *et al.* 2013). Future studies should clarify whether relatively higher speciation rates in hummingbird-pollinated species/clades (Lagomarsino *et al.* 2017) contribute to diversification and endemism in the *campo rupestre* flora.

The high percentage of hummingbird-pollinated plants in *campo rupestre* (Silveira *et al.* 2016) supports the idea that highly mobile pollinators are important to maximize gene flow in species with limited seed dispersibility, as predicted by OCBIL theory (Hopper *et al.* 2021). Nevertheless, territorial behaviour in hummingbirds restricting movement within habitat patches (Sazima 1977, Jacobi and Antonini 2008, Guerra *et al.* 2014) might constrain gene flow among plants (Maruyama *et al.* 2016), generating strong population genetic structure (Franceschinelli

Table 2. Research priorities to improve our understanding of the biogeography, ecology, and evolution of *campo rupestre* vertebrates.

Theme	Knowledge gaps	Research priorities
Diversity and endemism	Overall lack of faunistic studies and undersampled sites and lineages Lack of specimens and all their extensions (sounds, parasites, DNA) Closing the Linnean and Wallacean shorfalls Published checklists for *campo rupestre* areas frequently include other habitats and adjacent lowlands, preventing the distinction of species occurring in *campo rupestre*	Funding research in overlooked sites (especially in geomorphologically isolate sites) and clades to sample species and their extensions to build comprehensive biogeographical and phylogeographical databases Phylogeographical studies to uncover potential cryptic species and to elucidate diversification processes, and studies on niche evolution Strengthening museums and zoological collections
Diversification dynamics	Trait and niche shifts have been overlooked during biome shifts Lack of knowledge about the tree of life and the evolution of species and their traits (Darwinian shortfall)	Trait- and niche-based approaches coupled with time-calibrated phylogenies across different taxa
Functional ecology	General lack of knowledge about species-specific traits and their ecological functions (Raunkiaeran shortfall) prevents understanding of ecological strategies and adaptations	Building functional trait spectra across different taxa, establishment of meaningful trait–environmental correlations
Palaeoecology	Extinct fauna and their role in shaping ecosystems are unknown, paucity of data of fossil specimens	Establishing stratigraphic data and dating fossil specimens, establishing field experiments reintroducing megafauna to test for effects on ecosystem functioning
Ecological interactions	Lack of general knowledge on species interactions and their effects on individual survival and fitness (Eltonian shortfall) Few natural history studies	Support natural history studies, unravelling how ecological interactions shape eco-evolutionary dynamics
Climate change	Lack of species elevational distribution data Lack of knowledge about the responses and tolerances of species to abiotic conditions (Hutchinsonian shortfall)	Establishing long-term monitoring and elevation-based species distribution to support modelling approaches Assessing species thermotolerance
Conservation	Paucity of species assessment Effectiveness of protected areas in protecting species Identification of key biodiversity areas	Accelerating species conservation status, examining effectiveness of protected areas, promoting conservation genetic studies
Population monitoring for detection of declines	Few data on species abundance and population dynamics and their spatial and temporal changes (Prestonian shortfall) Low species detectability Lack of long-term studies	Implementation of new monitoring tools aiming for complementarity, efficiency, and precision, such as environmental DNA. Efforts need to be directed to the improvement of genomic libraries for comparison with environmental samples, because these will determine which species can be identified

et al. 2006). Such behaviour might contribute to higher speciation rates in hummingbird-pollinated species (Kessler *et al.* 2020), an idea that remains to be tested in *campo rupestre*.

Nectarivorous bats (Sazima and Sazima 1975) and chiropterophilous flowers are rare in *campo rupestre* (Monteiro *et al.* 2021). Specialized bat pollination is reported between *Lonchophylla bokermanni* (Phyllostomidae) and the endemic bromeliad *Encholirium glaziovii* (Sazima *et al.* 1989). In contrast, the use of flowers with intermediate characteristics between chiropterophilous and ornithophilous syndromes by hummingbirds seems to be common, suggesting that flower-visiting bats might also pollinate flowers not typically associated with them.

Frugivory and seed dispersal

In contrast to tropical forests and savannas, large birds and mammals, such as primates and tapirs, are absent or occur at very low densities in *campo rupestre*. Specialized avian frugivores are rare (*Antilophia galeata*, Pipridae) and restricted to forest islands, occasionally foraging on grasslands. Widespread birds, such as tyrant flycatchers (*Elaenia cristata*, Tyrannidae), tanagers, finches (*Schistochlamys ruficapillus*, Thraupidae), sparrows (*Zonotrichia capensis*, Passerellidae), mockingbirds (*Mimus saturninus*, Mimidae), and thrushes (*Turdus leucomelas*, Turdidae) represent major primary seed dispersers (Faustino and Machado 2006, Guerra *et al.* 2016). Generalist frugivores feed on insects and fruits from the few fleshy-fruited species in Melastomataceae, Myrtaceae, and Loranthaceae (Guerra *et al.* 2016). In particular, some *Miconia* species produce copious amounts of fruits during dry seasons, attracting a wide assemblage of frugivores (Guerra *et al.* 2017, 2018), underlying their role as keystone resources for birds.

Frugivores differ greatly in seed dispersal effectiveness, showing different fruit-handling behaviours, removal rates, and gut passage effects (Silveira *et al.* 2012, Guerra and Pizo 2014). Fruit removal rates are strongly influenced by fruiting phenology of neighbouring plants (Guerra *et al.* 2017). Moreover, although post-feeding flights are usually within 30 m from fruiting plants, birds occasionally transport seeds ≤80 m (Guerra *et al.* 2018). Even mashers (species dropping fruits beneath maternal plants) contribute indirectly to seed dispersal, by allowing secondary dispersal by *Tropidurus montanus* (Guerra *et al.* 2018). Nevertheless, gut passage effects are species specific, hence no general conclusions can be drawn at present (Silveira *et al.* 2012, Lessa *et al.* 2013).

Although seed dispersal by bats remains unexplored, 16 species of Rodentia and Didelphimorphia have been reported as seed dispersers in the *campo rupestre* (Lessa *et al.* 2013, Genrich *et al.* 2017). Vertebrate exclosure experiments confirmed significant seed removal by small non-volant mammals (Guerra *et al.* 2018), but interaction outcomes for consumed seeds range from dispersal to predation (Lessa *et al.* 2013, Genrich *et al.* 2017). The maned wolf (*Chrysocyon brachyurus*), a large carnivore feeding mostly on rodents and marsupials, is an effective disperser of *Solanum lycocarpum*, and potentially of other fleshy-fruited species.

Secondary seed dispersal appears to be relatively more important in *campo rupestre* compared with more productive ecosystems. For example, saurochory, thought to be important in island-like ecosystems (Correcher *et al.* 2023), has been demonstrated in short-distance dispersal for *campo rupestre* endemics (Fonseca *et al.* 2012, Guerra *et al.* 2018). Such short-distance dispersal by small mammals and lizards provides support to the reduced dispersibility hypothesis (Hopper *et al.* 2021), posing that optimum sites for seed deposition are near, rather than away from maternal plants.

CONCLUSIONS AND FUTURE RESEARCH AVENUES

Despite huge shortfalls knowledge of biodiversity (Table 2), the vertebrate fauna of *campo rupestre* is characterized by disproportionally high levels of biodiversity and endemism across most taxa. Its biota can be described as a continuum ranging from ancient to recent lineages (Fig. 4), related to adjacent biomes and distant cold and dry environments (Fig. 5), indicating that a combination of isolation, diversification, and species persistence played key roles in shaping diversification dynamics in these ancient mountains. The available studies on species adaptations to mountaintops point to a few mechanisms in fishes and anurans, but data for other taxa are lacking. In *campo rupestre*, hummingbirds are key pollinators, interacting with a wide variety of plants, playing key roles in gene flow and speciation owing to their high mobility and territorial behaviour. Conversely, seed dispersal is performed primarily by generalist birds, small mammals, and lizards, with secondary dispersal being significant, supporting the reduced dispersibility hypothesis that optimal seed-deposition sites are near maternal plants. Such biodiversity and vital ecosystem services are increasingly threatened (Fernandes *et al.* 2018), with approximately one-fifth of endemic species listed on the IUCN Red List. Unfortunately, conservation efforts are hindered by persistent knowledge gaps and biases.

Our study adds to previous knowledge indicating that the *campo rupestre* is home not only to the highest plant diversity per area in Brazil (Rapini *et al.* 2021) but also harbours a highly diverse and endemic vertebrate fauna. Our synthesis is the first step towards a more detailed and quantitative synthesis that will guide a future research agenda for the *campo rupestre* biota (Table 2). Future genetic studies are likely to uncover cryptic species and shed light on biogeographical patterns shaping the evolution of *campo rupestre* biota. It is also clear that more effective conservation programmes will benefit from such studies, considering that conservation of the Espinhaço Range should be prioritized immediately.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

All data are incorporated into the article and its online supplementary material.

REFERENCES

Abreu EF, Casali D, Costa-Araújo R *et al.* Lista de Mamíferos do Brasil (2023-1). *Zenodo* 2023. https://doi.org/10.5281/zenodo.10428436

Albert JS, Tagliacollo VA, Dagosta F. Diversification of neotropical freshwater fishes. *Annual Review of Ecology, Evolution, and Systematics* 2020;**51**:27–53. https://doi.org/10.1146/annurev-ecolsys-011620-031032

Altig R, McDiarmid RW. Body plan, development, and morphology. In: McDiarmid RW, Altig R (eds), *Tadpole: the Biology of Anuran Larvae*. Chicago, IL: The University of Chicago Press, 1999, 24–51.

Alves CBM, Leal CG, Brito MFG *et al.* Biodiversidade e conservação de peixes do Complexo do Espinhaço. [Biodiversity and conservation of fishes in the Espinhaço complex]. *Megadiversidade* 2008;**4**:178–96.

Amorim MD, Maruyama PK, Baronio GJ *et al.* Hummingbird contribution to plant reproduction in the rupestrian grasslands is not defined by pollination syndrome. *Oecologia* 2022;**199**:1–12. https://doi.org/10.1007/s00442-021-05103-6

Andrade PCB, Lessa LG, Geise L *et al.* Survey of small mammals (Rodentia and Didelphimorphia) in a cerrado reserve: central

Espinhaço mountain range, Brazil. *Oecologia Australis* 2017;**21**:147–55. https://doi.org/10.4257/oeco.2017.2102.05

Antonelli A, Kissling WD, Flantua SGA *et al*. Geological and climatic influences on mountain biodiversity. *Nature Geoscience* 2018;**11**:718–25. https://doi.org/10.1038/s41561-018-0236-z

Azevedo JAR, Valdujo PH, Nogueira CC. Biogeography of anurans and squamates in the Cerrado hotspot: coincident endemism patterns in the richest and most impacted savanna on the globe. *Journal of Biogeography* 2016;**43**:2454–64.

Azevedo JAR, Collevatti RG, Jaramillo CA *et al*. On the young savannas in the land of ancient forests. In: Rull V, Carnaval AC (eds), *Neotropical Diversification: Patterns and Processes*. Cham, Switzerland: Springer International, 2020a, 271–98.

Azevedo JAR, Guedes TB, Nogueira CC *et al*. Museums and cradles of diversity are coincident for narrowly distributed Neotropical snakes. *Ecography* 2020b;**43**:328–39.

Bandeira LN, Villalobos F, Werneck FP *et al*. Different elevational environments dictate contrasting patterns of niche evolution in Neotropical *Pithecopus* treefrog species. *Biotropica* 2021;**53**:1042–51. https://doi.org/10.1111/btp.12929

Barros-Souza Y, Borges LM. Spatial- and lineage-dependent processes underpin floristic assembly in the megadiverse Eastern South American mountains. *Journal of Biogeography* 2023;**50**:302–15.

Bernard E, Penna LA, Araújo E. Downgrading, downsizing, degazettement, and reclassification of protected areas in Brazil. *Conservation Biology* 2014;**28**:939–50. https://doi.org/10.1111/cobi.12298

Brandão RA, Magalhães RF, Garda AA *et al*. A new species of *Bokermannohyla* (Anura: Hylidae) from highlands of Central Brazil. *Zootaxa* 2012;**3527**:28–42.

Brunes TO, Pinto FC, Taucce PP *et al*. Traditional taxonomy underestimates the number of species of *Bokermannohyla* (Amphibia: Anura: Hylidae) diverging in the mountains of southeastern Brazil since the Miocene. *Systematics and Biodiversity* 2023;**21**:2156001.

Carstensen DW, Sabatino M, Trojelsgaard K *et al*. Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. *PLoS One* 2014;**9**:e112903. https://doi.org/10.1371/journal.pone.0112903

Carvalheiro LG, Bartomeus I, Rollin O *et al*. The role of soils on pollination and seed dispersal. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2021;**376**:20200171. https://doi.org/10.1098/rstb.2020.0171

Carvalho ALG, Rivas LR, Céspedes R *et al*. A new collared lizard (*Tropidurus*: Tropiduridae) endemic to the western Bolivian Andes and its implications for seasonally dry tropical forests. *American Museum Novitates* 2018;**3896**:1–56.

Carvalho TR, Seger KR, Magalhães FM *et al*. Systematics and cryptic diversification of *Leptodactylus* frogs in the Brazilian campo rupestre. *Zoologica Scripta* 2021;**50**:300–17. https://doi.org/10.1111/zsc.12470

Centeno FC, Antoniazzi MM, Andrade DV *et al*. Anuran skin and basking behavior: the case of the treefrog *Bokermannohyla alvarengai* (Bokermann, 1956). *Journal of Morphology* 2015;**276**:1172–82. https://doi.org/10.1002/jmor.20407

Chaves AV, Freitas GHS, Vasconcelos MF *et al*. Biogeographic patterns, origin and speciation of the endemic birds from eastern Brazilian mountaintops: a review. *Systematics and Biodiversity* 2014;**13**:1–16. https://doi.org/10.1080/14772000.2014.972477

Chaves AV, Vasconcelos MF, Freitas GHS *et al*. Vicariant events in the montane hummingbird genera *Augastes* and *Schistes* in South America. *Ibis* 2020;**162**:1060–7. https://doi.org/10.1111/ibi.12777

Colli GR, Fenker J, Tedeschi LG *et al*. In the depths of obscurity: knowledge gaps and extinction risk of Brazilian worm lizards (Squamata, Amphisbaenidae). *Biological Conservation* 2016;**204**:51–62. https://doi.org/10.1016/j.biocon.2016.07.033

Colli-Silva M, Vasconcelos TNC, Pirani JR. Outstanding plant endemism levels strongly support the recognition of *campo rupestre* provinces in mountaintops of eastern South America. *Journal of Biogeography* 2019;**46**:1723–33.

Correcher EJ, Hervías-Parejo S, Ruíz de Ybáñez Carnero R *et al*. Environmental and morphological drivers of mutualistic plant–lizard interactions: a global review. *Ecography* 2023;**2**:e06425.

Costa LM, Rodrigues M. Bird community structure and dynamics in the campos rupestres of southern Espinhaço Range, Brazil: diversity, phenology and conservation. *Revista Brasileira de Ornitologia* 2012;**20**:132–47.

Damasceno R, Strangas ML, Carnaval AC *et al*. Revisiting the vanishing refuge model of diversification. *Frontiers in Genetics* 2014;**5**:108535.

Datovo A, Bockmann FA. Dorsolateral head muscles of the catfish families Nematogenyidae and Trichomycteridae (Siluriformes: Loricarioidei): comparative anatomy and phylogenetic analysis. *Neotropical Ichthyology* 2010;**8**:193–246. https://doi.org/10.1590/s1679-62252010000200001

de Pinna MCC. Phylogenetic relationship of neotropical Siluriformes (Teleostei, Ostariophysi): historical overview and synthesis of hypotheses. In: Malabarba LR, Reis RE, Vari RP *et al.* (eds), *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre: EDIPUCRS, 2018, 279–330.

Derryberry EP, Claramunt S, Derryberry G *et al*. Lineage diversification and morphological evolution in a large-scale continental radiation: the Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution* 2011;**65**:2973–86. https://doi.org/10.1111/j.1558-5646.2011.01374.x

Domingos FMCB, Colli GR, Lemmon A *et al*. In the shadows: phylogenomics and coalescent species delimitation unveil cryptic diversity in a Cerrado endemic lizard (Squamata: *Tropidurus*). *Molecular Phylogenetics and Evolution* 2017;**107**:455–65. https://doi.org/10.1016/j.ympev.2016.12.009

Eterovick PC, Brandão RA, Brandao RA. A description of the tadpoles and advertisement calls of members of the *Hyla pseudopseudis* group. *Journal of Herpetology* 2001;**35**:442–50. https://doi.org/10.2307/1565962

Faivovich J, Haddad CF, Garcia PC *et al*. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. *Bulletin of the American Museum of Natural History* 2005;**294**:1–240.

Faustino TC, Machado CG. Frugivoria por aves em uma área de campo rupestre na Chapada Diamantina, BA. *Ararajuba* 2006;**14**:137–43.

Fernandes GW, Barbosa NPU, Alberton B *et al*. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. *Biodiversity and Conservation* 2018;**27**:2587–603. https://doi.org/10.1007/s10531-018-1556-4

Flantua SGA, Hooghiemstra H. Historical connectivity and mountain biodiversity. In: Hoorn C, Perrigo A, Antonelli A (eds), *Mountains, Climate and Biodiversity*. Oxford, UK: Wiley-Blackwell, John Wiley & Sons Ltd, 2018, 171–85.

Flantua SGA, O'Dea A, Onstein RE *et al*. The flickering connectivity system of the north Andean páramos. *Journal of Biogeography* 2019;**46**:1808–25.

Flantua SG, Payne D, Borregaard MK *et al*. Snapshot isolation and isolation history challenge the analogy between mountains and islands used to understand endemism. *Global Ecology and Biogeography* 2020;**29**:1651–73.

Fonseca RBS, Funch LS, Borba EL. Dispersão de sementes de *Melocactus glaucescens* e *M. paucispinus* (Cactaceae), no Município de Morro do Chapéu, Chapada Diamantina–BA. [Seed dispersal in *Melocactus glaucescens* and *M. paucispinus* (Cactaceae) at Morro do Chapúe, Chapada Diamantina, Bahia]. *Acta Botanica Brasilica* 2012;**26**:481–92. https://doi.org/10.1590/s0102-33062012000200024

Foote M. The evolution of morphological diversity. *Annual Review of Ecology and Systematics* 1997;**28**:129–52. https://doi.org/10.1146/annurev.ecolsys.28.1.129

Franceschinelli EV, Jacobi CM, Drummond MG *et al*. The genetic diversity of two Brazilian *Vellozia* (Velloziaceae) with different patterns of spatial distribution and pollination biology. *Annals of Botany* 2006;**97**:585–92. https://doi.org/10.1093/aob/mcl007

Freitas GHS, Chaves AV, Costa LM *et al*. A new species of *Cinclodes* from the Espinhaço Range, southeastern Brazil: insights into the biogeographical history of the South American highlands. *Ibis* 2012;**154**:738–55. https://doi.org/10.1111/j.1474-919x.2012.01268.x

García-Rodríguez A, Martínez PA, Oliveira BF *et al.* Amphibian speciation rates support a general role of mountains as biodiversity pumps. *The American Naturalist* 2021;**198**:E68–79. https://doi.org/10.1086/715500

Genrich CM, Mello MAR, Silveira FAO *et al.* Duality of interaction outcomes in a plant–frugivore multilayer network. *Oikos* 2017;**126**:361–8. https://doi.org/10.1111/oik.03825

Gonçalves PR, Christoff AU, Machado LF *et al.* Unraveling deep branches of the Sigmodontinae tree (Rodentia: Cricetidae) in eastern South America. *Journal of Mammalian Evolution* 2020;**27**:139–60. https://doi.org/10.1007/s10914-018-9444-y

Graboski R, Grazziotin FG, Mott T *et al.* The phylogenetic position of Ridley's worm lizard reveals the complex biogeographic history of New World insular amphisbaenids. *Molecular Phylogenetics and Evolution* 2022;**173**:107518. https://doi.org/10.1016/j.ympev.2022.107518

Guedes TB, Azevedo JAR, Bacon CD *et al.* Diversity, endemism, and evolutionary history of montane biotas outside the Andean region. In: Rull V, Carnaval AC (eds), *Neotropical Diversification: Patterns and Processes*. Cham, Switzerland: Springer International, 2020, 299–328.

Guedes TB, Entiauspe-Neto OM, Costa HC. Lista de répteis do Brasil: atualização de 2022. *Herpetologia Brasileira* 2023;**12**:56–161.

Guerra TJ, Pizo MA. Asymmetrical dependence between a Neotropical mistletoe and its avian seed disperser. *Biotropica* 2014;**46**:285–93. https://doi.org/10.1111/btp.12112

Guerra TJ, Galetto L, Silva WR. Nectar secretion dynamic links pollinator behavior to consequences for plant reproductive success in the ornithophilous mistletoe *Psittacanthus robustus*. *Plant Biology* 2014;**16**:956–66. https://doi.org/10.1111/plb.12146

Guerra TJ, Carstensen DW, Morellato LPC *et al.* Mutualistic interactions among free-living species in Rupestrian Grasslands. In: Fernandes GW (ed.), *Ecology and Conservation of Mountaintop Grasslands in Brazil*. Cham, Switzerland: Springer International, 2016, 291–314.

Guerra TJ, Dayrell RLC, Arruda AJ *et al.* Intraspecific variation in fruit–frugivore interactions: effects of fruiting neighborhood and consequences for seed dispersal. *Oecologia* 2017;**185**:233–43. https://doi.org/10.1007/s00442-017-3943-z

Guerra TJ, Messeder JVS, Arruda A *et al.* Handling by avian frugivores affects diaspore secondary removal. *PLoS One* 2018;**13**:e0202435.

Guillory WX, de Medeiros Magalhães F, Coelho FEA *et al.* Geoclimatic drivers of diversification in the largest arid and semi-arid environment of the Neotropics: perspectives from phylogeography. *Molecular Ecology* 2024;**33**:e17431. https://doi.org/10.1111/mec.17431

Haffer J. Speciation in Amazonian Forest birds: most species probably originated in forest refuges during dry climatic periods. *Science* 1969;**165**:131–7. https://doi.org/10.1126/science.165.3889.131

Hendry AP, Nosil P, Rieseberg LH. The speed of ecological speciation. *Functional Ecology* 2007;**21**:455–64. https://doi.org/10.1111/j.1365-2435.2007.01240.x

Heyer WR. A new genus and species of frog from Bahia, Brazil (Amphibia: Anura: Leptodactylidae) with comments on the zoogeography of the Brazilian campos rupestres. *Proceedings of the Biological Society of Washington* 1999;**112**:19–39. https://biostor.org/reference/74268

Hopper SD, Lambers H, Silveira FAO *et al.* OCBIL theory examined: reassessing evolution, ecology and conservation in the world's ancient, climatically buffered and infertile landscapes. *Biological Journal of the Linnean Society* 2021;**133**:266–96. https://doi.org/10.1093/biolinnean/blaa213

ICMBio. *Sistema de Avaliação do Risco de Extinção da Biodiversidade – SALVE*, 2024. https://salve.icmbio.gov.br/

Immerzeel WW, Lutz AF, Andrade M *et al.* Importance and vulnerability of the world's water towers. *Nature* 2020;**577**:364–9. https://doi.org/10.1038/s41586-019-1822-y

IUCN - IUCN SSC Amphibian Specialist Group & Instituto Boitatá de Etnobiologia e Conservação da Fauna. *The IUCN Red List of Threatened Species, 2023*. 2023. https://www.iucnredlist.org/

Jacobi CM, Antonini Y. Pollinators and defense of *Stachytarpheta glabra* (Verbenaceae) nectar resources by the hummingbird *Colibri serrirostris* (Trochilidae) on ironstone outcrops in south-east Brazil. *Journal of Tropical Ecology* 2008;**24**:301–8. https://doi.org/10.1017/s0266467408005051

Jansson R, Dynesius M. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. *Annual Review of Ecology and Systematics* 2002;**33**:741–77. https://doi.org/10.1146/annurev.ecolsys.33.010802.150520

Kessler M, Abrahamczyk S, Krömer T. The role of hummingbirds in the evolution and diversification of Bromeliaceae: unsupported claims and untested hypotheses. *Botanical Journal of the Linnean Society* 2020;**192**:592–608. https://doi.org/10.1093/botlinnean/boz100

Lagomarsino LP, Forrestel EJ, Muchhala N *et al.* Repeated evolution of vertebrate pollination syndromes in a recently diverged Andean plant clade. *Evolution* 2017;**71**:1970–85. https://doi.org/10.1111/evo.13297

Leite FSF, Eterovick PC. Description of the tadpole of *Bokermannohyla martinsi* (Bokermann, 1964) (Anura: Hylidae), morphological and ecological comparison with related *Bokermannohyla* tadpoles. *Journal of Herpetology* 2010;**44**:431–40. https://doi.org/10.1670/09-079.1

Leite FSF, Eterovick PC, Juncá FA. Status do conhecimento, endemismo e conservação de anfíbios anuros da Cadeia do Espinhaço, Brasil. [Knowledge, endemism and conservation of anurans in the Espinhaço Range, Brazil]. *Megadiversidade* 2008;**4**:158–76.

Lessa LG, Costa BMA, Rossoni DM *et al.* Mamíferos da Cadeia do Espinhaço: riqueza, ameaças e estratégias para conservação. [Mammals from the Espinhaço Range> richness, threats and conservation strategies]. *Megadiversidade* 2008;**4**:218–32.

Lessa LG, Geise L, Costa FN. Effects of gut passage on the germination of seeds ingested by didelphid marsupials in a Neotropical savanna. *Acta Botanica Brasilica* 2013;**27**:519–25. https://doi.org/10.1590/s0102-33062013000300009

Lins ACR, de Magalhães RF, Costa RN *et al.* The larvae of two species of *Bokermannohyla* (Anura, Hylidae, Cophomantini) endemic to the highlands of central Brazil. *Zootaxa* 2018;**4527**:501–20. https://doi.org/10.11646/zootaxa.4527.4.3

Lopes LE, Marçal BF, Chaves AV. The patchy distribution of the Pale-throated Serra-Finch *Embernagra longicauda* (Aves: Thraupidae) in the eastern Brazilian mountaintops: the overlooked campos rupestres of the Rio Doce valley. *North-Western Journal of Zoology, Oradea* 2016;**12**:373–6.

Lopes LE, Vasconcelos MF, Gonzaga LP. A cryptic new species of hummingbird of the *Campylopterus largipennis* complex (Aves: Trochilidae). *Zootaxa* 2017;**4268**:1–33. https://doi.org/10.11646/zootaxa.4268.1.1

Love SJ, Schweitzer JA, Woolbright S *et al.* Sky Islands are a global tool for predicting the ecological and evolutionary consequences of climate change. *Annual Review of Ecology, Evolution, and Systematics* 2023;**54**:219–36.

Lujan NK, Conway KW. Life in the fast lane: a review of rheophily in freshwater fishes. In: Riesch R, Tobler M, Plath M (eds), *Extremophile Fishes*. Cham, Switzerland: Springer, 2015, 107–36.

Lundberg J, Moberg F. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 2003;**6**:0087–98. https://doi.org/10.1007/s10021-002-0150-4

Machado CG, Coelho AG, Santana CS *et al.* Beija-flores e seus recursos florais em uma área de campo rupestre da Chapada Diamantina, Bahia. *Revista Brasileira de Ornitologia* 2007;**15**:267–79.

Magalhães RF, Lemes P, Santos MTT *et al.* Evidence of introgression in endemic frogs from the *campo rupestre* contradicts the reduced hybridization hypothesis. *Biological Journal of the Linnean Society* 2021;**133**:561–76.

Magalhães RF, Ramos EK, Bandeira LN *et al.* Integrative species delimitation uncovers hidden diversity within the *Pithecopus hypochondrialis* species complex (Hylidae, Phyllomedusinae) and its phylogeography reveals Plio-Pleistocene connectivity among Neotropical savannas. *Molecular Phylogenetics and Evolution* 2024;**190**:107959.

Maianne M, Fieker CZ, Dias MM *et al.* Hummingbird-plant networks in rupestrian fields and riparian forests in altitudinal areas of the Serra da Canastra National Park, Minas Gerais, Brazil. *Biota Neotropica* 2022;**22**:e20211284. https://doi.org/10.1590/1676-0611-BN-2021-1284

Mângia S, Amaral G, Müller M *et al.* New species of *Rupirana* (Heyer, 1999) (Anura, Leptodactylidae) from Serra do Assuruá, center-north of Bahia state, Brazil. *Journal of Vertebrate Biology* 2025;**74**:24121–1.

Marques RB, Haddad CFB, Garda AA. There and back again from monotypy: a new species of the casque-headed *Corythomantis* Boulenger 1896 (Anura, Hylidae) from the Espinhaço mountain range, Brazil. *Herpetologica* 2021;**77**:56–71.

Maruyama PK, Oliveira GM, Ferreira C *et al.* Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften* 2013;**100**:1061–8. https://doi.org/10.1007/s00114-013-1111-9

Maruyama PK, Justino DG, Oliveira PE. Does intraspecific behavioural variation of pollinator species influence pollination? A quantitative study with hummingbirds and a Neotropical shrub. *Plant Biology* 2016;**18**:913–9. https://doi.org/10.1111/plb.12492

Matzke NJ. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers in Biogeography* 2013;**5**:242–8.

McCormack JE, Huang H, Knowles LL. Sky islands. In: Gillespie RG, Clague D (eds), *Encyclopedia of Islands*. Berkeley, CA: University of California Press, 2009, 839–43.

Miola DTB, Ramos VDV, Silveira FAO. A brief history of research in *campo rupestre*: identifying research priorities and revisiting the geographical distribution of an ancient, widespread Neotropical biome. *Biological Journal of the Linnean Society* 2021;**133**:464–80. https://doi.org/10.1093/biolinnean/blaa175

Monteiro BL, Camargo MGG, Loiola PDP *et al.* Pollination in the *campo rupestre*: a test of hypothesis for an ancient tropical mountain vegetation. *Biological Journal of the Linnean Society* 2021;**133**:512–30. https://doi.org/10.1093/biolinnean/blaa205

Morrone JJ, Escalante T, Rodríguez-Tapia G *et al.* Biogeographic regionalization of the Neotropical region: new map and shapefile. *Anais da Academia Brasileira de Ciencias* 2022;**94**:e20211167. https://doi.org/10.1590/0001-3765202220211167

Nascimento AC, Chaves AV, Leite FSF *et al.* Past vicariance promoting deep genetic divergence in an endemic frog species of the Espinhaço Range in Brazil: the historical biogeography of *Bokermannohyla saxicola* (Hylidae). *PLoS One* 2018;**13**:e0206732. https://doi.org/10.1371/journal.pone.0206732

Nogueira CC, Argôlo AJ, Arzamendia V *et al.* Atlas of Brazilian snakes: verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *South American Journal of Herpetology* 2019;**14**:1–274.

Norões AM, Ursine RL, Souza ALM *et al.* Small mammals (Didelphimorphia, Chiroptera and Rodentia) of Espinhaço Range in eastern Brazil: checklist updates and implications for species conservation. *Revista Espinhaço* 2023;**12**:1–21.

Ochoa LE, Roxo FF, DoNascimiento C *et al.* Multilocus analysis of the catfish family Trichomycteridae (Teleostei: Ostariophysi: Siluriformes) supporting a monophyletic Trichomycterinae. *Molecular Phylogenetics and Evolution* 2017;**115**:71–81. https://doi.org/10.1016/j.ympev.2017.07.007

Ochoa LE, Datovo A, DoNascimiento C *et al.* Phylogenomic analysis of trichomycterid catfishes (Teleostei: Siluriformes) inferred from ultraconserved elements. *Scientific Reports* 2020;**10**:2697. https://doi.org/10.1038/s41598-020-59519-w

Oliveira FR, Gehara M, Solé M *et al.* Quaternary climatic fluctuations influence the demographic history of two species of sky-island endemic amphibians in the Neotropics. *Molecular Phylogenetics and Evolution* 2021;**160**:107113.

Oswald CB, Lemes P, Thome MTC *et al.* Colonization rather than fragmentation explains the geographical distribution and diversification of treefrogs endemic to Brazilian shield sky islands. *Journal of Biogeography* 2022;**49**:682–98. https://doi.org/10.1111/jbi.14320

Oswald CB, Magalhães RF, Pezzuti TL *et al.* Knowledge status, endemism, and conservation of anuran amphibians from Espinhaço Range, Brazil: what we know and what are the main opportunities for future studies? *Biota Neotropica* 2024;**24**:e20241640.

Pardiñas UF, Lessa G, Teta P *et al.* A new genus of Sigmodontine rodent from eastern Brazil and the origin of the tribe Phyllotini. *Journal of Mammalogy* 2014;**95**:201–15.

Perrigo A, Hoorn C, Antonelli A. Why mountains matter for biodiversity. *Journal of Biogeography* 2020;**47**:315–25. https://doi.org/10.1111/jbi.13731

Pezzuti TL, Teixeira-Santos MT, Velasquez-Martins S *et al.* The tadpoles of two species of the *Bokermannohyla circumdata* group (Hylidae, Cophomantini). *Zootaxa* 2015;**4048**:151–73.

Pezzuti TL, Leite FSF, Rossa-Feres DC *et al.* The tadpoles of the Iron Quadrangle, southeastern Brazil: a baseline for larval knowledge and anuran conservation in a diverse and threatened Region. *South American Journal of Herpetology* 2021;**22**:1–107.

Provan J, Bennett KD. Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology & Evolution* 2008;**23**:564–71. https://doi.org/10.1016/j.tree.2008.06.010

Rahbek C, Borregaard MK, Colwell RK *et al.* Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* 2019;**365**:1108–13. https://doi.org/10.1126/science.aax0149

Rapini A, Bitencourt C, Luebert F *et al.* An escape-to-radiate model for explaining the high plant diversity and endemism in campos rupestres. *Biological Journal of the Linnean Society* 2021;**133**:481–98. https://doi.org/10.1093/biolinnean/blaa179

Recoder R, Prates I, Marques-Souza S *et al.* Lizards from the Lost World: two new species and evolutionary relationships of the Pantepui highland *Riolama* (Gymnophthalmidae). *Zoological Journal of the Linnean Society* 2020;**190**:271–97. https://doi.org/10.1093/zoolinnean/zlz168

Ribeiro AC. Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. *Neotropical Ichthyology* 2006;**4**:225–46. https://doi.org/10.1590/s1679-62252006000200009

Rodrigues LC, Rodrigues M. Flowers visited by hummingbirds in the open habitats of the southeastern Brazilian mountaintops: species composition and seasonality. *Brazilian Journal of Biology* 2014;**74**:659–76. https://doi.org/10.1590/bjb.2014.0097

Rodrigues M, Freitas GHS, Costa LM *et al.* Avifauna, Alto do Palácio, Serra do Cipó National Park, state of Minas Gerais, southeastern Brazil. *Check List* 2011;**7**:151–61.

Rosauer DF, Jetz W. Phylogenetic endemism in terrestrial mammals. *Global Ecology and Biogeography* 2015;**24**:168–79. https://doi.org/10.1111/geb.12237

Rull V, Vegas-Vilarrúbia T, Huber O *et al. Biodiversity of Pantepui: the Pristine Lost World of Neotropical Guiana Highlands*. London: Academic Press, 2019.

Santana DJ, Ragalzi E, Koroiva R *et al.* Lineage diversification of the Sky Island treefrog *Scinax curicica* (Anura, Hylidae) in the Espinhaço Mountain range. *Biological Journal of the Linnean Society* 2024;**142**:58–67. https://doi.org/10.1093/biolinnean/blad125

Santos MTT, Magalhães RF, Lyra ML *et al.* Multilocus phylogeny of Paratelmatobiinae (Anura: Leptodactylidae) reveals strong spatial structure and previously unknown diversity in the Atlantic Forest hotspot. *Molecular Phylogenetics and Evolution* 2020;**148**:106819. https://doi.org/10.1016/j.ympev.2020.106819

Sazima M. Hummingbird pollination of *Barbacenia flavia* (Velloziaceae) in Serra do Cipó, Minas Gerais, Brazil. *Flora* 1977;**166**:239–47. https://doi.org/10.1016/s0367-2530(17)32141-2

Sazima I, Sazima M. Quiropterofilia em *Lafoensia pacari* St. Hil. (Lythraceae) na Serra do Cipó, Minas Gerais. *Ciência e Cultura* 1975;**27**:404–16.

Sazima I, Vogel S, Sazima M. Bat pollination of *Encholirium glaziovii*, a terrestrial bromeliad. *Plant Systematics Evolution* 1989;**168**:167–79.

Segalla MV, Berneck B, Canedo C *et al.* List of Brazilian amphibians. *Herpetologia Brasileira* 2021;**10**:121–216.

Silveira FAO, Mafia P, Lemos-Filho JP *et al.* Species-specific outcomes of avian gut passage on germination of Melastomataceae seeds. *Plant Ecology and Evolution* 2012;**145**:350–5.

Silveira FAO, Negreiros D, Barbosa NPU *et al*. Ecology and evolution of plant diversity in the endangered *campo rupestre*: a neglected conservation priority. *Plant and Soil* 2016;**403**:129–52. https://doi.org/10.1007/s11104-015-2637-8

Simon MF, Grether R, de Queiroz LP *et al*. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by *in situ* evolution of adaptations to fire. *Proceedings of the National Academy of Sciences of the United States of America* 2009;**106**:20359–64. https://doi.org/10.1073/pnas.0903410106

Smith MA, Green DM. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 2005;**28**:110–28.

Stroud JT, Losos JB. Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* 2016;**47**:507–32. https://doi.org/10.1146/annurev-ecolsys-121415-032254

Tenorio EA, Montoya P, Norden N *et al*. Mountains exhibit a stronger latitudinal diversity gradient than lowland regions. *Journal of Biogeography* 2023;**50**:1026–36. https://doi.org/10.1111/jbi.14597

Uchôa LR, Delfim FR, Mesquita DO *et al*. Lizards (Reptilia: Squamata) from the Caatinga, northeastern Brazil: detailed and updated overview. *Vertebrate Zoology* 2022;**72**:599–659. https://doi.org/10.3897/vz.72.e78828

Vanzolini PE. A new *Gymnodactylus* from Minas Gerais, Brasil, with remarks on the genus, on the area and on montane endemisms in Brazil (Sauria, Gekkonidae). *Papéis Avulsos de Zoologia* 1982;**34**:403–13. https://doi.org/10.11606/0031-1049.1982.34.p403-413

Vanzolini PE, Williams EE. The vanishing refuge: a mechanism for ecogeographic speciation. *Papéis Avulsos de Zoologia* 1981;**34**:251–5. https://doi.org/10.11606/0031-1049.1980.34.p251-255

Vasconcelos MF. Mountaintop endemism in eastern Brazil: why some bird species from campos rupestres of the Espinhaço Range are not endemic to the Cerrado region? *Revista Brasileira de Ornitologia* 2008;**16**:348–62.

Vasconcelos MF, Rodrigues M. Patterns of geographic distribution and conservation of the open-habitat avifauna of southeastern Brazilian mountaintops (campos rupestres and campos de altitude). *Papéis Avulsos de Zoologia* 2010;**50**:1–29.

Vasconcelos MF, Maldonado-Coelho M, Buzzetti DRC. Range extensions for the Gray-backed Tachuri (*Polystictus superciliaris*) and the Pale-throated Serra-finch (*Embernagra longicauda*) with a revision on their geographic distribution. *Ornitología Neotropical* 2003;**14**:477–89.

Vasconcelos MF, Chaves AV, Santos FR. First record of *Augastes scutatus* for Bahia refines the location of a purported barrier promoting speciation in the Espinhaço Range, Brazil. *Revista Brasileira de Ornitologia* 2012;**20**:443–6.

Vasconcelos TN, Alcantara S, Andrino CO *et al*. Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. *Proceedings of the Royal Society B: Biological Sciences* 2020;**287**:20192933.

Wagner PJ, Estabrook GF. Trait-based diversification shifts reflect differential extinction among fossil taxa. *Proceedings of the National Academy of Sciences of the United States of America* 2014;**111**:16419–24. https://doi.org/10.1073/pnas.1406304111

Weksler M, Bonvicino CR. Taxonomy of pigmy rice rats genus *Oligoryzomys* Bangs, 1900 (Rodentia, Sigmodontinae) of the Brazilian Cerrado, with the description of two new species. *Arquivos do Museu Nacional* 2005;**63**:113–30.

Zanata AM, Primitivo C. Natural history of *Copionodon pecten*, an endemic trichomycterid catfish from Chapada Diamantina in northeastern Brazil. *Journal of Natural History* 2013;**48**:203–28. https://doi.org/10.1080/00222933.2013.809168