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REVIEW ARTICLE

Indian rock outcrops: review of flowering plant diversity, adaptations, floristic composition and endemism

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Abstract

Rock outcrops are unique habitats in terms of their geological and ecological specializations, soil availability, water seasonality, and environmental extremes. These habitats have attracted the attention of many researchers worldwide in the last few decades. Indian rock outcrops spread throughout the country with more concentration in the Western Ghats region, supporting many endemic and unique habitat specialist species. Despite Indian outcrops having become hotspots for novel species discoveries in recent times, ecological studies on them are still in their infancy. In the present review, we discuss studies, research gaps, and the scope for future investigations on Indian outcrops. We also compare outcrop studies across the world with the Indian systems in order to understand their uniqueness and peculiarities. Literature and observations revealed the presence of 390 taxa on rock outcrops of the Western Ghats with various adaptive traits such as desiccation tolerance, succulence, carnivory, and geophytism, a trend common to most of the tropical outcrops. The dominance of Poaceae endemics, large extents of monocotyledonous mats, and underrepresentation of succulence are unique features of Indian rock outcrops. In the light of various disturbances, faced by Indian outcrops, further studies that would lay a foundation on which conservation strategies can be formulated are a want of time.

Keywords Ephemeral vegetation · Ferricretes · India · Rock outcrops · Western Ghats

Introduction

Rock outcrops is a general term used for a wide array of landscapes with the majority of their area as exposed rock and are of different geological origin as well as history (Porembski and Barthlott 2000a). Inselbergs are dome-like monolithic structures; cliffs are vertical rocky areas whereas plateaus are rocky flat structures. Technically, rock outcrops can be distinguished from surrounding areas by having an average of 55% of the area as exposed rock (Wiser and White 2007). Due to this exposed rock, the environment is extreme and is generally characterized by scorching and arid seasons for the majority of the time in a year and short precipitation spells creating seasonal wet conditions (Porembski 2007). As rock outcrops are also characterized by surface depressions that are water-filled during the wet season, they are considered as ephemeral wetlands (Johnson and Rogers 2003). This cyclic availability of water results in the ephemeral nature of vegetation marked by an alteration between the aquatic and terrestrial phases (Deil 2005).

Rock outcrops are distributed throughout the world and have diverse base rocks ranging from granites to ferricretes to ironstones (Fig. 1). West Africa, Brazil, and Madagascar shelter inselbergs, a subtype of rock outcrops, with granite or gneiss as a base rock (Porembski and Barthlott 1996). Brazil is home to a variety of outcrops such as ferricretes, ironstones (commonly known as 'canga'), sandstones, and inselbergs (Porembski et al. 1994, 1997; Jacobi et al. 2007; Jacobi and Carmo 2008). Ferricretes are also found in other parts of the world, such as Central and West Africa and India (Porembski et al. 1994; Ollier and Sheth 2008). Sandstone outcrops are distributed in parts of Guinea, Brazil,

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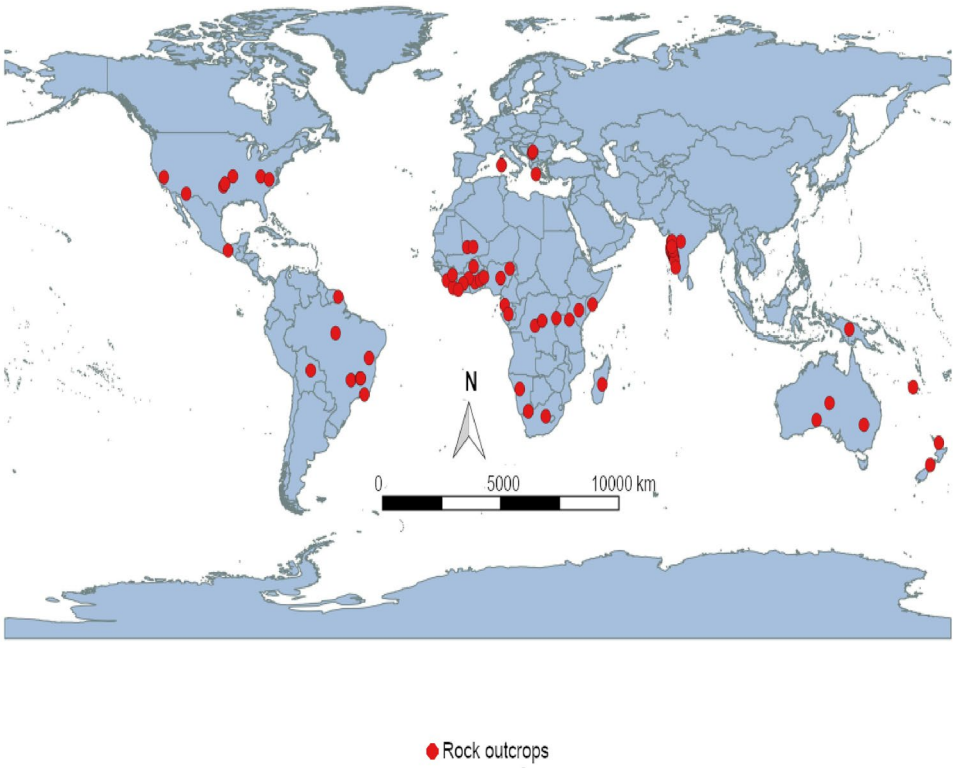

Fig. 1 Distribution of rock outcrops throughout the world based on georeferenced data from the published literature

Madagascar and Australia (Porembski et al. 1994; Hopper et al. 2016; Silveira et al. 2016; Rabarimanarivo et al. 2017). Granite inselbergs with dolerite dykes from Namibia (Burke 2002), and Quartizitic outcrops in Central Africa (Porembski et al. 1994) are also considered as subtypes of rock outcrops. The northeastern region of the United States of America (USA) consists of serpentine outcrops that are poor in minerals required by plants and rich in heavy toxic metals (Harrison and Inouye 2002; Anderson et al. 2007; Rajakaruna et al. 2009). Rock outcrops are often referred to as terrestrial islands because of their unique structure and ecological distinctness from the surrounding areas (Porembski and Barthlott 2000a; Porembski 2007). Pantropical outcrops of West Africa, Madagascar, Australia, Brazil, NE USA and SE USA have been well studied ecologically presenting detailed observations on flora, vegetation composition and special life-history adaptations associated with outcrop plants (Porembski et al. 1996, 1997, 1998; Porembski and Barthlott 1997; Hopper 2000; Burke 2002; Porembski 2005, 2007; Anderson et al. 2007; Jacobi et al. 2007; Silveira et al. 2016; de Paula et al. 2017).

India, like other tropical regions, is a mega-diverse country having a variety of habitats supporting unique flora and fauna. It is home to four of the world's 36 biodiversity hotspots (Mittermeier et al. 2011; Noss et al. 2015). Western Ghats escarpment, one of these four hotspots, is a mountain chain parallel to the west coast of India (Myers et al. 2000; Mittermeier et al. 2011). The Western Ghats are divided into northern, central, and southern parts based on peculiar features associated with varying levels of wetness resulting due to uneven precipitation. A decrease in the amount of rainfall with an increase in the dry period length from south to north is a peculiar feature of Western Ghats (Pascal 1988). The magnitude of precipitation received separates these three regions and affects associated biological entities (Mani 1974; Karthikeyan 1996). Within the Western Ghats escarpments, there are many biologically significant habitats like forests, sholas supporting many rare and endemic species that are the focus of exploratory studies in the last few decades (Ramesh and Pascal 1997; Kumar et al. 2012; Nayar et al. 2014; Singh et al. 2015; Shigwan et al. 2020). Along with these habitats, rock outcrops are present at both low and high elevations and form an essential component of the landscape of Western Ghats. The vegetation of Indian outcrops has been documented in the regional floras for a long time, but only a few of them (Potdar et al. 2012; Datar and Lakshminarasimhan 2013) consider outcrops as a distinct habitat. However, in the last two decades, their ecological importance and uniqueness have been recognized, which has resulted in sporadic floristic inventories and novel species descriptions. Despite these scattered studies documenting the endemic and rare species of plants, rock outcrop ecology has largely remained understudied.

In the present review, we have attempted to cover the distribution, types, and current classification of outcrops in India, focusing on the Western Ghats where they are

concentrated. We provide an overview of research on vegetation describing plant communities inhabiting Indian outcrops with their spatial and temporal patterns, classification of adaptive strategies shown by outcrop plants from India, and their current state of research comparing them with the studies from the other parts of the world. For comparison with Indian outcrops, we have considered studies from inselbergs, ferricretes, sandstone and ironstone outcrops in tropical regions mainly from Africa, Madagascar, Brazil, and Australia in order to evaluate the present situation of research in India. We discuss the past and present research, research gaps, and future research opportunities for Indian outcrops.

Materials and methods

Literature survey

Understanding the geological classification of Indian rock outcrops

The literature on the geology of India was consulted to understand the uniqueness, features, and classification of rock outcrops. Particular emphasis was laid on Western Ghats geology as this region supports a large number of outcrops (Widdowson and Cox 1996; Gunnell and Radhakrishna 2001; Ollier and Sheth 2008).

Floristic checklist preparation and analysis

Species inventory data from ferricretes and basalt mesa of Western Ghats were pooled together, combining various sources such as regional floras and publications documenting floristic diversity and novel species discoveries from outcrops (Lekhak and Yadav 2012; Watve 2013; Datar and Lakshminarasimhan 2013; Borude et al. 2016; Chandore et al. 2016a, b; Darshetkar et al. 2017; Kolte et al. 2018, 2019; Bokil et al. 2020, Chandore et al. 2021a, b). Major herbaria like Agharkar Herbarium of Maharashtra Association (AHMA), Botanical Survey of India, Western Regional Center, Pune (BSI), Blatter herbarium, Mumbai (BLAT) were consulted. The data obtained from the literature (Lekhak and Yadav 2012; Watve 2013), and herbarium studies, supplemented with our observations were used for preparing a working list of 390 taxa (385 species) from 31 plateaus of Western Ghats (henceforth referred to as 'outcrop checklist'). The outcrop checklist consists of only herbaceous species. Endemic status was assigned to the 'outcrop checklist' following Nayar et al. (2014) and Singh et al. (2015). Besides, the 'outcrop checklist' included information under various heads, such as the name of the family, the occurrence on a particular type of outcrop. The dominance of plant families, similarities, and differences in the vegetation based on the characteristics such as elevation, base rock composition, and the proportion of endemics on various types of outcrops were analyzed from the 'outcrop checklist.' Literature about the vegetation of Indian outcrops was studied to understand general features of vegetation, specialized adaptations, conditions required for plant establishment, and types of vegetation that dominate these habitats (Watve 2007, 2008, 2013; Bhattarai et al. 2012; Lekhak and Yadav 2012; Aphale et al. 2019; Kulkarni et al. 2021, 2022a, b).

Comparison of studies from India and other parts of the world

Spatial and temporal pattern

In order to understand spatial and temporal patterns of research carried out on rock outcrops through meta-analysis, the Web of Science database was accessed (April 2020). This database was preferred because of its authoritative and easy-to-use nature compared to other databases. Specific keywords such as 'rock outcrop,' 'inselberg', 'India', and 'Western Ghats' were used. Studies were grouped into different subject categories, such as Geology, Ecology, Plant Sciences, Paleontology, Physical geography, Anthropology, Evolutionary biology, etc. The search results were used for various comparisons and the results are presented in figures and tables. Figures were made in RStudio version 3.6.3 (R Core Team 2020). To find out the temporal and geographical patterns of studies on rock outcrops worldwide, along with the Web of Science database, other literature prior to 1985 using google scholar and backreferencing was also included. Localities from published literature were geo-referenced, and the data were categorized into intervals of ten years to give a better understanding of the region in the focus and longevity of the studies. Maps for the distribution of rock outcrops were prepared in Q-GIS (version-3.4.13), and a photo plate was prepared in LaTex.

Vegetation

Studies on pan-tropical rock outcrops were thoroughly scrutinized for understanding various broad categories of vegetation on outcrops and microhabitat classification. Data were analyzed to find out the diversity and distribution of plant families that are dominant on the outcrops by comparing the checklists from some studies such as de Paula et al. (2017), Porembski and Barthlott (2000a) and Watve (2013).

Endemism

The 'outcrop checklist' was utilized for the understanding of endemism on Indian rock outcrops by categorizing species

into local, regional, and national endemics for regions like northern Western Ghats (NWG), Western Ghats, and India respectively. The term local endemic was adapted after Isik (2011). Species not falling under these endemic categories were considered as widespread.

Adaptive strategies

Various vegetative, reproductive as well as eco-physiological adaptive traits, have been described for inselberg plants (Biedinger et al. 2000; Kluge and Brulfert 2000; Deil 2005). The adaptive trait classification used in the present review for grouping plants of Indian outcrops was adopted after Biedinger et al. (2000), Kluge and Brulfert (2000) and Deil (2005) with slight modification based on our understanding and their occurrence on Indian outcrops.

Results and discussion

Outcrops in India and their current classification

Outcrops is the term applied for habitats composed of freely exposed bedrock that protrudes out above the soil level due to natural reasons like weathering (Allaby 2013). India is home to diverse types of outcrops, including ferricretes, inselbergs, and flat plateaus of certain rock types such as basalt, limestone, and sandstone (Fig. 2). Despite outcrops being a dominant habitat in the country, the Wastelands Atlas of India classifies them under barren rocky/stony waste areas (Watve 2013). Outcrops are particularly dominant habitats of the Western Ghats, where large areas are covered with plateaus, cliffs, and inselbergs. Western Ghats outcrops are geologically well studied and are classified depending on the base rock content and the elevation at which they are located (Widdowson and Cox 1996). Based on geology, different classes of outcrops from the Western Ghats can be summarized as follows (Fig. 2).

1. High-level ferricretes (HLF).

According to Ollier and Sheth (2008), ferricretes is the term used for duricrusts that are rich in iron. High-level ferricretes are lateritic plateaus occurring at higher elevations (800–1000 m a.s.l.) and are located in the northern and the central Western Ghats.

2. Low-level ferricretes (LLF)

Laterite formation is also observed on the Konkan and Malabar Coast, an area bordering the Arabian sea placed at lower elevations (50–200 m a.s.l.) as compared to the Western Ghats (Widdowson and Cox 1996).

3. Basalt Mesa (BM)

Basalt plateaus that occur in predominance between 900 and 1100 m a.s.l. in the northern part of Western Ghats are treated under this class. High-level laterites that cap the basalt summits are absent in the northern part of Western Ghats (Ollier and Sheth 2008) between 18° to 21° N. Instead, the basalt itself is observed.

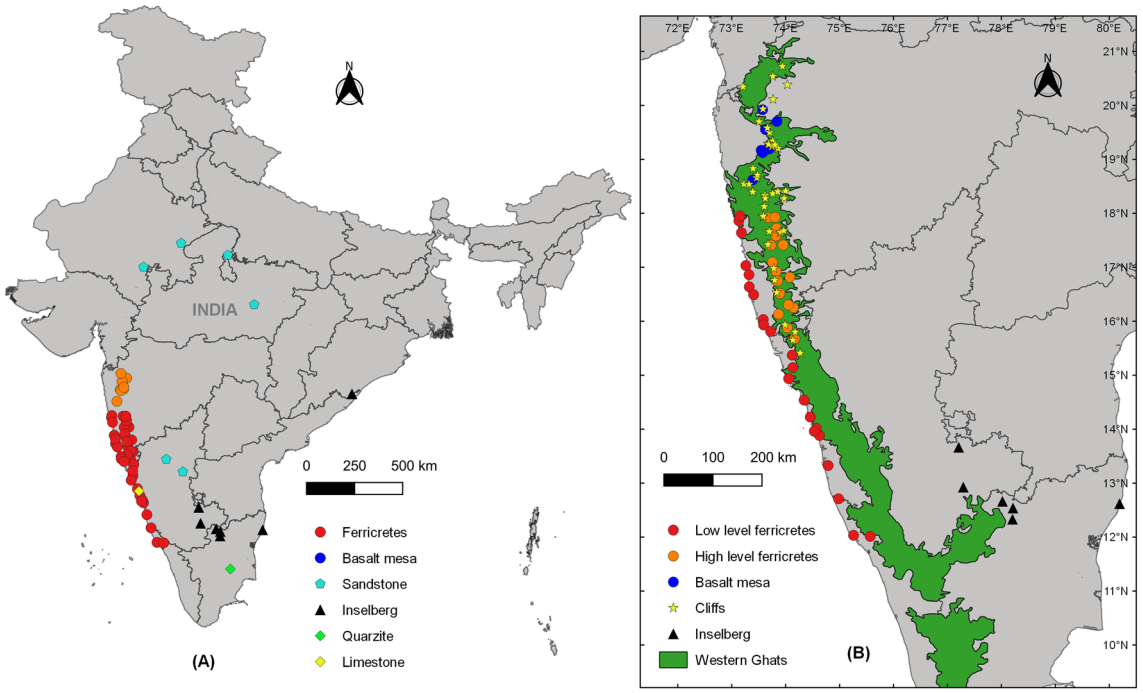

Fig. 2 Occurrence of various types of rock outcrops based on literature and personal observations (**A**) in India (**B**) in Western Ghats, India

4. Inselberg

These are dome-like monolithic structures made of granite or gneiss present in Peninsular India in Karnataka, Tamil Nadu, Kerala, and Odisha. They are the most studied rock outcrops worldwide but least studied in India despite their broader distribution in the country.

5. Cliffs

Cliffs are steep rocky slopes found throughout the country formed naturally along hills, riverbanks, and coastal areas and artificially in the mountain passes as a result of human activities. Except for a solitary study by Datar and Watve (2018), there are hardly any works on cliffs in India, focusing on their biological features and unique vegetation.

Although diverse types of rock outcrops are spread all over India, apart from a few studies in the Western Ghats, there is hardly any literature available from other parts of the country. Moreover, the majority of the studies carried out on rock outcrops in the Western Ghats are focusing on taxonomy with little importance given to its habitat ecology, relating it with the geology of the region.

Spatial and temporal patterns of studies on rock outcrops worldwide

In order to understand the spatial and temporal patterns of studies on outcrops, an analysis based on the data obtained from the Web of Science (1985–2000) was carried out. Searches on the "Web of Science" using keywords such as "Inselberg" or "Rock outcrops' yielded about 8575 results. When these results were categorized based on the subjects, it has been observed that more than 70% of the published literature is focusing on topics related to geology (Fig. 3). Ecology and plant sciences have less than a 10% share in the total publications. We checked the use of different keywords in the publications related to rock outcrops. It was noticed that "rock outcrops" is a widely used term and mostly in publications on geology; whereas "Inselbergs" is mostly used in publications on biology. Two hundred and thirty publications using the combination of keywords "Rock outcrops" and "India" are related to geology or geochemistry. The searches using keywords such as "India" or "Western Ghats" in combination with "Inselbergs" show that studies from India are scarce (Table 1).

The distribution of vegetation and ecology-related publications on outcrops showed an interesting pattern when the publications were classified decade-wise, starting from 1950 till now. Africa, the USA, and parts of Australia are the areas that have pioneered these studies. Several works seem to be concentrating on these regions from 1955 to 1980. After 1980, studies from serpentine outcrops of the USA continued (Fig. 4). Around the 1990s, there were many simultaneous studies from Africa, the USA as well as Brazil, mainly due to efforts of the Inselberg Research group, which involved several researchers from Europe, Africa, and the

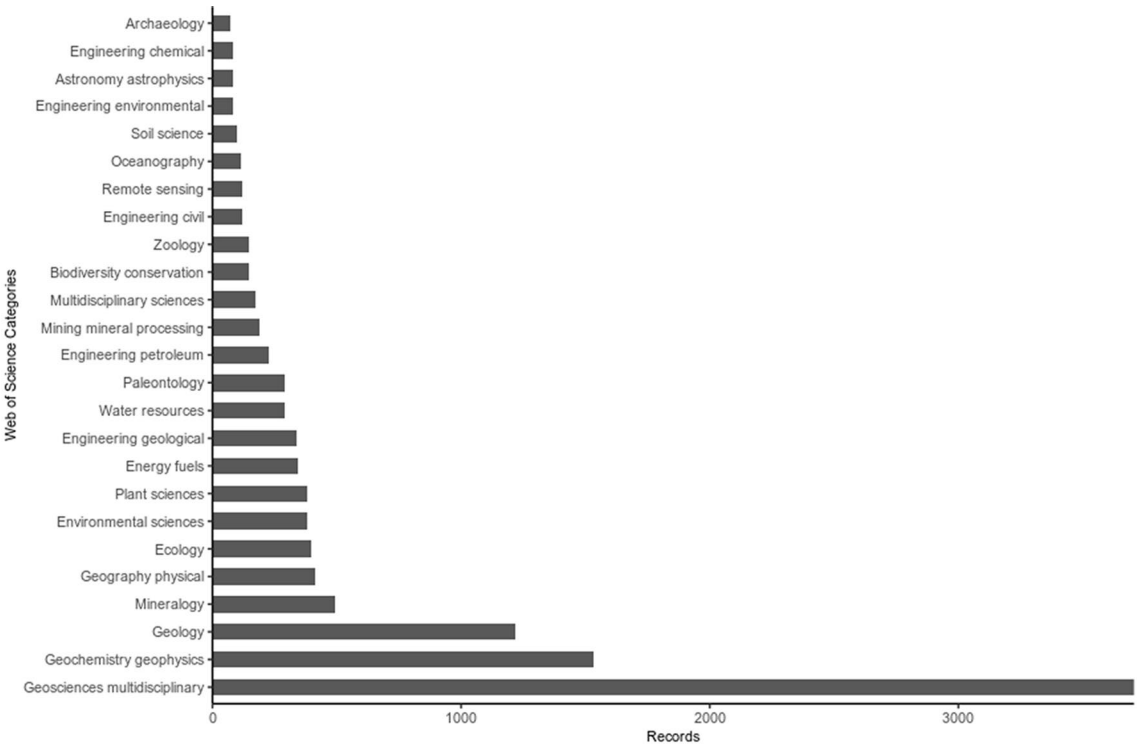

Fig. 3 Subject wise categorization of the published literature using keywords "Inselberg" or "Rock outcrops" on the Web of Science

Table 1 Usage of different keywords in published literature based on Web of Science searches (based on the searches done in April 2020)

Keywords/no. of publications	As topic	As title
Rock outcrops	8334	184
Rock outcrops and India	230	0
Rock outcrops and Western Ghats	17	0
Inselbergs	418	117
Inselbergs and India	5	0
Inselbergs and Western Ghats	0	0

USA. Since the year 2000, a lot of studies from all over the world, including some studies from India, have appeared.

There is an overall increasing trend of publications on the ecology of rock outcrops with maximum publications between 2000 and 2010, with significant contributions from studies on inselbergs of Africa, Brazil, and Madagascar (Fig. 5). Among the tropical outcrops, inselbergs from Africa and Brazil seem to be well worked out, followed by Australia. In India, Watve (2003, 2007) showed the necessity to study these habitats as a unique entity, and a few published works followed these studies. However, the understudies of rock outcrops in India are also reflected in the Web of Science results (Table 1).

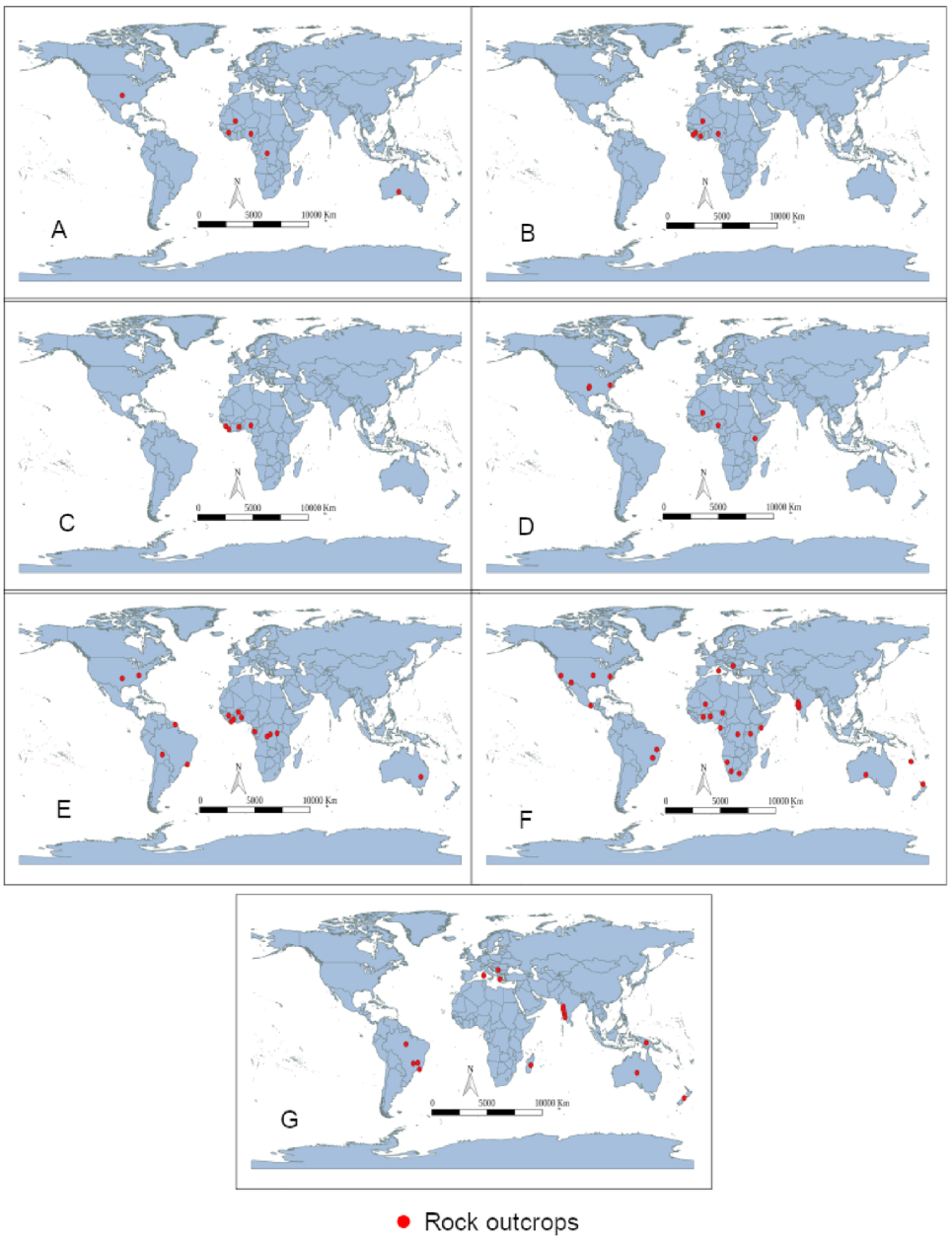

Fig. 4 Decade wise geographical focus of studies on rock outcrops **A** studies during 1950–1960, **B** 1961–1970, **C** 1971–1980, **D** 1981–1990, **E** 1991–2000, **F** 2001–2010, **G** 2011 onwards

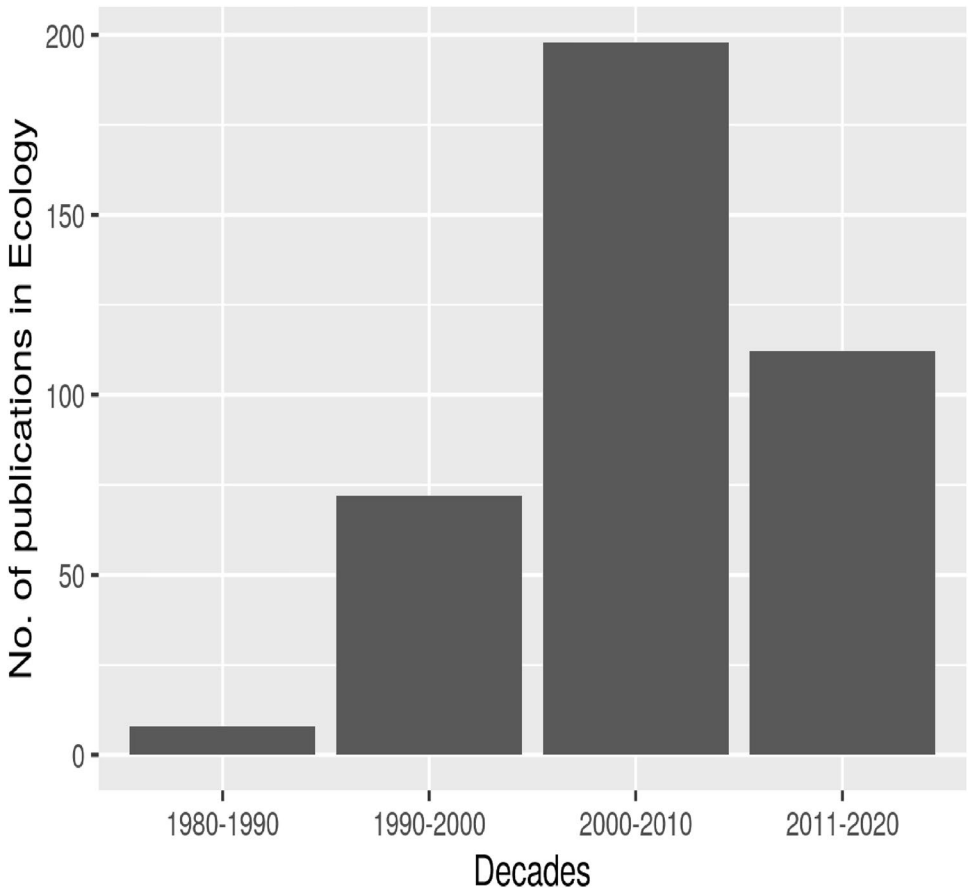

Fig. 5 Decade wise progress in the number of publications focusing on ecology of rock outcrops (Based on subject categories of 'Web of Science')

Vegetation on outcrops

Pantropical (tropical regions of both hemispheres) outcrops have many similarities in vegetation composition. Vegetation data compiled from Porembski and Barthlott (2000a), Watve (2013) and de Paula et al. (2017) revealed that families such as Cyperaceae, Poaceae, Orchidaceae, and Fabaceae are among the ten most species-rich families that are present on all the outcrops (Table 2). Family Poaceae is either dominant (India, North America) or at least subdominant (Africa, Madagascar, South America, Australia) on rock outcrops worldwide except in Seychelles. Following the grass family, Cyperaceae and Fabaceae are dominant in certain regions, whereas Bromeliaceae and Cyperaceae are the most species-rich in Brazil (de Paula et al. 2017). There are many species of Velloziaceae inhibiting outcrops in Brazil. However, this family, along with Bromeliaceae is totally absent from Indian outcrops.

Based on the soil availability and water permanence, specific microhabitats can be identified on the outcrops, and the vegetation is often described based on these features (Porembski et al. 1994, 1997, 2000; Seine et al. 1998). Plant communities on Indian outcrops can be described and compared with the outcrops from other parts of the world based on the microhabitats categories described for the inselbergs. Studies by Watve (2007, 2013) and Bhattarai et al. (2012) are among the pioneering works describing microhabitats on Indian rock outcrops.

Exposed bare rock covered with non-flowering plants such as lichens, cyanobacteria, algae, fungi etc. It is a pioneer layer in terms of nutrient cycling. Cryptogams are predominantly found on bare rocks that cover larger areas on outcrops. On African inselbergs, *Peltula* Nyl., *Stigonema* C.Agardh ex Bornet & Flahault and species of *Scytonema* C.Agardh ex É.Bornet & C.Flahaul. are the commonly found taxa. On the outcrops in the NWG, the members belonging to the genera *Graphis* Adans. and *Lecanora* Ach. are the commonly occurring taxa. Cryptogamic crust support many vascular plants such as species of Bromeliaceae on African inselbergs while species such as *Indopoa paupercula* (Stapf) Bor ex Ramamoorthy, *Murdannia semiteres* (Dalzell) Santapau, species of *Glyphochloa* Clayton spp. and species of *Lepidagathis* Willd. spp. are commonly observed on the NWG outcrops (Watve 2013; Personal observations).

One of the dominant vegetation types on tropical outcrops is monocotyledonous mats, where plant communities have characteristic species of Bromeliaceae and Cyperaceae. Monocotyledonous mats occur sporadically on the NWG

Table 2 Ten species rich families from the rock outcrops across various regions

Family	South America	Africa	Madagascar	Seychelles	Australia	USA	Brazil	India
Cyperaceae	1	3	5	3	9	2	2	9
Poaceae	2	2	2	8	2	1	4	1
Bromeliaceae	3						1	
Rubiaceae	4	6		5		10		
Melastomataceae	5							
Orchidaceae	6	8	3	6	8		3	4
Fabaceae	7	1	10	9	10			2
Apocynaceae	8			1			5	7
Euphorbiaceae	9	7	6	4			9	
Myrtaceae	10							
Scrophulariaceae		4	8					
Asteraceae		5	1		1	3	6	5
Commelinaceae		9				5		
Lentibulariaceae		10						10
Asclepiadaceae			4					
Aloaceae			7					
Gentianaceae			9					
Arecaceae				2				8
Pandanaceae				7				
Sapotaceae				10				
Stylidiaceae					3			
Centrolepidaceae					4			
Boryaceae					5			
Apiaceae					6			
Droseraceae					7			
Liliaceae						4		6
Caryophyllaceae						6		
Rosaceae						7		
Hypericaceae						8		
Portulacaceae						9		
Velloziaceae							7	
Cactaceae							8	
Gesneriaceae							10	
Eriocaulaceae								3

Data compiled from de Paula et al. 2017, Porembski and Barthlott 2000a, and Watve 2013

ferricretes and BM. They are dominated by the members of the family Poaceae and Eriocaulaceae. However, these mats are dominant on vertical cliffs in the Western Ghats, composed mainly of species of grass genus *Tripogon* Roem. & Schult. Besides this, other monocots from the family Cyperaceae and Eriocaulaceae are also found on cliffs (Datar and Watve 2018; Porembski et al. 2021).

Certain species of *Dopatrium* Buch.-Ham. ex Benth. commonly habituate rock pools on the African inselbergs. Whereas, species belonging to Poaceae and Cyperaceae are dominant in the rock pools of inselbergs in the Ivory coast (Krieger et al. 2000). Rock pools on Indian outcrops commonly contain species of *Eriocaulon* L., *Pogostemon deccanensis* (Panigrahi) Press, *Wiesneria triandra* (Dalzell) Micheli and grasses such as *Oryza rufipogon* Griff., *Coelachne* spp., *Panicum* spp. and *Isachne lisboae* Hook. f. (Pramod et al. 2014).

Areas on crevices of African inselbergs commonly consist of *Bulbostylis coleotricha* (Hochst. ex A.Rich.) C.B.Clarke, *Fimbristylis dichotoma* (L.) Vahl, *Sporobolus festivus* Hochst. ex A.Rich., *Aeschynomene lateritia* Harms. and crevices of ferricretes and BM, where the soil gets accumulated, offer a safe site for the geophytes and other perennial species. On Indian outcrops geophytes such as *Habenaria rariflora* A.Rich., *Habenaria suaveolens* Dalzell and *Ceropegia jainii* Ansari & B.G.Kulk are reported from crevices (Watve 2013). While endemic grasses such as *Glyphochloa acuminata* (Hack.) Clayton, *Dimeria stapfiana*

C.E.Hubb. ex Pilg. and *Ischaemum yadavii* Gad & Janarth. are also observed growing in the crevices.

On Australian inselbergs, several species of *Eucalyptus* L'Hr. grow on deep soil areas (Hopper 2000). Trees such as *Bombax costatum* Pellegr. & Vuillet, *Hymenodictyon floribundum* (Hochst. & Steud.) B.L.Rob., *Ficus* spp. along with certain arborescent monocots of families Velloziaceae and Bromeliaceae are found on African inselbergs. Indian ferricretes show the presence of certain tree species such as *Memecylon umbellatum* Burm.f., *Eleocarpus* sp., *Terminalia elliptica* Willd., *Ficus arnottiana* (Miq.) Miq. on similar microhabitats (Chandran et al. 2012; Watve 2013; Sreejith et al. 2016).

"Ephemeral flush vegetation (EFV)" is a highly seasonal plant community that develops at the base of more or less inclined rocky slopes. It is present on the inselbergs as well as ferricretes in parts of Africa, Madagascar, and India (Porembski and Watve 2005). There are many species shared among EFV on inselbergs and ferricretes throughout the world. Continued seepage of water is essential for the development and sustenance of EFV. On inselbergs, EFV occurs on the downslopes of monocotyledonous mats to get a continuous supply of water (Richards 1957). On ferricretes, it grows in places where water can remain accumulated for a longer time. Small herbaceous plants of Eriocaulaceae, Xyridaceae, Lentibulariaceae dominate EFV while various species of Cyperaceae and Poaceae are also observed. EFV in India and tropical Africa are physiognomically and floristically similar. Both regions possess various carnivorous taxa, such as *Drosera* L. and *Utricularia* L. indicating nutrient-poor soils. There are few common species such as *Drosera indica* L. as well as local endemics like *Trithuria konkanensis* S.R.Yadav & Janarth. from LLF and *Utricularia purpurescens* J.Graham on HLF on Indian outcrops and *Genlisea barthlottii* Porembski, Eb.Fisch. & Gemmel on EFV from Guinea outcrops (Porembski and Watve 2005).

Gravelly patches dominated by small gravel and pebbles are frequently observed on Indian ferricretes and basalt mesa. They support species like *Murdannia semiteres, Eriocaulon cinereum* R.Br., *Eriocaulon parvicephalum* Darsh., R.K.Choudhary, Datar & Tamhankar, *Utricularia malabarica* Janarth. & A.N.Henry.

A meta-analysis based on floristic studies from Indian rock outcrops

A meta-analysis based on the 'outcrop checklist' showed that the highest number of species (309) were recorded from High-Level Ferricrete, followed by Basalt mesa (177) and Low-Level Ferricrete (123). HLF and BM have 134 shared species, whereas HLF and LLF have 82 shared species. Sixty-four species are shared among all types (Fig. 6). Plants inhabiting Indian rock outcrops were reported in the

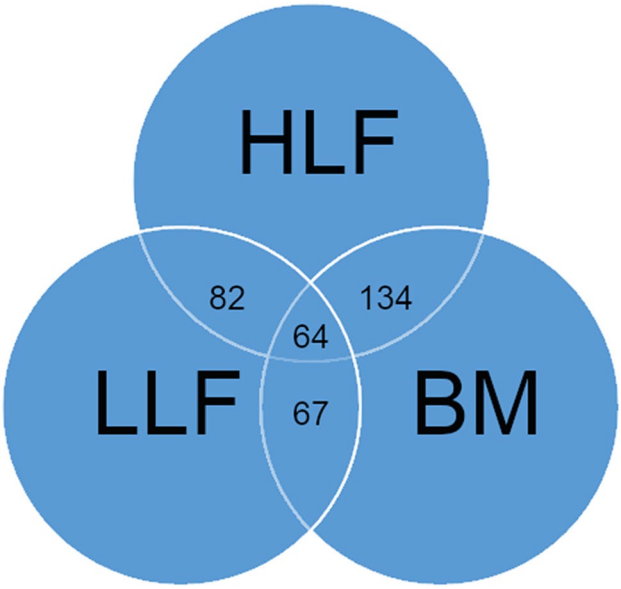

Fig. 6 Number of shared species across various outcrops of different elevations and base rock types (*HLF* High-Level Ferricrete, *LLF* Low-Level Ferricrete, *BM* Basalt Mesa)

regional and local floras for a very long time. Even in the last decade, many taxonomic studies documenting novel plant species (Borude et al. 2016; Chandore et al. 2016a, b; Darshetkar et al. 2017; Kolte et al. 2018,2019; Bokil et al. 2020; Chandore et al. 2021a, b) from the outcrops of Western Ghats with no attention on their ecology have been published (Fig. 7).

Though taxonomists have explored these habitats for species discoveries, recognition of rock outcrops as a unique habitat is very recent (Watve 2003, 2007, 2013). A few works that documented the diversity of specific ferricretes and basalt mesa in the Western Ghats have emerged in recent years (Apate et al. 2009; Bhattarai et al. 2012; Chandran et al. 2012; Lekhak and Yadav 2012; Shenai et al. 2013; Rahangdale and Rahangdale 2014; Sreejith et al. 2016, 2020). All these studies unanimously highlighted herbaceous dominance on Indian outcrops, which is very similar to the African inselbergs and iron outcrops of Brazil (Watve 2007, 2013). The dominance of Poaceae is not only restricted to ferricretes but to basalt mesa also. Orchidaceae and Asteraceae are co-dominant exclusively on ferricretes (Lekhak and Yadav 2012) and Fabaceae and Eriocaulaceae on both ferricretes and basalt mesa combined (Watve 2007). HLF, LLF, and BM share a large number of species; however, some species like *Ceropegia anjanerica* Malpure, M.Y. Kamble & S.R. Yadav occur exclusively on BM, while *Impatiens lawii* Hook. f. & Thomson, *Eriocaulon epedunculatum* Potdar, Anil Kumar Bis, Otaghvari & Sonkar and *Ceropegia jainii* occur exclusively on HLF and *Dipcadi goaense* Prabhug., U.S.Yadav

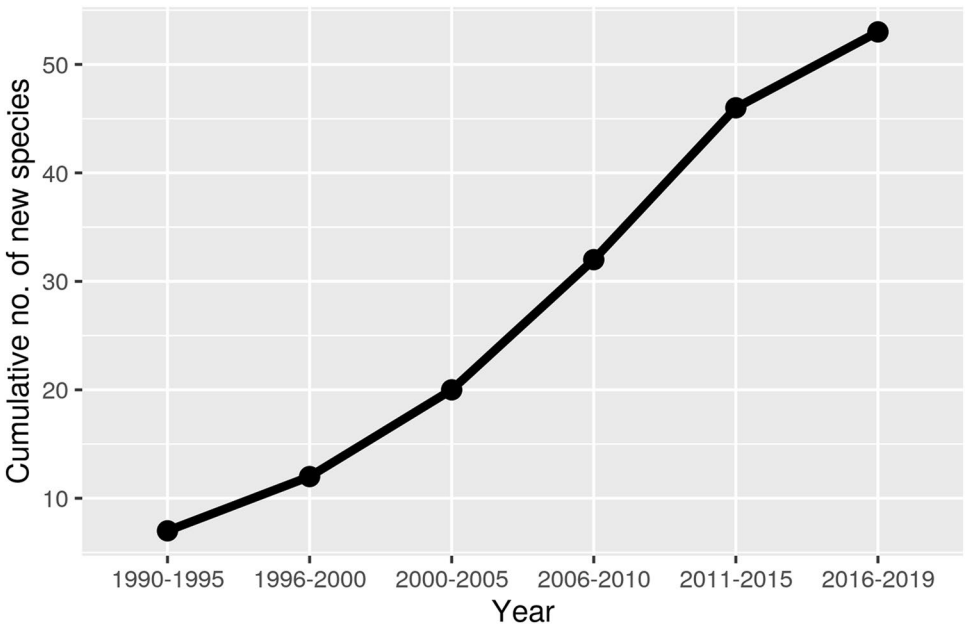

Fig. 7 Cumulative number of novel species described from Western Ghats, India from the year 1990

& Janarth., *Glyphochloa santapaui* (S.K. Jain & Deshp.) Clayton occur exclusively on LLF.

Vertical outcrops or cliffs are among the least studied habitats in India. Datar and Watve (2018) recorded a total of 102 species from cliffs out of which about 50% are endemic. Family Poaceae (16 species) is dominant, followed by Apocynaceae and Rubiaceae with seven species each and Asteraceae (six species) on cliffs. The study showed that cliffs are fascinating habitats that harbor many rare and endemic plants and need attention from plant taxonomists and ecologists.

Vegetation data is available only for a few outcrops, and many are yet to be studied for even baseline floristic information. The available vegetation data for Indian outcrops are in the form of floristic documentation, and there are hardly any quantitative studies revealing the diversity of the habitats and describing the adaptations. Though novel species discoveries from the outcrops in recent years have indicated the importance of Western Ghats as the center of diversity and radiation, very few works (Shigwan et al. 2020) highlighted outcrops as a prime habitat of Western Ghats.

Species adaptive traits

Extreme environmental conditions and low nutrient availability have a massive influence on the vegetation that grows on rock outcrops (Porembski 2007; de Paula et al. 2015, 2021). Various physical, environmental, and habitat characteristics such as insolation, temperature, soil texture, depth, and water availability govern the establishment of plant communities on rock outcrops (Porembski and Watve 2005; Sarthou et al. 2017; Pinto-Junior et al. 2020; Kulkarni et al. 2021, 2022b). Though herbaceous plants dominate these habitats, trees and shrubs are also found in places where the soil depth is at least one meter and above. Outcrop species show many specific adaptive traits at morphological, physiological and life-history levels (Biedinger et al. 2000; Deil 2005; de Paula et al. 2019; Porembski et al. 2021). These adaptations which help species survive the extreme conditions are summarized here.

Succulence

Succulence is one of the desiccation avoidance strategies which is commonly observed in desert-like habitats. Succulent plants have thick and fleshy parts which are used to retain water in plant tissues of leaves, stems, and roots (Biedinger et al. 2000). Many species that grow on bare rock surfaces are found on the inselbergs of East Africa and Madagascar (Porembski 2007). Inselbergs show the presence of leaf succulents such as *Cyanotis lanata* Benth. from Africa and *Sedum smallii* (Britton) H.E. Ahles from SE USA. *Solanostemon graniticola* A. Chev. is one such example that has deciduous leaves. Species of *Alcantarea* (É.Morren ex Mez) Harms and *Vriesea* Lindl. have specially developed tanks that can store up to 20 L of water and organic debris (Biedinger et al. 2000). Vertical outcrops (cliffs) of India, show the presence of deciduous leaf-bearing succulents (Datar and Watve 2018) like *Frerea indica* Dalzell and *Sarcostemma intermedium* Decne, whereas, horizontal outcrops (ferricretes) have leaf succulents like *Cyanotis concanensis* Hassk., *Cyanotis fasciculata* (B. Heyne ex Roth) Schult. & Schult. f. and *Euphorbia fusiformis* Buch.-Ham. Ex D. Don (Lekhak and Yadav 2012). Along with these species that

are desiccation avoiders, there are many species that can tolerate desiccation.

Desiccation tolerance

Desiccation tolerance is the ability to recover from almost complete loss (80–90%) of protoplasmic water (Alpert 2000; Oliver et al. 2000). Desiccation-tolerant plants can survive periods of drought and recover without losing viability. This property has enabled many plants to occupy habitats of extreme environmental characteristics. It is estimated that approximately 1500 species of vascular plants are desiccation-tolerant, including ferns such as *Selaginella* P. Beauv., monocots belonging to the families Cyperaceae, Poaceae, Velloziaceae and dicots such as members of Scrophulariaceae (Porembski 2011).

This ability is particularly advantageous on the rock outcrops where the dry period length is about eight months. Madagascar and Brazil are particularly rich in desiccation-tolerant vascular plants (de Paula et al. 2017). Scrophulariaceae and Velloziaceae dominate the desiccation-tolerant flora followed by Cyperaceae and Poaceae on inselbergs (Porembski and Barthlott 2000b).

In India, there has been a solitary attempt till now to test desiccation tolerance by Gaff and Bole (1986), who recorded nine species of grasses belonging to the genera *Eragrostiella* Bor, *Oropetium* Trin, and *Tripogon*. Various species of these genera that are desiccation-tolerant are replaced in other parts of the world. Species of *Eragrostiella* from Australia, *Oropetium* from South Africa and *Tripogon* from Africa, the USA and Australia are proven to be desiccation-tolerant (Biedinger et al. 2000). It is known that seasonal water availability and property of desiccation tolerance are advantageous for Indian outcrops, no single study has been carried out after Gaff and Bole (1986). It is estimated that the vertical cliffs in the Western Ghats form the largest growth sites of desiccation-tolerant plants in the world (Porembski 2011), detailed studies are needed to prove it empirically. Along with the strategies for water management, plants also possess strategies to deal with the nutrient requirements as outcrops are essentially oligotrophic habitats.

Carnivory

Carnivory is an adaptation for nutrient-poor substrates wherein plants obtain certain nutrients such as nitrogen and phosphorus through phytoplanktons, zooplanktons, small insects, and nematodes. They have peculiar anatomical and morphological structures to attract, ingest, and digest the prey (Givnish 1989; Juniper et al. 1989). Carnivory is also found in water-logged habitats. Tropical outcrops shelter species-rich families such as Droseraceae and Lentibulariaceae representing carnivory. Seine et al. (1996) have reported around 45 species of carnivorous plants from various inselbergs in Australia, Benin, French Guyana, Guinea, Ivory Coast, Seychelles, and Zimbabwe. Australian outcrops have at least 15 species of *Drosera*. *Drosera indica* is a common carnivorous species occurring on both inselbergs and ferricretes.

On Indian outcrops, *Drosera* is represented by two species namely *D. indica* and *D. burmanni* whereas, *Utricularia* has eight species, *U. albocoerulea* Dalzell, *U. cecilii* P. Taylor, *U. malabarica* Janarth. & A. N. Henry, *U. purpurascens* J. Graham, *U. caerulea* L., *U. reticulata* Sm. and *U. striatula* Sm. (Janarthanam and Henry 1992; Lekhak and Yadav 2012).

Dwarfism

Another adaptive strategy observed on inselbergs where plants tend to be small (a few centimeters high) and are phenologically plastic is termed "dwarfism". Inselbergs have species of Eriocaulaceae, Scrophulariaceae, Juncaceae, Cyperaceae, which show dwarfism. For Indian outcrops, such evaluation is yet to be carried out. However, species like *Eriocaulon epedunculatum, E. parvicephalum* Darsh., R. K. Choudhary, Datar & Tamhankar, *Lindernia ciliata* (Colsm.) Pennell and *Trithuria konkanensis* may be categorized as dwarf annuals. However, detailed autecological studies are needed for the classification.

Diversity in photosynthetic pathways

The presence of dual photosynthetic pathways is an adaptive strategy to deal with the scarcity of water. Crassulacean Acid Metabolism (CAM) and C_4 pathways are known to show an advantage for survival in high insolation, avoiding water loss, and sustaining through the desiccation cycles. Members of diverse families such as Apocynaceae, Cactaceae, Crassulaceae, Euphorbiaceae, Agavaceae, Orchidaceae, Bromeliaceae, and Araceae found on inselbergs show CAM as a photosynthetic pathway (Kluge and Brulfert 2000). CAM-C_3 intermediates like *Clusia* Plum. ex L. are also recorded from inselbergs (Lüttge et al. 2011).

From the rocky cliffs of the Western Ghats, *Frerea indica* belonging to family Apocynaceae has been recorded showing a combination of CAM-C_3 (Datar and Watve 2018), which is beneficial to deal with the prolonged dry period. Leafless during the winters and summers and foliated during the monsoon, the stems of *Frerea indica* have been recorded to follow CAM pathway, whereas the leaves show C_3 pathway (Lange and Zuber 1977). Though it is known that Indian outcrops have the dominance of C_4 grasses, the shift between CAM and C_3 and temporal and spatial spread of C_4 grasses are yet to be understood in detail.

Studies on various adaptive traits for the Indian outcrop dwelling plants for dealing with water scarcity, high light intensities and low nutrient availability are yet to be carried out to understand how adaptations help the survival of the species in extreme conditions. Though it is known from the present 'outcrop checklist' that succulence, desiccation tolerance, geophytic nature of plants and carnivory are overall helpful in survival, the detailed dynamics is yet to be understood.

Pollination and dispersal syndromes

Studies on the rock outcrops such as tropical inselbergs, sandstone and ironstone outcrops showed that entomophily is the dominant mode of pollination followed by anemophily (Biedinger et al. 2000; Conceição et al. 2007; Jacobi and Carmo 2011).

Mass flowering, a peculiar feature of rock outcrops, is useful to the species as millions of individuals flowering simultaneously attract a large number of pollinators, and at the same time, the cost of individual floral reward is reduced (Hobbhahn et al. 2006).

Mass flowering species of *Utricularia* on rock outcrops were earlier believed to be following autogamy. However, experiments and observation by Hobbhahn et al. (2006) confirmed that the three *Utricularia* species from the Western Ghats are incapable of selfing on their own. The structure of the flower limits autonomous selfing and promotes insect visitation. These species prefer bee pollination because the flower structure limits access to the other pollinators. A minimal quantity of nectar having a high concentration of sugars is present. Similar results were observed in a study by Balachandran et al. (2014), which looked at the plant–insect interactions on LLF of the central Western Ghats. This investigation revealed that insects are the dominant pollinators recording 58 different taxa, including 38 butterfly species, three flies, four wasp species, three beetles and seven species of bees.

Concerning the seed dispersal ability of outcrop plants, there are contrasting views. One view suggests that a majority of plants show long-distance dispersal as it might be advantageous for plants occupying a favorable habitat in a heterogeneous landscape (Mathias et al. 2001) whereas, Wyatt (1997) assumes rock outcrops species, possess adaptations against long-distance dispersal to prevent dispersal to sites where they are unlikely to be established. However, his studies are restricted to the southeastern USA. In plants situated on tropical African inselbergs, the highest number of species show endozoochory followed by anemochory and epizoochory (Biedinger et al. 2000). There are literally no studies available on seed dispersal for Indian outcrops.

Endemism

Rock outcrops are known to contain a high proportion of endemic species (Smith and Cleef 1988; Alves and Kolbek 1994; Couto et al. 2017; Shigwan et al. 2020; de Paula et al. 2021). As environmental extremes and short-term favorable conditions demand specific adaptations, several plants become specialized and are often restricted to their habitats. Rock outcrops are known to act as the refuge for the species with habitat-specific adaptive traits.

At the global level, the first study on the endemism of rock outcrops was carried out in the eastern USA (Baskin and Baskin 1988). This work highlighted the importance of rock outcrops in terms of endemism, examining the causes of endemism by off the field and on the field plant studies. The study confirmed that endemic plants on the rock outcrops of the eastern USA prefer high-intensity light conditions, are shade-intolerant and are weak competitors. It was the first elaborate study that pioneered the investigation of the causes of rock outcrop endemism (Baskin and Baskin 1988). There are many species restricted to inselbergs, ironstones, sandstones and other types of outcrops. Ironstone outcrops in Iron Quadrangle (IQ), Southeastern Brazil have endemic species of Bromeliaceae such as *Aechmea maculata* L.B.Sm., *Dyckia consimilis* Mez, *D. schwakeana* Mez and *Vriesea minarum* L.B.Sm. that are endemic to IQ (Jacobi et al. 2007). A study on outcrops in Guinea showed that sandstone outcrops have high diversity and endemism as compared to the granitic inselbergs and ferricretes (Porembski et al. 1994). Stehmann et al. (2009) observed that 42% of the species from the Atlantic forest, Brazil area are endemic to rock outcrops. The floristic survey conducted in northeastern Minas Gerais, Brazil recorded 89 species out of which 24 are endemic to inselbergs (de Paula et al. 2017). Family Myrothamnaceae is a desiccation-tolerant family with two species endemic to Africa and Madagascar (Porembski and Barthlott 2000b).

Indian outcrops also shelter a high proportion of endemic species. Watve (2013) listed 188 endemic species occurring on ferricretes, while Datar and Watve (2018) documented about 50% endemism to cliffs. A recent study by Shigwan et al. (2020) showed that out of 181 taxa endemic to the northern Western Ghats, 101 taxa occur on rock outcrops highlighting the prime significance of this habitat. 'Outcrop checklist' analysis for endemism revealed that 52% of the total species found on outcrops are endemic (Fig. 8). HLF shows the presence of 39% endemic species whereas, BM and LLF have 25% and 17% endemic species, respectively (Fig. 9). Owing to the harsh environments in which they grow, many outcrop species are habitat specialists and are often restricted to the area. Though habitat specialists and endemic species increase the uniqueness of habitats, disturbances in those habitats make these species vulnerable.

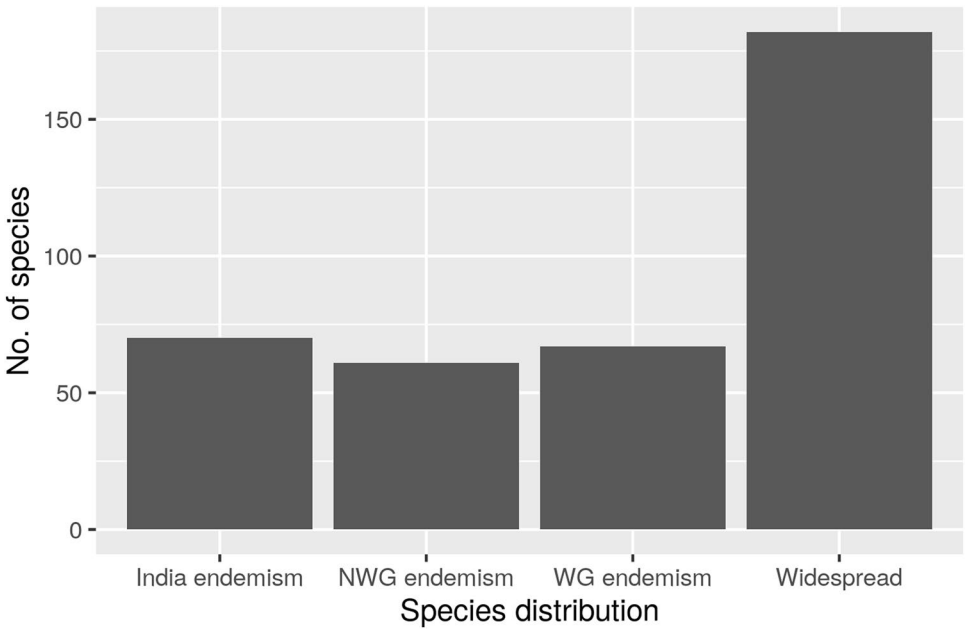

Fig. 8 Endemic species richness at local and regional scales on rock outcrops in northern Western Ghats. (*NWG* Northern Western Ghats, *WG* Western Ghats)

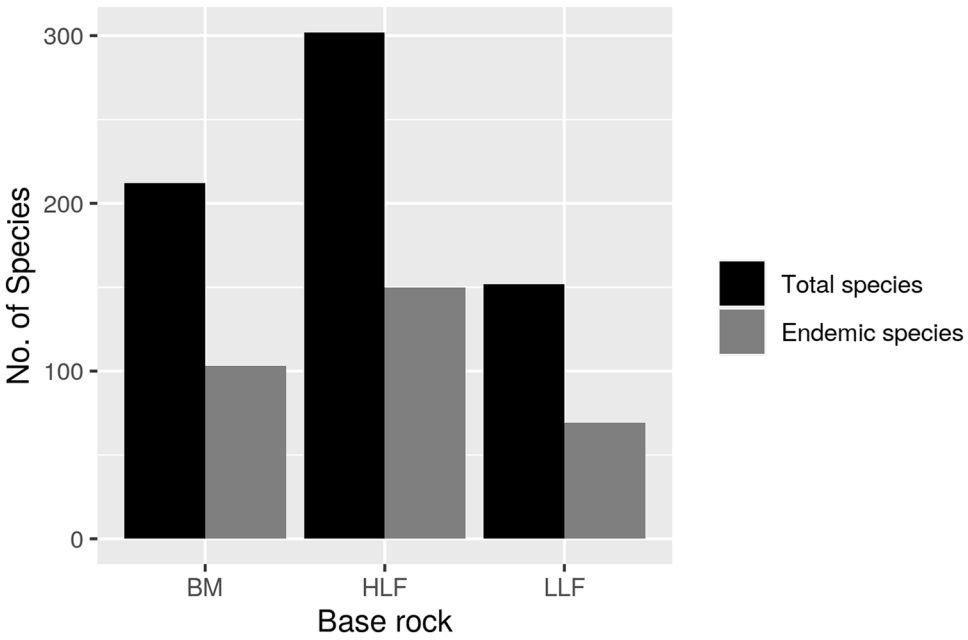

Fig. 9 Proportion of endemic species on each outcrop type (*HLF*: High-Level Ferricrete, *LLF*: Low-Level Ferricrete, *BM*: Basalt Mesa)

Therefore, such species are of considerable significance for the biodiversity value of the area and its conservation.

Future scope of research

Rock outcrops has been a paradise for taxonomic inventories over many decades. Recently few ecological studies investigated the vegetation-bedrock relationship (Kulkarni et al. 2021), the population structure of *Impatiens* spp. (Rahim et al. 2021) and microhabitats specific studies such as rock pools (Kulkarni et al. 2022a, b) have also been carried out. However, rock outcrops of Western Ghats still provide large avenues for studies on various aspects such as:

- Temporal and spatial vegetation dynamics and its triggering factors
- Pollination and seed dispersal syndromes of rock outcrop species and testing various hypotheses related to these interactions.
- Competition within and between species/ communities to occupy niches available on the outcrops

- Nutrient uptake mechanism to overcome nutrient scarcity of the soils
- Evolution, migration and speciation of the outcrop species
- Habitat integrity, fragmentation and disturbance studies to inform conservation area prioritization
- Molecular and omic studies of plants species inhibiting rock outcrops
- Studies on the functional ecology of rock outcrops
- Exploration of outcrops for its diversity of desiccation-tolerant plants.
- Real-time climate data and its correlation with vegetation
- Threat status assessment of rock outcrop species using IUCN criteria.

Conclusion

Rock outcrop species have tuned their morphological, physiological and life-history traits to suit the changing environments of alternating desiccation and inundation cycles. Though spread across the country, Indian outcrops are neglected and are often treated as wastelands. Species discoveries are made from these habitats for centuries, but their importance as a distinct habitat from an ecological point of view is very recent. Species here show many habitat-specific adaptations, hence the vegetation is exclusively composed of species showing adaptive strategies like geophytism, carnivory, succulence and desiccation tolerance. Indian outcrop species exhibit many tropic specific trends like the dominance of Poaceae, desiccation tolerance, insectivory, and geophytism.

Indian outcrops are facing many disturbances due to ignorance in terms of their biodiversity value and ecological significance. Many of these areas are either private or government revenue lands with very few under legal protection. Anthropogenic activities such as mining, construction (houses, temples, airports, and windmills), and tourism have initiated the process of destruction of the outcrops (Watve 2013; Datar and Pande 2014; Thorpe and Watve 2015). It is negatively affecting the plants, animals and overall ecosystem. However, apart from early geological studies and some sporadic floristic inventories, the published literature on Indian outcrops is still at its infancy. Hence for better conservation of these unique habitats, they are needed to be understood and studied for various open-ended questions related to ecology, taxonomy, evolution and population genetics.

Systematic efforts to carry out necessary ecological studies will hugely improve our understanding of the specialized processes and mechanisms operating in these unique habitats. This knowledge can be used as a template on which conservation strategies can be developed.

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