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Between a rock and a hard place: Comparing rock-dwelling animal prevalence across abandoned paddy, orchards, and rock outcrops in a biodiversity hotspot

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A R T I C L E I N F O

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A B S T R A C T

Rock outcrops are geologically and ecologically unique ecosystems that harbour threatened and endemic biodiversity. These underappreciated, open ecosystems are undergoing rapid land-use changes and the impacts of these changes on the threatened and endemic biodiversity are poorly understood, compared to the forested ecosystems. The unprotected, low-elevation lateritic plateaus of the northern Western Ghats of India are a case in point; they have high levels of endemism but are experiencing agricultural land-use change to orchards on the one hand and abandonment of traditional paddy cultivation on the other. We compared 1) the availability of loose rocks, a critical microhabitat for saxicolous animals, 2) the prevalence of an endemic caecilian (*Gegeneophis seschachari),* an endemic gecko (*Hemidactylus albofasciatus*), and a wide-spread snake (*Echis carinatus*), and 3) the composition and abundance of other rock-dwelling animals across 12 less-disturbed natural rock outcrop sites and 10 sites each in agroforestry plantations and abandoned paddies using time-constrained searches. By surveying 7179 surface rocks, we encountered 5738 individuals from 38 animal taxa. We found that the abundance of large rocks, which were the most-preferred size class of rocks by animals, was higher in abandoned paddy compared to plateaus and orchards. However, the prevalence of the reptiles *H. albofasciatus* and *E. carinatus* was highest on undisturbed plateaus. Contrastingly, the prevalence of *G. seshachari*, a caecilian, was significantly higher under rocks in abandoned paddy than in less-disturbed plateau or orchards. We also found significant differences between the rock-dwelling faunal assemblages across the three agricultural land-use types. Despite being adapted to persist in extremely variable climates on lateritic plateaus, multiple species/groups are vulnerable to land-use changes. However, *G. seshachari* and a few other taxa appear to benefit from certain kinds of agricultural land-use change, highlighting the context-specificity in species responses. This is one of the first studies to determine the impacts of the agricultural conversion of rock outcrops, thereby highlighting the conservation value of habitats that are often classified as wastelands.

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1. Introduction

Rock outcrops, which are habitats with more than 55% of exposed rocks, are geologically and ecologically unique open ecosystems (Goldingay and Newell, 2017; Kulkarni et al., 2022; Madhusudan and Vanak, 2022). These habitats, with poor tree cover, are exposed to extreme climates during the dry and wet seasons. These seemingly homogeneous habitats offer a diverse array of microhabitats that harbour unique, endemic, and threatened biodiversity, and provide critical livelihood resources for humans such as agricultural and grazing lands (Singh et al., 2006; Watve, 2013; Bond, 2019). Within these rock outcrops, loose rocks of varying sizes offer critical microhabitats for biodiversity, protecting them from extreme climate (Shah et al., 2004; Webb et al., 2009). These rocks are particularly critical for ectotherms that are unable to intrinsically regulate their body temperatures and must do so behaviourally by sheltering under rocks to protect themselves from unfavourable climates. Patterns of species occupancy under these loose rocks are influenced by the size of the rocks, with larger rocks likely providing a more stable climate than smaller ones, and other features such as the substrate and sun exposure (Goldsbrough et al., 2006; Becker and Brown, 2016). Unfortunately, the rock outcrops are facing diverse threats, including land-use changes that negatively impact microhabitat availability. Unlike land-use changes in forested ecosystems, open ecosystems have received scant attention (Porembski, 2000; Burke, 2003; Fitzsimons and Michael, 2017).

Land-use change is one of the major drivers of biodiversity loss in the tropics (Gibson et al., 2011). Typically, the understanding of agricultural-driven land-use change on biodiversity, especially of increasing land abandonment and agricultural intensification, is mostly from forested ecosystems. Additionally, existing information on the impact of land-use change mostly focuses on bird and plant communities (Cramer et al., 2008; Shahabuddin et al., 2021; Appiah-Badu et al., 2022), with relatively little information on ectotherms (Michael et al., 2008; McGrath et al., 2015). As rock outcrops are often classified as wastelands and therefore receive limited protection, they face rapid land-use changes (Fitzsimons and Michael, 2017; Bond, 2019; Madhusudan and Vanak, 2022). This is exacerbated by other threats such as habitat degradation, physical damages due to quarrying, and boulder removal (Michael et al., 2010, 2021; Watve, 2013; Fitzsimons and Michael, 2017). Habitat conversion and degradation on rock outcrops alter the availability of loose rocks. The large-scale movement of "bush-rocks" for landscaping and other uses impacts the availability of critical microhabitats for animals and, consequently, the abundance of animals (Webb and Shine, 2000; Goldingay and Newell, 2017). Removal and displacement of surface rocks from outcrops are known to have a long-lasting impact on saxicolous taxa such as reptiles (Shine et al., 1998; Goode et al., 2005; Michael et al., 2008, 2021; Goldingay and Newell, 2000). For example, loose rocks that are generally found on the rocky substrate of the outcrops in our study area are moved to paddy with soil substrate, affecting the number and quality of rock microhabitats in the landscape. However, the impact of such habitat modifications as part of agricultural practices on rock-dwelling fauna has been rarely quantified in the existing literature, and our understanding of how ectotherms respond to such changes in rock outcrops in agricultural landscapes is minimal (but see Michael et al., 2021; O'Sullivan et al., 2023). Therefore, it is critical to determine how human activities impact the availability of critical microhabitats, like rocks, and the ectotherms that depend on these rocks for refuge.

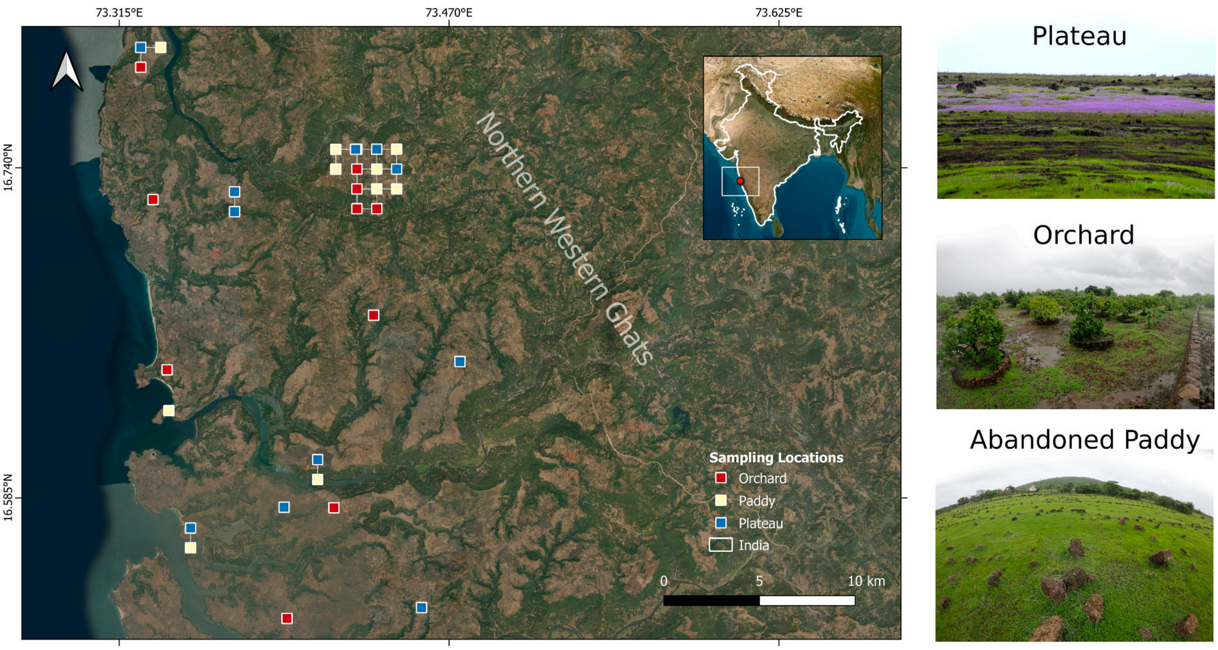

Fig. 1. Map showing sampling sites across different land-use types on lateritic plateaus in the northern Western Ghats region of Ratnagiri District of Maharashtra in India. The line joining the sites is indicative that the sites were on the same plateau. The plateau with multiple sites across the three treatments is the Devihasol plateau. One can see the boulders lining the trees in orchards and being used for lining the paddy fields. Satellite imagery source: Esri, Maxar, Earthstar Geographics, and the GIS User Community.

The rock outcrops or low-elevation ferricretes or lateritic plateaus of the northern Western Ghats are being converted to other land-uses at an alarming rate (Bhattacharyya et al., 2019). They harbour unique flora and fauna compared to wooded habitats in the neighbourhood, thereby forming habitat islands in the larger landscape (Porembski and Barthlott, 2000; Watve, 2013). Plateaus are critical habitats for multiple taxa, and new species of herbaceous plants, invertebrates, and vertebrates continue to be discovered in these habitats (Sayyed et al., 2018; Joshi et al., 2020; Kulkarni et al., 2022). More than 50% of plant species on the lateritic plateaus are endemic (Kulkarni et al., 2022). These lateritic plateaus are mostly privately owned or governed by the revenue department of the Government of India. Conversion to agricultural lands is one of the main threats to these lateritic plateaus (Thorpe, 2018; Kulkarni et al., 2022). Parts of these areas have been historically converted to rice paddy and, more recently, into mango or cashew orchards (Bhattacharyya et al., 2019). Thus, the landscape is a mosaic, with relatively less disturbed plateaus, forest patches, paddy, orchards, and human settlements.

In the northern Western Ghats, especially in the coastal belt, large rocks sourced from the lateritic plateau are used as construction material for houses and compound walls, and lining paddy fields (to prevent soil erosion) and plant pits in orchards on lateritic plateaus (Fig. 1; Fig. A4 & A5 in Appendix). In addition, soil is added to these plateaus for paddy cultivation, thereby altering the substrate from hard rock to soft soil. While previous studies have focused explicitly on boulder removal impacts on reptile populations (Shine et al., 1998; Pike et al., 2010), the impacts, and implications for management of agricultural habitat modification on rock-dwelling fauna, especially at the community level are poorly understood (Sainsbury et al., 2021). Ectotherms respond strongly to abiotic factors (Hofer et al., 1999; Naniwadekar and Vasudevan, 2007) and land-use change (Gardner et al., 2007; Paoletti et al., 2018; Cordier et al., 2021), and thus are ideal models for such studies.

The boulders on low-elevation lateritic plateaus in the northern Western Ghats provide refuge to the 'Vulnerable' White-striped viper gecko *Hemidactylus albofasciatus*, 'Data Deficient' Seshachari's caecilian *Gegeneophis seshachari*, and Saw-scaled viper *Echis carinatus* among other taxa. *Gegeneophis seshachari* is a fossorial caecilian endemic to the northern Western Ghats and is found in forested and plateau ecosystems. This lesser-known amphibian is encountered during the short-rainy season of the northern Western Ghats under rocks on the plateau, loose soil under boulders, and agricultural soil of approximately 10 cm depth (Gower et al., 2007; Katwate and Apte, 2019). It was re-discovered 36 years after the holotype collection from a mixed plantation habitat near a lateritic plateau (Gower et al., 2007). *Hemidactylus albofasciatus* is an uncommon, small, slender gecko found only in the open, rocky areas of lateritic plateaus of Maharashtra (Grandison and Soman, 1963; Amberkar, 2022). This ground-dwelling, nocturnal species is known to hide primarily under the rocks during the daytime, and is patchily distributed (Gaikwad et al., 2009; Mirza and Sanap, 2012). The species is facing continuing decline due to rock collection for construction, stone quarrying, livestock grazing, and mining (Srinivasulu and Srinivasulu, 2013). The Saw-scaled viper, locally known as *'Phoorsa'*, occurs in forests, shrublands, grasslands, rocky areas, and deserts (Ananjeva et al., 2021). However, the species can be found commonly under the rocks in plateaus during the monsoon (Sengupta et al., 1994). The species was heavily harvested for antivenin production, and the government organised destruction campaigns in the past, considering the health hazard to people (Sengupta et al., 1994; Whitaker and Whitaker, 2012). Between 1971 and 1991, almost 60,000 snakes were collected for antivenin production near our study area (Sengupta et al., 1994). Apart from the three taxa, several invertebrates, including spiders, scorpions, centipedes, beetles, and ants, are also commonly found under these rocks. Prior to this study, there has been no systematic research focusing on the composition of rock-dwelling fauna and their response to land-use change in the region.

In this study, we compared, across relatively less-disturbed lateritic plateaus (reference sites), orchards, and abandoned paddy on lateritic plateaus, 1) the availability of different-sized rocks, 2) the occurrence of *G. seshachari*, *H. albofasciatus,* and *E. carinatus*, and 3) composition and abundance of other vertebrate and invertebrate taxa. Given that large rocks are used extensively in modified habitats, we expected that modifying the original plateau habitat to paddy and orchards would negatively impact the abundance of rocks of the more preferred (by humans) size classes (larger rocks) across land uses. In addition, land-use change can be expected to alter the occurrence of the caecilian, gecko, and viper due to altered microhabitats. We expected differences in the composition and abundance of rock-dwelling faunal communities across the three land-use types.

2. Materials and methods

2.1. Study area

The Western Ghats is among the eight 'hottest' biodiversity hotspots due to high endemism (particularly of herpetofauna) and the intensity of anthropogenic threats (Myers et al., 2000). Vast expanses of ferricretes and basalt plateaus characterise the northern portions of the Western Ghats. The low-elevation ferricretes (25–200 m asl) occur from the sea coast to the foothills, and the high-level ferricretes (800–1400 m asl) occur on high-level laterites to the east of the crestline of Western Ghats (Watve, 2013). Such vast lateritic plateaus are absent in Western Ghats' central and southern portions (Kulkarni et al., 2022). The northern portion of the Western Ghats is seasonal, with rains primarily restricted to the four monsoon months from June to September (Watve, 2008, 2013). Heavy rains in the monsoon transform the dry and exposed habitat into a lush green cover of herbaceous vegetation. Hot and dry conditions during the dry season and water-logging during the monsoon expose the animals inhabiting the rock outcrops to extreme environments (Watve, 2008). The loose rocks on the lateritic plateaus provide refuge to a diverse array of invertebrate and vertebrate fauna (Thorpe and Watve, 2015).

We conducted the study in the low-level lateritic plateaus of Ratnagiri, in the Konkan region of Maharashtra state in west India (16°31′–16°48′N; 73°19′–73°29′E; Fig. 1). These plateaus are locally known as '*sada*' or '*jambha kaatal*'. The elevation of the sampled plateaus ranges between 24 and 197 m asl. The site experiences a tropical climate with temperatures ranging between 23 and 33 °C and an average annual rainfall of 3313 mm. The Arabian Sea and the Western Ghats escarpment are to the west and east of the plateaus, respectively. The sampling sites on lateritic plateaus were located in privately-owned areas. Portions of the plateaus have been modified to paddy fields and cashew/mango orchards. Traditionally, paddy is either grown in existing depressions on plateaus that have accumulated soil or by dumping soil from neighbouring areas on the plateau. Large rocks from the plateaus are lined along the paddy fields to prevent soil run-off.

Driven by stagnation in agriculture, poor returns from farming, and other socio-economic factors, many paddy fields have been abandoned and humans have migrated to urban centres (Yamin, 1989). However, the abandoned paddy fields continue to harbour a layer of soil and loose rocks in high numbers (Fig. 1, Fig. A4 in Appendix). In mango/cashew orchards on plateaus, the sites are blasted with explosives, and the pits are filled with soil and lined with rocks (Bhattacharyya et al., 2019). Mango/cashew saplings are planted in the pits and mangos grown on plateaus fruit at a desired time, well before the onset of monsoon, and are supposedly sweeter, fetching a higher price (Bhattacharyya et al., 2019). This has resulted in the rapid expansion of mango orchards, with more than 25, 000 ha of lateritic plateaus now under mango orchards (Bhattacharyya et al., 2019). We sampled such abandoned paddy fields and orchards along with existing natural lateritic plateaus. The relatively less-disturbed plateaus were our reference sites. The orchards included mango and mixed mango-cashew orchards. The orchards sampled included actively managed and harvested ones. The paddy fields sampled in the study were abandoned for at least two years and had a soil depth of at least 10 cm.

2.2. Sampling

Between June and September 2022, coinciding with the monsoon period, we conducted one-hour time-constrained searches at 32 sites spread across 11 unique plateaus and three land-use types (12 natural lateritic plateau sites [reference sites], 10 abandoned paddy fields, and 10 orchards) (Fig. 1; Table A1 in Appendix). The 20 modified sites (10 each in paddy and orchards) were on sites that were historically lateritic plateaus. To ensure that we captured spatial variability, we sampled multiple plateaus apart from the main Devihasol Plateau (Fig. 1). The 12 reference laterite plateau sites extended across eight plateaus, the 10 orchard sites were spread across seven plateaus, and the 10 abandoned paddy sites were spread across four plateaus (Fig. 1). While we had aimed for sampling all treatments across all plateaus, all plateaus did not comprise all treatments. Time-constrained searches enable the detection of more species and individuals per site than area-controlled plot methods (Kadlec et al., 2012). Given that our target species are rarely encountered, and our main interest in understanding the micro-habitat use, we felt that time-constrained searches were a more appropriate strategy than belt transects, which are area-constrained.

One observer (VJ) conducted the searches between 0900 and 1700 hr during the daytime, and well after sunrise and before sunset, in clear climate, barring rare incidences of slight rains between sampling to ensure similar sampling conditions across the searches that were conducted over a single season. The sampling effort was similar across the three land-use types (10 h each in orchards and abandoned paddy, and 12 h on reference plateau sites) (Table A1 in Appendix). We walked from a starting point away from the road or edge of the habitat turning all the rocks encountered in the 1 hr walk. The general direction of the walk ensured that we remained within the same land-use type even after one hour. For each turned rock, the observer recorded the size class of the rock. We classified the rocks into small (< 5 cm in diameter of the planar surface), medium (5–10 cm), and large (> 10 cm) sizes based on our observation that most rocks > 10 cm in size were moved from plateaus for various purposes. All large rocks that we could manually move were checked. We immediately placed all the rocks in their original positions after recording the faunal community. The observer recorded all visible fauna, including the focal animals, i.e., *G. seshachari*, *H. albofasciatus*, and *E. carinatus*.

All individual animals were counted, except in the case of ants (Formicidae), termites (Termitoidae), and mites (Acariformes) as they occurred in very high numbers making it difficult to count the exact number of individuals. Species-level identification in the field was difficult for *Minervarya* spp. froglets. Among arthropods, there was uncertainty in identifying one insect species that belonged to Dermaptera but was misclassified as Orthoptera in the field. Arthropods were identified to the order or family level wherever possible.

2.3. Analyses

We performed all analyses in R (v. 4.2.2) (R Core Team, 2022). We used a generalised linear model with a negative-binomial error structure (since Poisson error structure indicated overdispersion) to determine the differences in the number of rocks encountered across the different land-use types (lateritic plateaus, abandoned paddy, and orchards). Since rocks, particularly large- and medium-sized ones, are moved to paddy from lateritic plateaus, we expected interactive effects between rock size and land-use type. Predictors whose 95% CI on the estimated coefficients did not overlap zero were considered to have a significant influence on the response variable. We estimated the marginal means and assessed pairwise contrasts for rock and land-use types in the model with Tukey's method for *p*-value adjustment. We estimated Nagelkerke's pseudo R^2. We used the R packages 'MASS', 'emmeans', and 'performance' for this analysis (Venables and Ripley, 2002; Lüdecke et al., 2021).

We used generalised linear model with binomial error structure and each site as sampling unit to determine if the occurrence of the three focal herpetofaunal species (*G. seshachari*, *H. albofasciatus*, and *E. carinatus*) differed across the three land-use types. The analysis was carried out separately for each species. For *G. seshachari*, which was detected across the three land-use types, we used the regular binomial GLM in the 'MASS' package. For *H. albofasciatus* and *E. carinatus*, which were never detected in abandoned paddy, we initially assessed separation and infinite maximum likelihood estimates for log-binomial regression using the package 'detectseparation' (Kosmidis et al., 2022). Since we detected separation and biased estimates, we used package 'brglm2' (Kosmidis and Firth, 2021) for bias reduction with a mixed bias-reduction adjusted scores approach to model the influence of land-use type on these two species. To inspect if the focal species preferred large-sized rocks over medium-sized ones (none of the three focal species were detected under

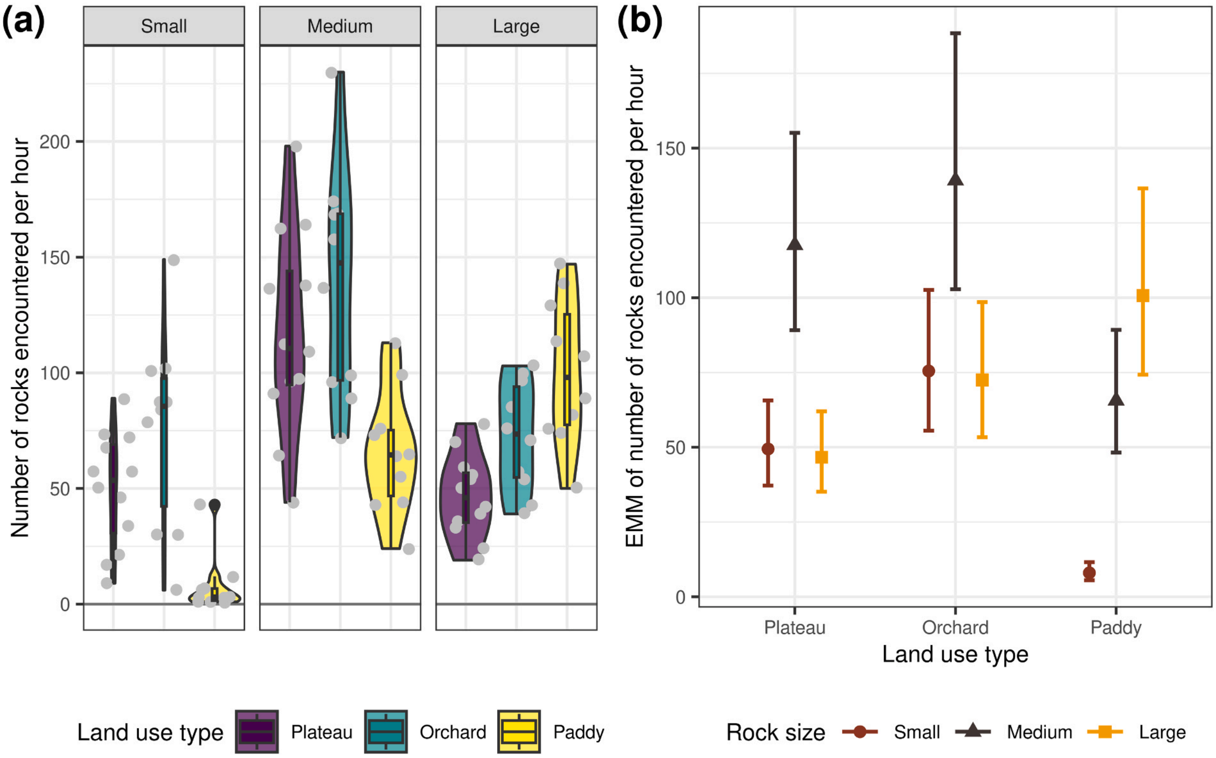

Fig. 2. (a) The violin plot shows the rock encounter rates (per hour) of small- (< 5 cm diameter), medium- (5–10 cm diameter) and large-sized rocks (> 10 cm) across the three land-use types. The grey dots are individual data points. While the number of small- and medium-sized rocks was least in paddy, the number of large-sized rocks was highest in paddy; (b) Estimated marginal means (EMM) with 95% CI from the generalized linear model used to assess the influence of land-use type on the encounter rate of rocks.

small-sized rocks), we used the Chi-square test for independence.

We visualised the co-occurrence of all taxa across the land-use types, and rock-size classes using the package 'UpSetR' (Gehlenborg, 2019). To determine if the composition of the rock-dwelling community of lateritic plateaus differed across land use types, we used Non metric multidimensional scaling (NMDS) analysis. This was performed using the *metaMDS* function of the 'vegan' package (Oksanen et al., 2022) with the presence-absence data (since we did not have abundance information for ants and mites) of the taxa recorded across sites. Since the two-dimensional stress value was higher than 0.2, we used a three-dimensional ordination with the Bray-Curtis dissimilarity index. We validated the assumption of homogeneity of multivariate dispersion using *betadisper* function and tested for the differences between the land-use types using the permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function in package 'vegan'. To assess the influence of land-use change on taxa with more than 100 detections, we used generalised linear models with negative-binomial error structure and count as response variable. We assessed pairwise contrasts for all three land-use types in each model as described earlier.

3. Results

3.1. Rock availability across land-use types

We turned 7179 rocks across the different land-use types in 32 sites. We found that the model that examined variation in rocks of different size classes across the different land-use types explained significant variation in the observed data (Nagelkerke's Psuedo $R^2 = 0.85$). The interaction term between rock size and land-use type was significant (Fig. 2a and b; Table A3a in Appendix). Compared to the less-disturbed lateritic plateaus, in the abandoned paddy, there were fewer small rocks but higher numbers of large rocks (Fig. 2a and b; and Table A3b in Appendix). Unlike plateaus and orchards, paddy fields tended to have fewer medium-sized rocks (Fig. 2b). The numbers of small-, medium-, and large-sized rocks did not differ between orchards and less-disturbed lateritic plateaus (Fig. 2a and b; Table A3b in Appendix).

3.2. Prevalence of caecilian, gecko, and viper across land-use types

We had 35 detections of *G. seshachari* from three plateaus, 24 detections of *H. albofasciatus* from seven plateaus, and 22 detections of *E. carinatus* from nine plateaus. We never detected these three species under small-sized rocks. The probability of occurrence of the

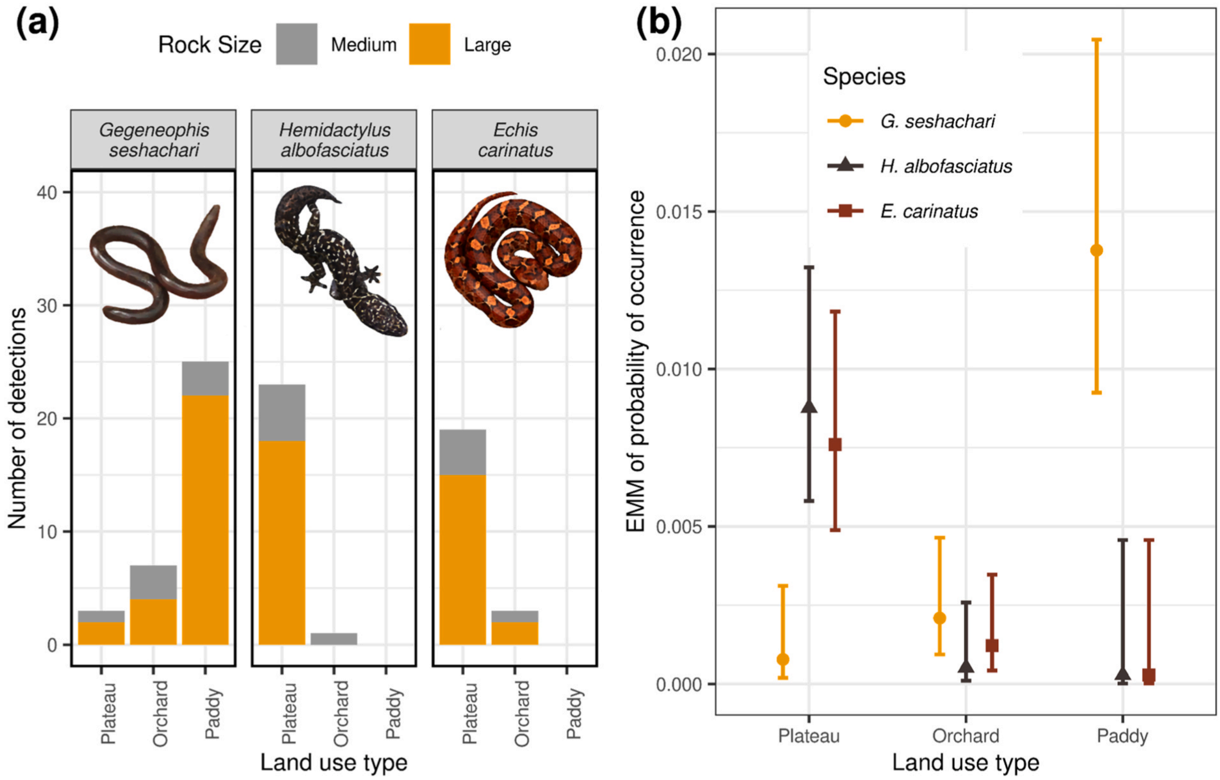

Fig. 3. (a) Number of detections of *Gegeneophis seshachari*, *Hemidactylus albofasciatus*, and *Echis carinatus* across land use types and rock size classes; (b) Estimated marginal means (EMM) with 95% CI from the generalized linear models used to assess the influence of land-use type on the probability of occurrence of focal species. Photographs by V. Jithin and A. Gadkari.

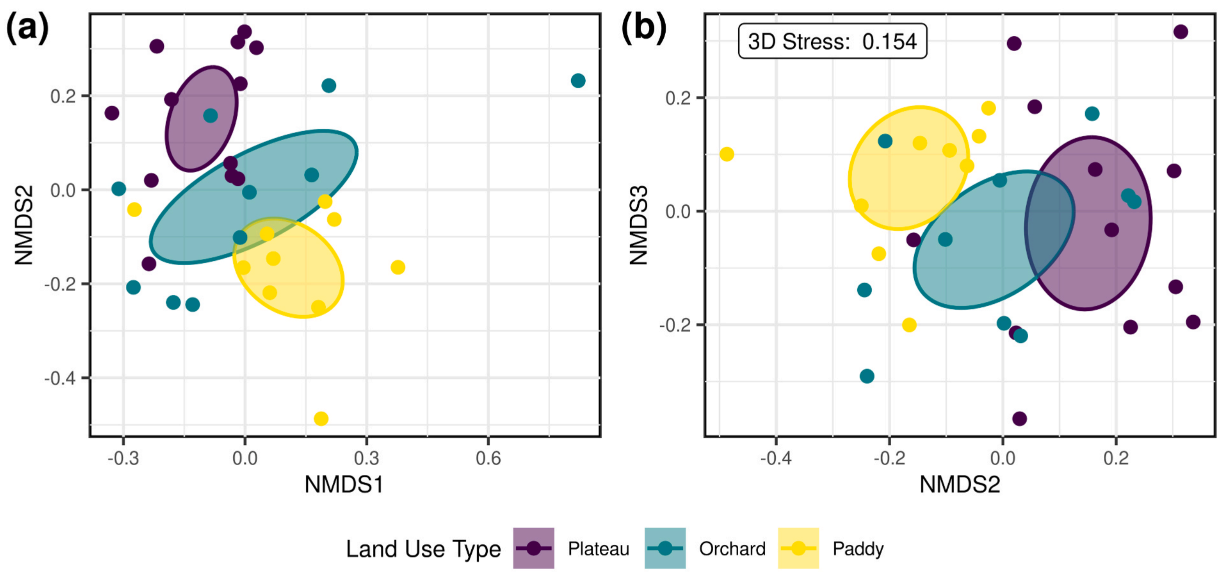

Fig. 4. Non metric multidimensional scaling (NMDS) in three dimensions showing dissimilarities between the three land-use types (less-disturbed plateaus, orchards, and abandoned paddy) in the overall taxonomic composition of rock-dwelling animals in the lateritic plateaus of the northern Western Ghats. Figure (a) represents the first two axes (NMDS1 & NMDS2) and (b) represents the second and third (NMDS2 & NMDS3) axes. The ellipses indicate multivariate 95% confidence intervals around the group centroid.

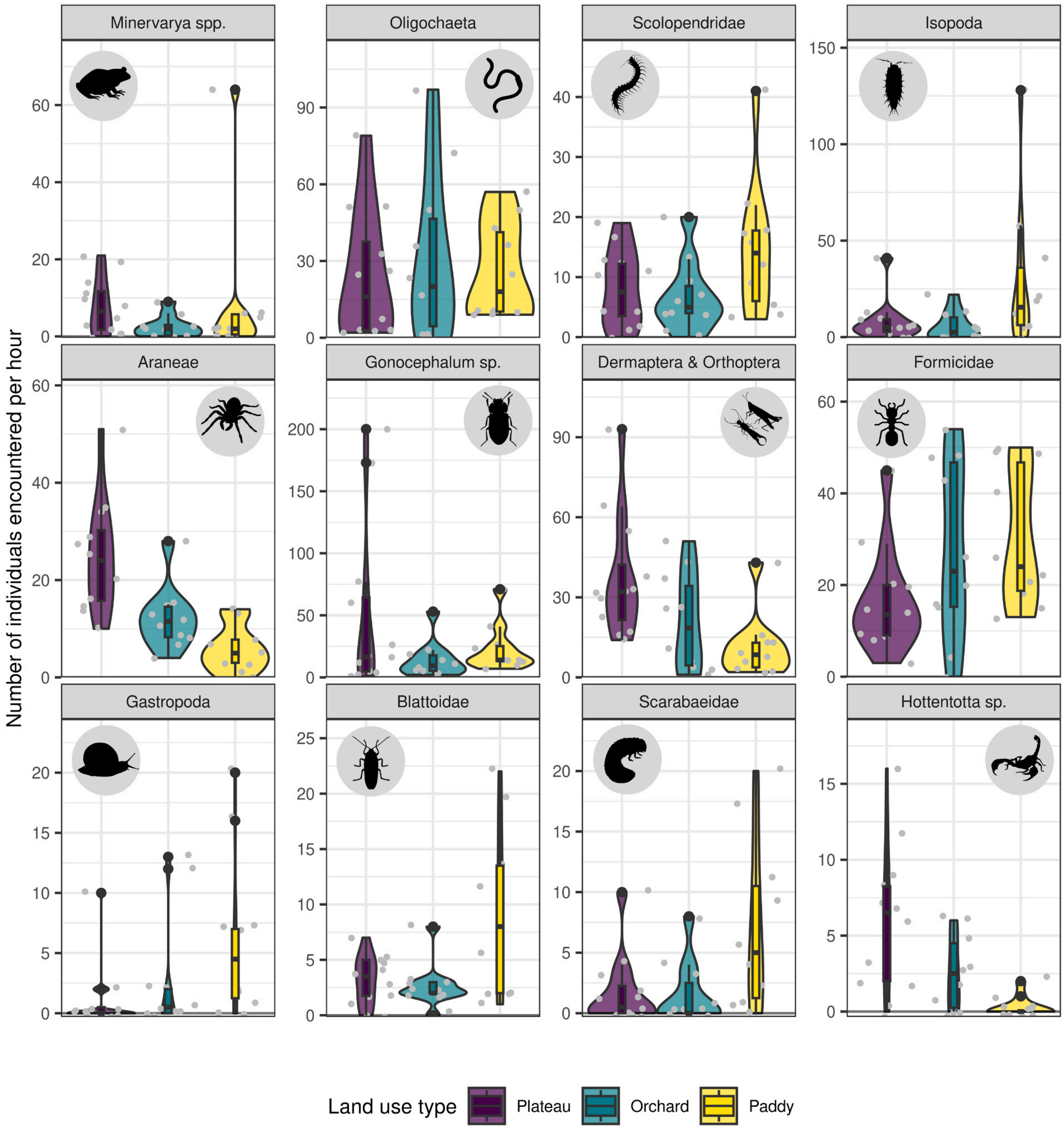

Fig. 5. Violin plots showing the encounter rates (per hour) of animals with greater than 100 detections during the survey across the three land-use types. The grey dots represent individual data points. Note that the numbers on the y-axis for Formicidae are the number of group encounters (per hour) (see Section 3.3 for details).

caecilian was significantly higher in abandoned paddy than in less-disturbed plateaus (Fig. 3; Table A4 in Appendix). However, we never detected the gecko and viper in paddy (Fig. 3a). The probability of occurrence of *H. albofasciatus* and *E. carinatus* was significantly higher in less-disturbed plateaus compared to the orchards and abandoned paddy (Fig. 3; Table A4 in Appendix). All three animals used large-sized rocks more than medium-sized ones (*G. seshachari*: $\chi2 = 12.6$, $df = 1$, $p < 0.001$; *H. albofasciatus*: $\chi2 = 6$, $df = 1$, $p = 0.01$; *E. carinatus*: $\chi2 = 6.55$, $df = 1$, $p = 0.01$; Fig. 3a).

Table A1
Sampling effort across different plateaus and land use types. Each site was independently subjected to one-hour time constrained searches.

Land Use	Plateau	Site Name	No. of Rocks Turned
Plateau	Bakale	Site 1	150
	Barsu	Site 1	260
	Devache Gothane	Site 1	249
	Devi Hasol	Site 1	131
	Devi Hasol	Site 2	324
	Devi Hasol	Site 3	171
	Devi Hasol	Site 4	86
	Gaokhadi	Site 1	240
	Nanar	Site 1	305
	Niveli	Site 1	231
	Runde	Site 1	222
	Runde	Site 2	195
Orchard	Ambolgad	Site 1	339
	Devache Gothane	Site 2	351
	Devi Hasol	Site 5	482
	Devi Hasol	Site 6	162
	Devi Hasol	Site 7	168
	Devi Hasol	Site 8	149
	Gaokhadi	Site 2	344
	Nanar	Site 2	299
	Niveli	Site 2	310
	Vetye	Site 1	268
Abandoned Paddy	Bakale	Site 2	161
	Devache Gothane	Site 3	190
	Devi Hasol	Site 9	147
	Devi Hasol	Site 10	187
	Devi Hasol	Site 11	142
	Devi Hasol	Site 12	116
	Devi Hasol	Site 13	120
	Devi Hasol	Site 14	224
	Gaokhadi	Site 3	270
	Musa Kazi	Site 1	186
Total		**32**	**7179**

3.3. Composition of the animal community under rocks across land-use types

Animals were detected under approximately 45% of the rocks turned (58%, 44%, and 24% under the large, medium, and small rocks, respectively). Apart from the *G. seshachari*, *H. albofasciatus*, and *E. carinatus,* we recorded eight genera of frogs, three genera of lizards, two species of snakes, and one mammal (Table A2). Overall, we documented 38 taxonomic groups spanning 10 classes and more than 20 orders under rocks across different land uses from 5738 encounters (Table A2 & Fig. A1 in Appendix). The most numerically dominant groups of animals found under the rocks were Insecta (2937), followed by Clitellata (861), Arachnida (671), Malacostraca (471), Chilopoda (320), Amphibia (283), and Gastropoda (106). Darkling beetles (*Gonocephalum* sp.), earthworms (Oligochaeta), ants, crickets, and earwigs were among the most abundant animals. The co-occurrence plots showed that paddy harboured six exclusive taxa, whereas less-disturbed plateaus had two, and orchards had none. Nine taxa occurred across all land-use types and rock-size classes (Fig. A2 in Appendix). NMDS analysis demonstrated that the animal communities found under rocks differ significantly across land-use types (PERMANOVA $R^2 = 0.21$, df = 2, $F = 3.82$, $p = 0.001$; Fig. 4). Animal composition under rocks in paddy was very distinct from that in orchards and lateritic plateaus (Fig. 4).

Less-disturbed plateaus had a significantly higher abundance of Araneae and *Gonocephalum* sp. than that in orchards; and Araneae, *Hottentotta* sp. and Dermaptera-Orthoptera groups than that in abandoned paddy (Fig. 5; Fig. A3 in Appendix). The abandoned paddy had a significantly higher abundance of Isopoda and Blattoidae than that in orchards; and Blattoidae than that in less-disturbed plateaus (Fig. 5; Fig. A3 in Appendix). The orchards showed a significantly higher abundance of *Hottentotta* sp. and Araneae than that in the abandoned paddy (Fig. 5; Fig. A3 in Appendix). The abundance of *Minervarya* spp., Oligochaeta, Scolopendridae, Formicidae, Gastropoda, and Scarabaeidae groups did not show any significant difference between any land-use types (Fig. 5; Fig. A3 in Appendix).

4. Discussion

Land-use change is among the biggest drivers of herpetofaunal declines worldwide (Ficetola et al., 2015; Doherty et al., 2020). Land-use change reduces the quantum of suitable habitat, and thereby negatively impacts the diversity and abundance of amphibians and reptiles, especially that of specialist species (Ficetola et al., 2015). However, previous studies have mainly examined the impacts of the conversion of forested landscapes to other land-uses (Kurz et al., 2014). In this study, we demonstrate the impacts of agricultural land-use conversion of the unique lateritic plateaus on select threatened and endemic species and on the community composition of

Table A2
Complete list of animals detected under the rocks turned across the land-use types with number of detections.

Class	Taxa	Number of detections			
		Plateau	Orchard	Paddy	Total
Amphibia	*Duttaphrynus melanostictus*	1	1	0	2
	Euphlyctis jaladhara	0	0	15	15
	Gegeneophis seshachari	3	7	25	35
	Hoplobatrachus tigerinus	8	0	0	8
	Microhyla cf. *nilphamariensis*	2	0	2	4
	Minervarya spp.	95	26	87	208
	Polypedates maculatus	0	0	1	1
	Sphaerotheca dobsonii	4	4	0	8
	Uperodon mormoratus	0	1	1	2
Arachnida	Acariformes	0	0	4	4
	Araneae	299	122	59	480
	Sahyadrimetrus sp.	28	10	48	86
	Hottentotta sp.	72	26	3	101
Chilopoda	Scolopendridae	98	68	147	313
	Scutigeromorpha	3	0	4	7
Clitellata	Oligochaeta	288	312	261	861
Diplopoda	Eugnatha	3	21	3	27
Gastropoda	Gastropoda	14	30	62	106
Insecta	*Acanthaspis* sp.	5	4	4	13
	Blattoidae	38	27	91	156
	Dermaptera & Orthoptera	447	208	115	770
	Erotylidae	3	18	15	36
	Formicidae	197	274	303	774
	Gonocephalum sp.	593	143	233	969
	Lepidoptera	7	18	10	35
	Scarabaeidae	21	16	71	108
	Termitoidae	6	17	43	66
	Zygentoma	7	1	2	10
Malacostraca	Brachyura	15	3	0	18
	Isopoda	99	57	297	453
Mammalia	*Mus* sp.	0	0	1	1
Reptilia	*Bungarus caeruleus*	0	0	1	1
	Echis carinatus	19	3	0	22
	Eutropis spp.	4	2	3	9
	Hemidactylus albofasciatus	23	1	0	24
	Hemidactylus sp. 1	2	0	0	2
	Ophisops spp.	1	1	0	2
	Typhlopidae	0	0	1	1
Total		**2405**	**1421**	**1912**	**5738**

rock-dwelling fauna. In the rock outcrop agroecosystem, land use change resulted in an influx of larger rocks in abandoned paddy. The two endemic species in the study exhibited contrasting responses to this land-use change. The conversion of lateritic plateaus to agroforestry plantations and abandoned paddy negatively impacted the threatened and endemic *H. albofasciatus* and the generalist *E. carinatus*. Interestingly, *G. seshachari*, an endemic amphibian that occurs in forests and plateaus, was more prevalent in the abandoned paddy than in less-disturbed plateaus and orchards. Habitat conversion significantly changes the composition of rock-dwelling faunal communities on the lateritic plateau. This is one of the first few studies to examine the impacts of land-use change on rock-dwelling fauna across a wide taxonomic breadth. The study also generates valuable baseline information on endemic and threatened species inhabiting the unique lateritic plateau habitat of the Western Ghats Biodiversity hotspot, one of which (*G. seshachari*) has been identified as 'Data Deficient' by the IUCN.

4.1. Large rocks as a refuge

Large-sized rocks on outcrops, which experience smaller daily temperature amplitudes, and can act as stable retreat sites, may be favoured by cold-blooded animals (Goldsbrough et al., 2003; Becker and Brown, 2016). In the rock outcrops of Australia, the broad-headed snake *Hoplocephalus bungaroides* and its principal prey, the Velvet gecko *Amalosia lesueurii*, depend on rocks with distinct thermal profiles as shelter sites (Webb and Shine, 1998). We found that the caecilian, gecko, and viper consistently preferred large rocks. Invertebrates were frequently encountered under large- and medium-sized rocks but were relatively rarer under small rocks (Fig. A1 in Appendix), highlighting the value of large rocks as important refuges on the open lateritic plateaus.

The presence of large rocks alone need not necessarily influence the occurrence of different animals. *Echis carinatus* and *Hemidactylus albofasciatus* preferred large rocks, yet they were not detected in abandoned paddy fields with the highest numbers of large rocks among the three land-use types. As the substratum under rocks is modified from hard rock to muddy soil with modification to paddy, microclimate under large rocks there can be unsuitable to some animals. Webb and Whiting (2006) found that the probability

Table A3

(**a).** The effect of land-use change and rock size on the encounter rate of rocks from the results of negative binomial GLM. Rows highlighted in bold indicate coefficients whose 95% CI do not overlap zero and thus were inferred to significantly influence the response variable.

Term	Coefficient	95% CI	*p*
Intercept: (Plateau & Small Size)	**3.9**	**3.63 – 4.2**	**< 0.001**
Orchard	**0.42**	**0.01 – 0.85**	**0.047**
Paddy	**-1.82**	**-2.29 – -1.35**	**< 0.001**
Medium Size	**0.87**	**0.47 – 1.26**	**< 0.001**
Large Size	-0.06	-0.46 – 0.35	0.78
Orchard x Medium Size	-0.26	-0.84 – 0.33	0.393
Paddy x Medium Size	**1.24**	**0.61 – 1.86**	**< 0.001**
Orchard x Large Size	0.02	-0.58 – 0.61	0.956
Paddy x Large Size	**2.59**	**1.96 – 3.22**	**< 0.001**

(**b).** Estimated marginal means for factor combinations in negative binomial GLM assessing the effect of land-use change and rock size on the encounter rate of rocks. Rows highlighted in bold indicate estimated marginal means whose 95% CI do not overlap zero and thus were inferred to significantly influence the response variable.

Size	Contrast	Estimate	SE	*z*	*p*
Small	Plateau – Orchard	-0.42	0.21	-1.99	0.12
	Plateau – Paddy	**1.82**	**0.24**	**7.65**	**< 0.001**
	Orchard – Paddy	**2.25**	**0.25**	**9.16**	**< 0.001**
Medium	Plateau – Orchard	-0.17	0.21	-0.81	0.7
	Plateau – Paddy	**0.58**	**0.21**	**2.76**	**0.02**
	Orchard – Paddy	**0.75**	**0.22**	**3.42**	**< 0.01**
Large	Plateau – Orchard	-0.44	0.21	-2.06	0.0976
	Plateau – Paddy	**-0.77**	**0.21**	**-3.62**	**< 0.001**
	Orchard – Paddy	-0.33	0.22	-1.49	0.3

Table A4

The effect of land-use changes on the proportion of detections of the focal species from the results of binomial GLMs (with a mixed bias-reduction adjusted scores approach for the models of *H. albofasciatus* and *E. carinatus*). Rows highlighted in bold indicate coefficients whose 95% CI do not overlap zero and thus were inferred to significantly influence the response variable.

Species	Land use type	Coefficient	95% CI	*p*	*Nagelkerke's* R^2
G. seshachari	**Intercept: Plateau**	**-7.16**	**-8.95 – -6.03**	**< 0.001**	**0.33**
	Orchard	0.99	-0.48 –2.91	0.23	
	Paddy	**2.88**	**1.67 – 4.71**	**< 0.001**	
H. albofasciatus	**Intercept: Plateau**	**-4.73**	**-5.14 – -4.31**	**< 0.001**	**0.58**
	Orchard	**-2.83**	**-4.48 – -1.18**	**< 0.001**	
	Paddy	**-3.43**	**-6.23 – -0.63**	**0.02**	
E. carinatus	**Intercept: Plateau**	**-4.87**	**-5.32 – -4.43**	**< 0.001**	**0.42**
	Orchard	**-1.84**	**-2.98 – -0.7**	**< 0.01**	
	Paddy	**-3.29**	**-6.09 – -0.48**	**0.02**	

of occurrence of snakes was higher under boulders on rock substrate than on soil substrate. To understand how agricultural land-use affects both the availability and the quality of microhabitats, future studies should determine the influence of substrate on species prevalence, an aspect that was not explored in this study. Previous studies have shown that both intensive land-use and abandonment lead to habitat and species assemblage homogenization in the case of Orthoptera (Fumy et al., 2021) and abandoned farmland provides alternate habitat for wetland ground beetles (Yamanaka et al., 2017). Similar studies across other taxa can provide insights into the habitat management and restoration of agricultural landscapes.

Apart from lining the paddy, large rocks are also used extensively to construct compound walls and mark land borders among other activities (Mirza and Sanap, 2012; Thorpe and Watve, 2015). Decreased availability of large rocks due to these activities might be detrimental to the prevalence of rock-dwelling fauna. Manipulative experiments involving rock addition could be carried out on disturbed plateaus to determine species recovery and plan restoration or management of these habitats (Goldingay and Newell, 2017; Palmer et al., 2022).

4.2. Contrasting responses of reptiles and caecilian

Herpetofaunal communities are known to respond differentially to habitat conversion to monocultures and polyspecific plantations (Trimble and van Aarde, 2014; Iglesias-Carrasco et al., 2022). Reptiles are known to be more resilient to agricultural land-use change than amphibians (Fulgence et al., 2022). Our results were in contrast with those of previous studies, and showed the caecilian was more common in abandoned paddy and reptiles were negatively impacted by land-use change. While the viper and the gecko were negatively affected by land-use change, the muddy soils of the abandoned paddy may have provided increased opportunity for burrowing and more amenable microhabitat conditions that may reduce water loss of the endemic and fossorial caecilian. Most of the past

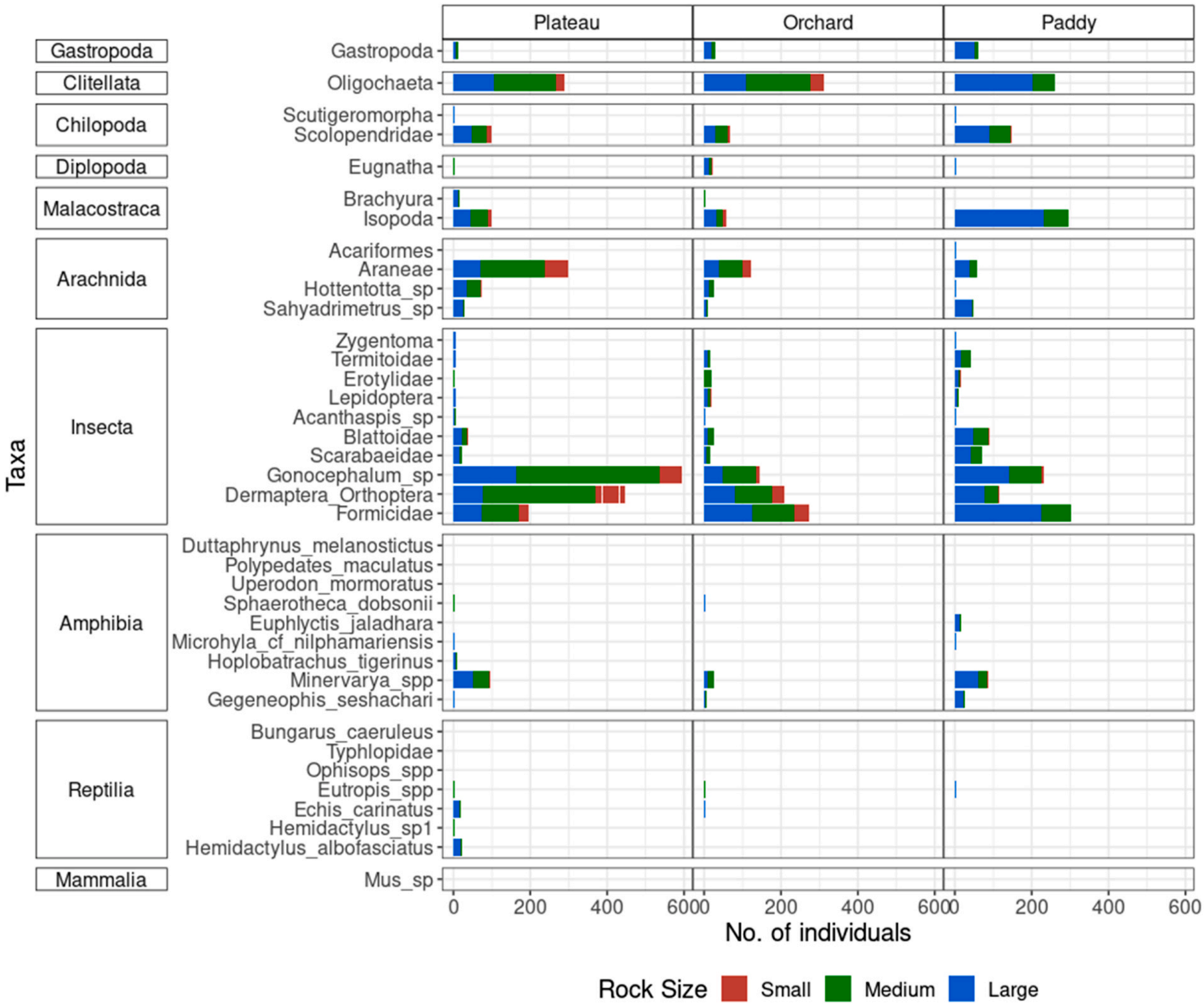

Fig. A1. Figure showing the number of different taxa belonging to the classes represented in the boxes on the left, encountered under rocks of varying sizes across land-use types. The number of individuals is depicted except in the cases of ants (Formicidae), termites (Termitoidae) and mites (Acariformes); their presence-absence data was considered.

research has focused on anurans with little information on the impacts of land-use change on caecilians (Valdez et al., 2021). The present study is one of the first to determine the responses of caecilians to land-use change.

Generally, land-use change negatively impacts endemic and habitat specialist species while benefiting generalist species (McKinney and Lockwood, 1999; Newbold et al., 2018). Instances of endemics benefitting from land-use change, like the caecilian in our case, are not common (Meijer et al., 2011). Unlike the habitat specialist *H. albofasciatus*, *G. seshachari* is a habitat generalist found in synanthropic habitats (Gower et al., 2007; Gaikwad et al., 2009). However, we must be cautious in interpreting this result since only certain kinds of land-use change (such as abandoned paddy in our case) in specific contexts (rock addition on soil substrate) provided a more favourable habitat for the caecilian. Farmland abandonment has varying consequences for biodiversity (Queiroz et al., 2014) as demonstrated in this study. Additionally, moving the relatively large rocks from abandoned paddy to plateaus may benefit species such as geckos and vipers, but may have the converse effect for caecilians.

4.3. Other factors influencing reptile prevalence

In our study, despite the similar availability of large rocks in plateaus and orchards, gecko and viper abundances were lower in orchards. This might be due to the altered habitat structure in orchards, due to the addition of trees in an otherwise treeless landscape (Gorissen et al., 2017; Amberkar, 2022). Apart from the modified microhabitat, human persecution could also be responsible for the rarity of the saw-scaled viper, which is one of the big four venomous snakes in India (Das, 2002). Humans fear venomous vipers and often vipers are persecuted when encountered, especially in the cattle grazing grounds of plateaus (Balakrishnan, 2010). Vipers are supposed to be very common in the study area, from where approximately 150 vipers in five hours was collected by a team of five

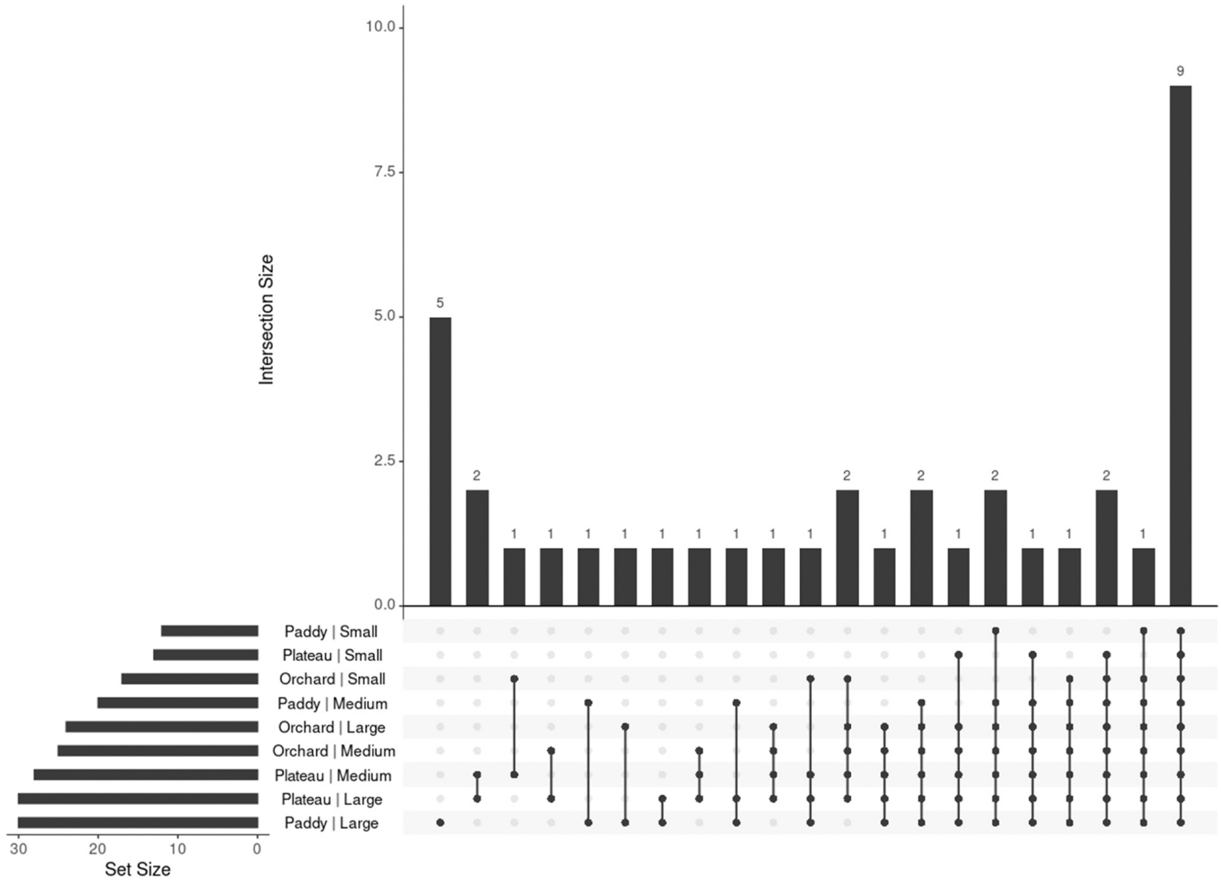

Fig. A2. Figure showing the rock dwelling animals composition across the land use types and rock size classes in the lateritic plateaus of the northern Western Ghats. Note that empty combinations are not shown in the figure. Vertical bars indicate the number of taxa recorded in each unique combination of land-use type and rock-size class shown with the connected points.

members, two decades ago (pers. comm. Sanjay Thakur). However, in a comparable effort, we found only 22 vipers. This underlines the need to systematically evaluate how viper collection and rock removal may have impacted their regional populations (Webb and Shine, 2000).

The most common prey item of *E. carinatus* and *Hemidactylus* sp. are arthropods (Cyriac and Umesh, 2021; Ghezellou et al., 2021); and of *Gegeneophis* are termites and earthworms (Measey et al., 2004). While agricultural land-use change did not alter the overall abundance of arthropods, we found a change in the community composition of rock-dwelling invertebrates. Replacement of Araneae, Dermaptera, and Orthoptera with Scolopendrid centipedes, Oligochaetes, Formicids, and Isopods possibly resulted in this turnover in the communities. We had expected encounters of invertebrates to be lower in orchards compared to the less-disturbed plateau due to the heavy use of pesticides in orchards. But, except for the lower numbers of spiders and darkling beetles, we did not find any significant differences. However, further studies are required on the pesticide effect on invertebrates accounting for the seasonality in pesticide use. Future studies should aim to generate fine-scale information on gecko, caecilian, and viper diets through metabarcoding and compare the abundance of preferred prey items across land-use types over a long-term to determine the potential role of prey availability in their distributions.

Information from locals suggested potential threats of illegal pet trade to the gecko, an aspect that needs to be studied in greater detail (Altherr and Lameter, 2020). Given the harvest, persecution, and other factors discussed above, it is critical to monitor populations of the vipers, gecko, and caecilian, particularly in sites where they are relatively common. In this study, using a non-invasive method, we have established baselines of the rock-dwelling faunal community that can be useful for periodic monitoring.

4.4. Conservation of lateritic plateaus

The low-elevation lateritic plateaus are not protected, have received poor conservation attention, and are being rapidly converted to orchards. Proposed development projects such as refineries and power plants have also been planned (Watve, 2013). Additionally, plateau rocks are being used extensively for multiple human activities. Therefore, there is a need for systematic biodiversity inventories of the lateritic plateaus, identifying key plateaus, and working with local communities towards their conservation. Habitat

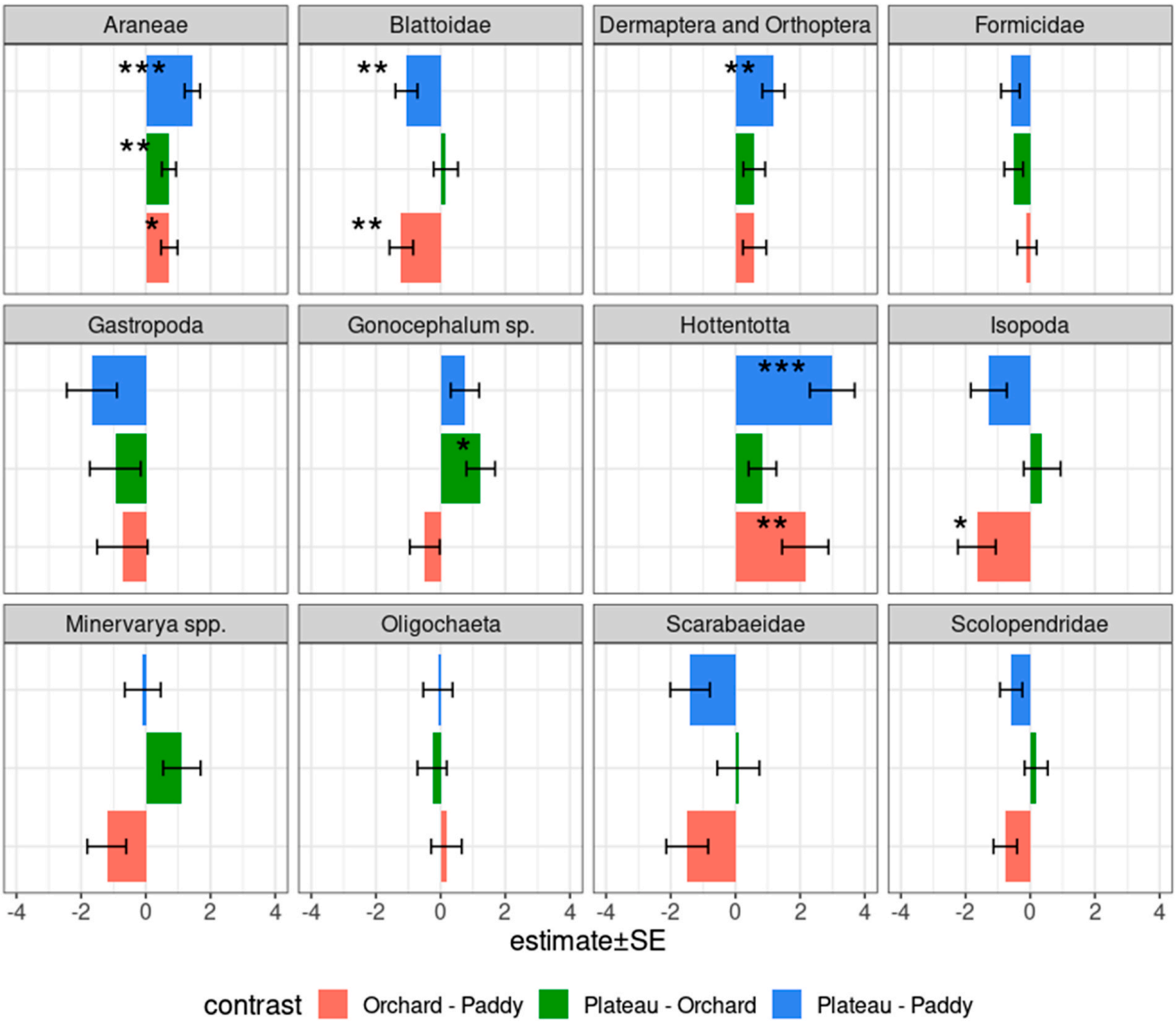

Fig. A3. Barplots showing the pairwise contrast coefficients from the generalized linear models used to assess the influence of land-use type on the encounter rate of animal groups with > 100 individuals detected during the whole survey. Significance levels: * **p < .001, * *p < .01, and *p < .05.

restoration in plateaus, where large rocks have been heavily depleted, can be explored through the introduction of aptly designed artificial rocks (Croak et al., 2010; Croak et al., 2013). The information collected in this study, in conjunction with other socio-ecological information collected as part of our larger research projects, will contribute to declaring select plateaus as 'Biodiversity Heritage Sites' with the due consent of local communities.

4.5. Limitations of the study

One limitation of the study is our failure to incorporate detection probability of animals while estimating the probability of occurrence. A previous study has demonstrated that detection probability of a lizard was very low, and species was missed despite being present (McGrath et al., 2015). We refrained from using occupancy sampling for the study since we used time-constrained searches. Repeat surveys using this method would have meant sampling different rocks during each re-visit which would have induced a bias in the study. If we had constrained for area and not time, we would have missed sampling suitable microhabitats that fell outside the plots. Additionally, we were sampling a diverse array of taxa and we were afraid that rock-turning would affect different taxa differently and would influence their occupancy. We also wanted to maximise spatial coverage since some species are extremely rare, lacking baseline information on their prevalence. Given these reasons, we did not use occupancy sampling methodology that would have allowed us to estimate detection probability. Given the baseline information generated in this study, future studies should demarcate areas and rocks and conduct repeat surveys to determine the influence of detection probability on species occurrence across land-use types. Invertebrate taxonomy in the region is still not resolved as new species continue to be described. This did not allow us to

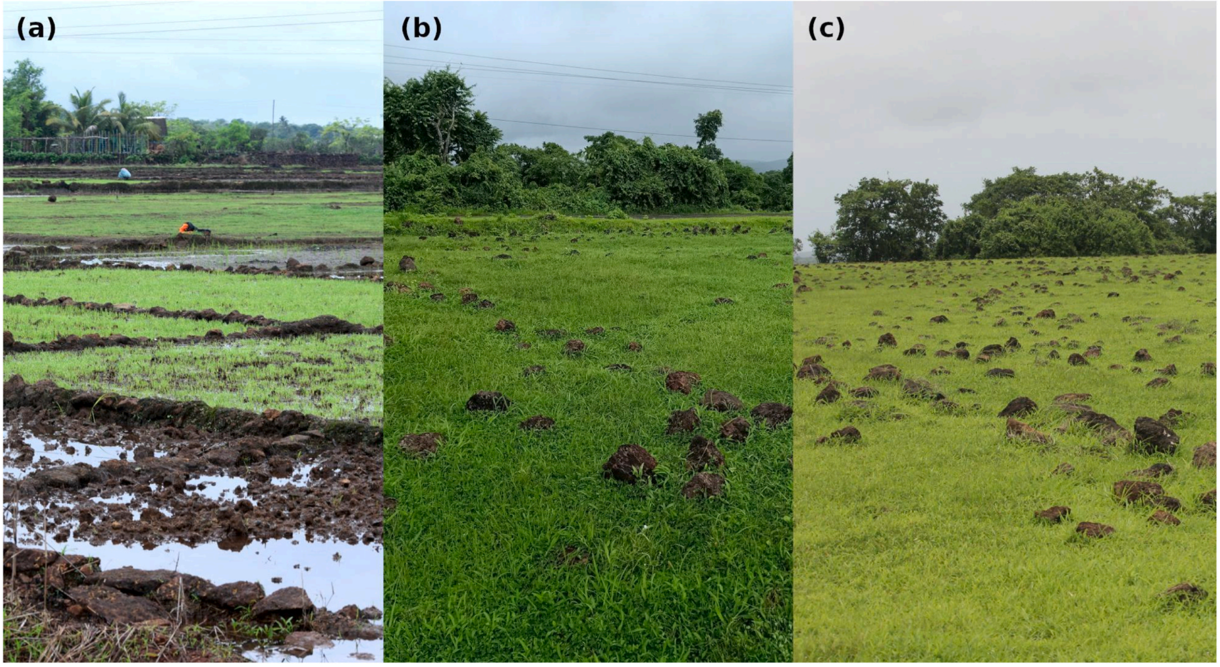

Fig. A4. Figure showing the use of rocks sourced from the plateau in paddy fields. Figure (a) shows an active paddy with rocks lined up to demarcate paddy boundaries; (b) and (c) shows gradual displacement of the boundary rocks creating scattered boulder grounds with wet soil after paddy abandonment. Photographs by V. Jithin.

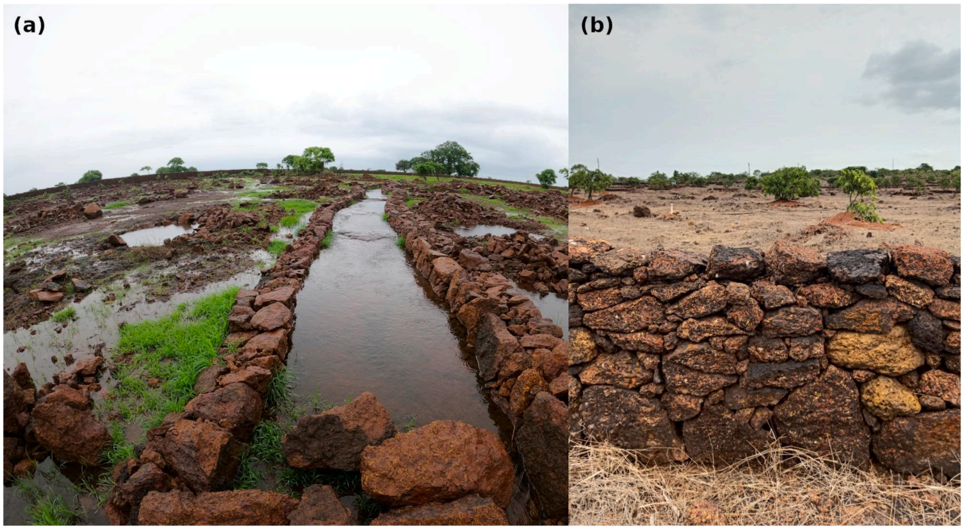

Fig. A5. Figure (a) showing a newly blasted plateau with plantation pits along a water diversion canal and (b) showing an establi37shed mango orchard with boundary rock wall around the property. Photographs by V. Jithin.

identify certain invertebrates at the species level. However, even with higher levels of taxonomic information, NMDS demonstrated significant compositional differences. Fine-scale taxonomic information will most likely exacerbate these differences. Since local communities extensively use all the plateaus, we did not have a completely undisturbed laterite plateau as a benchmark. Therefore, our inferences of different landscapes are, at best conservative, since undisturbed sites may have had much higher abundances of some of these animals.

5. Conclusions

We demonstrate that agricultural land-use change in open natural ecosystems can have drastic impacts even on species adapted to persist in extreme and variable environments. We also show that land-use change, while impacting specialist and generalist species, may also be advantageous to certain endemic species under certain circumstances. Land-use change is often seen in the light of the benefit to people due to agricultural intensification and development, though it results in biodiversity decline and the associated loss in ecosystem function and services to humans (Hooper et al., 2012; Newbold et al., 2015). Our study provides some of the first insights from the rock-dwelling fauna living in the least-explored open landscape in the Western Ghats, contributing to the understanding of ecology and conservation of Indian rock outcrops. Future studies need to systematically document the impacts of agricultural land-use change on biodiversity and ecosystem function in open natural ecosystems and identify thresholds that may facilitate the coexistence of humans and biodiversity.

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CRediT authorship contribution statement

VJ and *RN* conceived the ideas and designed the methodology with inputs from *AW* and *VG*; *VJ* collected the data; *VJ* and *RN* analysed the data; *VJ and RN* led the writing of the manuscript with inputs from *VG*, *AW,* and *MR*. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data and code used in this study are available at https://doi.org/10.5061/dryad.4j0zpc8j4

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Appendix

See Appendix Tables A1, A2, A3, A4.
See Appendix Fig. A1, A2, A3, A4, A5.

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