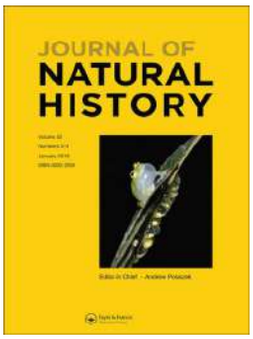

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Herpetofauna in Bromo Tengger Semeru National Park – underestimated diversity in East Java's upper montane forest

Luhur Septiadi[a,b], Muhammad Fathoni[a,c], Muhammad Asyraf Rijalullah[a,d], Miftah Farid Assiddiqy[a,d], Agus Nurrofik[a,d], Abdul Mutholib Shahroni[a,d,e,f], Afthoni Nur Fuadi[a,g], Berry Fakhry Hanifa[a,h], Muhammad Asmuni Hasyim[a,h], Mahmuddin Rahmadana[i], Hendro Widjanarko[i] and Nia Kurniawan[a,d*]

[a]Bromo Tengger Semeru Herpetofauna Conservation (BTSHC), Malang, Indonesia; [b]Wildlife Conservation Society – Indonesia Program, Bogor, Indonesia; [c]Manusela National Park, Masohi, Indonesia; [d]Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Brawijaya, Malang, Indonesia; [e]Kupunesia, Malang, Indonesia; [f]Yayasan Badak Indonesia (YABI), Bogor, Indonesia; [g]Department of Biology, Faculty of Science and Data Analytics, Institut Teknologi Sepuluh Nopember, Surabaya, Indonesia; [h]Biology Study Program, Faculty of Science and Technology, Universitas Islam Negeri Maulana Malik Ibrahim, Malang, Indonesia; [i]Bromo Tengger Semeru National Park, Malang, Indonesia

ABSTRACT

The East Java province is among the most vulnerable regions of Java and still possesses overlooked biodiversity. There are very few remaining areas of pristine forest, including the upper montane forests that are home to a wide variety of poorly known and endemic herpetofauna. From August 2022 to May 2023, a survey was carried out in the upper montane forest of Bromo Tengger Semeru National Park (BTSNP) to examine the herpetofauna's diversity and community along the elevational gradient. Out of 20 surveyed sites, we identified 47 herpetofauna species, comprising 20 amphibian and 27 reptile species, including three species of conservation importance, ie *Nyctixalus margaritifer, Sphenomorphus sanctus tenggeranus*, and *Tetralepis fruhstorferi*. We found that amphibian and reptile diversity decreased linearly with increasing altitude, with generalist species more abundant at relatively moderate and wide altitude ranges (750–1500 m) and specialist species (even endemics, eg *T. fruhstorferi*) found at higher and narrower altitudes (>1500 m). This study highlights hotspots for amphibian and reptile diversity where conservation efforts may require different approaches (sites with high species richness but many common species vs. sites with low species richness but including some endemic species). Expanding systematic surveys into currently underexplored areas will also help refine conservation priorities by uncovering hidden diversity and informing more effective, evidence-based management plans.

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Amphibian; community; conservation; highland forest; new record; reptile

Introduction

Java is the 13th largest island in the world, with biodiverse ecoregions, such as upper montane rainforests and lower montane rainforests in the west and east (Whitten *et al*. 1996; Supriatna and Margules 2025). As the central administrative hub, Java's population has increased rapidly with more than 50% of Indonesian population inhabiting this island, creating highly populated areas that pose various environmental threats (Kurniawan *et al*. 2021). The growing human population has put severe pressure on biodiversity in Java, as forest size is reduced and limited to upland slopes due to land-use change and human encroachment (Smiet 1990). Java is known to be home to many poorly known and endemic amphibian and reptiles, which have been studied since the nineteenth century (Boulenger 1890; Boettger 1892; de Rooij 1917; van Kampen 1923; Kopstein 1930; Mertens 1957; Hodges 1993; Iskandar 1998). More than 200 species of amphibians and reptiles have been described from Java (Frost 2023; Uetz *et al*. 2023), including both species widespread in Southeast Asia and endemic species. Nevertheless, former studies have mainly focused on West and Central Java, resulting in a sampling gap in East Java (Kurniawan *et al*. 2021; Kusrini *et al*. 2021).

Few upper montane forests remain in East Java, including Bromo Tengger Semeru National Park (BTSNP), a popular tourist destination characterised by the sea of sand and the caldera of Mount Bromo, as well as Java's

CONTACT Luhur Septiadi luhur.septiadi@gmail.com
*Deceased on 28 September 2025

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highest active volcano, Mount Semeru, which is a favourite hiking spot (Departemen Kehutanan 2009). The BTSNP offers diverse upper montane rainforest habitats and is considered an area of high biodiversity, but data on the region's biodiversity is lacking, including amphibians and reptiles (or herpetofauna) (Fathoni *et al*. 2022). Recently, rediscoveries of endemic species and new distribution records of herpetofauna in BTSNP and its surroundings have been reported (Erfanda *et al*. 2019; Hanifa *et al*. 2023a; Septiadi *et al*. 2023), indicating that the area may have more herpetofauna diversity than is currently known. However, survey efforts are still limited, and a comprehensive species list of herpetofauna in BTSNP does not yet exist.

Understanding patterns of herpetofauna diversity can give us insights into how best to protect them, which is critical to supporting conservation management, especially in upper mountain ecosystems such as BTSNP. Comprehensive herpetofauna surveys suggested that herpetofauna can be useful and cost-effective indicators of environmental change (Kusrini 2008), for example, in BTSNP during continuous volcanic eruptions (Hanifa *et al*. 2024), and in Bali Barat National Park (Amarasinghe *et al*. 2021). Our current knowledge of the distribution of herpetofauna in the mountain ecosystems of BTSNP is based on recent research outside the conservation area (Elzain *et al*. 2018; Hidayah *et al*. 2018; Indrawati *et al*. 2018; Septiadi *et al*. 2018; Arroyyan *et al*. 2020; Fathoni *et al*. 2022; Hanifa *et al*. 2023a) that mostly focused on checklists of species diversity, composition, and abundance. However, a comprehensive understanding of how diversity patterns shift with elevation, particularly in the upper montane forests of East Java, remains limited. Given the pressures of land-use change and the importance of montane regions for endemic species conservation, studying these patterns is essential for guiding future conservation efforts.

Here we conducted a thorough survey in BTSNP and surrounding areas to better understand herpetofauna diversity and investigate the relationship between species diversity across a tropical forest elevational gradient. We also identified species of conservation importance based on endemicity and information gaps, as well as sites of conservation importance based on the degree of species diversity and generalist–specialist species found. This baseline data of herpetofauna diversity will help strengthen future management interventions for these poorly known and threatened animal groups in the face of climate and environmental change.

Methods

Study area

Bromo Tengger Semeru National Park (8.024°S, 112.952°E) covers an area of 502.763 km^2 and is dominated by sub-alpine, sub-montane, and montane forests, with elevation ranging from 750–3676 m asl, and temperature ranging from 3 to 20°C (reaching subzero in extreme conditions) (Figure 1). As an active volcanic area (two volcanoes present, ie Mount Bromo [2329 m asl] and Mount Semeru [3676 m asl]), this natural landscape suffers from continuous yearly eruption (Rachmawati *et al*. 2007). BTSNP is also a tourist destination for Mount Bromo's sea of sand and caldera, six natural lakes, tropical upper montane forest, endemic flora species (eg edelweiss and orchids) and threatened vertebrates (eg Javan leopard, East Javan langur, and Javan-hawk eagle) (Hakim and Soemarno 2017). Administratively, BTSNP are located adjacent to four regencies, ie Malang, Lumajang, Probolinggo, and Pasuruan. Within the national park, there is an enclaved zone (an area where human settlements existed prior to the formal establishment of the national park), particularly around the Ranu Pani and Jarak Ijo villages. Survey sites inside the national park represent relatively intact forest with minimal human disturbance, whereas sites in the buffer zone are characterised by higher levels of human influence, including agriculture, settlements, and resource extraction.

Sampling

Sampling was conducted at 20 survey sites (16 sites inside the national park and four sites in the buffer zone; Figure 1; Table 1) considered to be representative of the local amphibian and reptile fauna on the basis of habitat type, temperature, humidity, altitude, and disturbance level. Furthermore, sites were chosen by considering preliminary data, team resources, access to the location, and surveyor safety (given the location is quite extreme and there is frequent volcanic activity).

We used the standard Visual Encounter Survey method with purposive sampling method (Kusrini 2008; Dorcas and Willson 2009) at night (6.00pm to 12.00am), between August 2022 and May 2023 (60 days of fieldwork). At

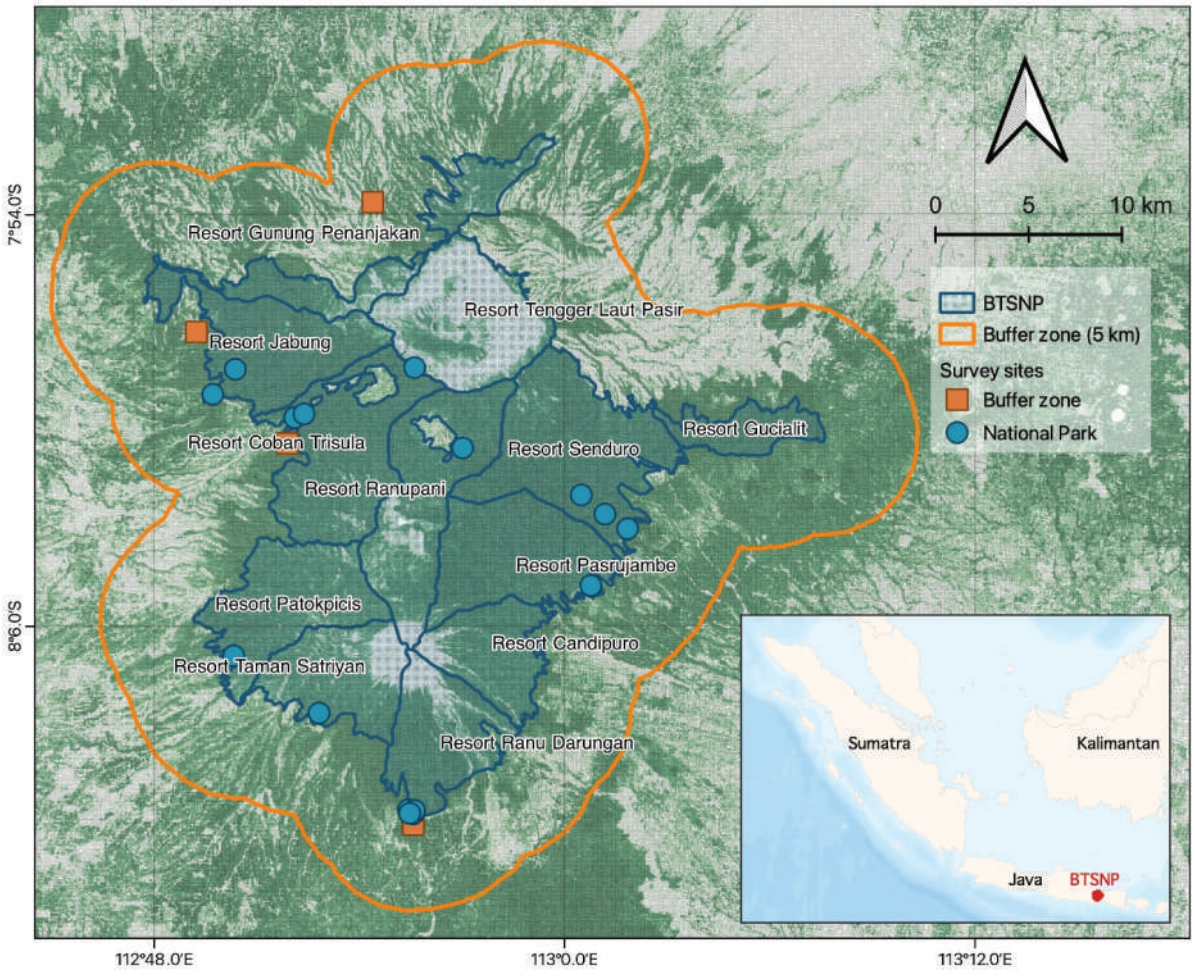

Figure 1. Map of Bromo Tengger Semeru National Park in Java Island (inset map) showing the location of 20 surveyed sites across national park boundaries and the buffer zone. The tree cover is represented by green colours (Hansen *et al*. 2013). BTSNP: Bromo Tengger Semeru National Park.

each site, we defined three subsample points with a radius of 150 m each (with total area covered ± 4.24 km^2) to avoid double counting. We surveyed each subsample point for 3 consecutive days (1 day per subsample point), where six trained surveyors (equipped with boots, headlamps, snake hooks and other safety equipment) combed through areas potentially inhabited by reptiles and amphibians. We collected data on species encounters, location, elevation and habitat. Some of the specimens, whose collection was deemed important, were captured by hand and immediately transferred to the laboratory for examination. We recorded habitat information and elevation using a Garmin eTrex 10 GPS receiver with the WGS84 datum. Detailed photographs of the live specimens were taken ex situ. Specimens were euthanised using a 7.5% benzocaine solution, preserved in 10% formalin for 24 h, and then stored in 70% ethanol. These specimens were deposited at the Laboratory of Animal Diversity and Ecology Collection, Biology Department, Universitas Brawijaya, Indonesia (NK). This procedure followed the guidelines set by Kurniawan *et al*. (2022).

Species identification

We identified herpetofauna species by examining the external morphological characters and following the nomenclature from the literature (de Rooij 1917; Iskandar and Colijn 2000; McKay 2006; Das 2015; Figueroa *et al*. 2016; de Lang 2017; Streicher and Ruane 2018; Burbrink *et al*. 2020; Frost 2023; Uetz *et al*. 2023). We grouped the herpetofauna by taxon and report the conservation status based on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2022).

Table 1. List of 20 surveyed sites in Bromo Tengger Semeru National Park including latitude and longitude in degree minutes second (datum WGS84), elevation in metres above sea level (m), and result of diversity index (H').

Survey site	Longitude (DMS)	Latitude (DMS)	Elevation (m)	H'
National Park				
Coban Jodo	7°59′14″S	112°49′43″E	1.034	1.68
Bendolawang	7°58′30″S	112°50′23″E	1.254	2.24
Jarak Ijo Sumber	7°59′48″S	112°52′24″E	1.547	0.50
Trisula	7°59′55″S	112°52′07″E	1.456	1.35
Jemplang	7°58′28″S	112°55′37″E	2.364	0.00
Ranu Darungan	8°11′28″S	112°55′35″E	827	2.84
Sungai Besuk	8°11′21″S	112°55′26″E	861	2.09
Loji	8°11′22″S	112°55′36″E	856	1.87
Sudetan	8°11′27″S	112°55′28″E	833	1.61
Resort Senduro	8°03′10″S	113°01′51″E	1.102	1.75
Blok Ireng-ireng	8°02′44″S	113°01′11″E	1.151	1.60
Kali Cilik	8°02′11″S	113°00′29″E	1.240	1.91
Kopirejo	8°06′51″S	112°50′20″E	1.084	0.45
Ranu Regulo	8°00′48″S	112°57′02″E	2.100	0.00
Kali Tempuk	8°04′49″S	113°00′46″E	934	1.83
Taman Satriyan 1	8°08′32″S	112°52′49″E	1.306	1.49
Buffer zone				
Coban Pelangi	8°00′40″S	112°51′54″E	1.238	1.53
Coban Siuk	7°57′25″S	112°49′15″E	1.019	1.93
Pronojiwo	8°11′46″S	112°55′34″E	795	2.52
Wonokitri	7°53′39″S	112°54′25″E	1.890	0.00

Data analysis

We reported species composition of encountered amphibian and reptiles (encounters [*n*] and relative frequency [F %]) and compared them between surveyed sites in the national park and buffer zone using Venn diagrams. We analysed the diversity of amphibian community data using asymptotic and non-asymptotic analyses based on widely used Hill numbers on the order of q = 0 (species richness, Chao1) for various datasets, ie (a) herpetofauna across all sites, (b) between amphibians and reptiles across all sites, and (c) herpetofauna between national park and buffer zone sites. Individual-based rarefaction and extrapolation (R/E) curves based on diversity order (q = 0) and a sample completeness curve were computed and plotted with 95% confidence intervals. The analysis was done in the R package provided in iNEXT Online (Hsieh *et al*. 2016; Chao *et al*. 2023; https://chao.shinyapps.io/iNEXTOnline/), with 200 bootstrap replicates for confidence interval estimation. Extrapolation was performed for up to twice the minimum observed sample size, following standard recommendations. Our analysis combined all individuals collected from all survey sites to estimate overall species diversity across the study area, rather than assessing sampling sufficiency at each individual site. Survey completeness was evaluated following the approach of Marthy *et al*. (2017). Species richness was then estimated using the Chao1 estimator, and survey completeness was calculated as the ratio of observed to estimated species richness (S_{obs}/S_{Chao1}), to account for the overall adequacy of the survey.

We analysed the species diversity index (H') using Shannon-Weaver diversity index (Shannon and Weaver 1949). A linear regression model was also fitted to investigate the relation between elevation and species diversity index (H') across surveyed sites, analysed in R base (R Core Team 2023). All data and R scripts used for the analyses in this study are provided as supplementary files (https://doi.org/10.5281/zenodo.17358752).

Results

Diversity and species of conservation importance

A total of 1125 individuals were recorded, with an encounter rate of 18.7 individuals/day and 265.3 individuals/km^2. This included 47 species (20 amphibian and 27 reptile species) from 14 families (six amphibian and eight reptile families) (Tables 2, and 3), where reptiles (57%) had higher species richness than amphibians (43%) (Figure 2(A)). Twenty-one species (11 amphibian and 10 reptile species) were present within both national park

Table 2. List of herpetofauna species found during our surveys in Bromo Tengger Semeru National Park. Table entries include taxon family and species, presence/absence indicated by + (encountered) and – (not encountered), conservation status by International Union for Conservation of Nature (IUCN), encounters (*n*), and relative frequency in percentage (F %).

Taxon	National Park	Buffer zone	IUCN	n	F (%)
AMPHIBIAN					
Bufonidae					
Duttaphrynus melanostictus	+	+	LC	12	1.07
Ingerophrynus biporcatus	+	–	LC	1	0.09
Leptophryne borbonica	+	+	LC	128	11.38
Phrynoidis asper	+	–	LC	25	2.22
Dicroglossidae					
Fejervarya limnocharis	+	–	LC	18	1.60
Limnonectes microdiscus	+	+	LC	64	5.69
Occidozyga sumatrana	+	–	LC	11	0.98
Megophrydae					
Leptobrachium hasseltii	+	+	LC	16	1.42
Megophrys montana	+	–	LC	31	2.76
Microhylidae					
Kaloula baleata	+	–	LC	1	0.09
Microhyla achatina	+	+	LC	28	2.49
Microhyla palmipes	+	–	LC	18	1.60
Ranidae					
Hylarana nicobariensis	+	–	LC	17	1.51
Hylarana chalconota	+	+	LC	52	4.62
Odorrana hosii	+	+	LC	223	19.82
Wijayarana masonii	+	+	LC	88	7.82
Rhacophoridae					
Nyctixalus margaritifer	+	–	LC	3	0.27
Philautus aurifasciatus	+	+	LC	162	14.40
Polypedates leucomystax	+	+	LC	29	2.58
Rhacophorus reinwardtii	+	+	LC	29	2.58
REPTILE					
Agamidae					
Bronchocela jubata	+	+	LC	35	3.11
Draco volans	+	+	LC	7	0.62
Gonocephalus kuhlii	+	–	VU	18	1.60
Gekkonidae					
Cyrtodactylus petani	+	+	DD	25	2.22
Scincidae					
Dasia olivacea	+	–	LC	2	0.18
Eutropis multifasciata	+	+	LC	12	1.07
Eutropis rugifera	+	–	LC	1	0.09
Sphenomorphus puncticentralis	+	–	LC	2	0.18
S. sanctus tenggeranus	+	+	LC	3	0.27
Tytthoscincus temmincki	+	+	LC	27	2.40
Colubridae					
Calamaria linnaei	+	+	LC	3	0.27
Ahaetulla prasina	+	+	LC	2	0.18
Coelognathus flavolineatus	–	+	LC	1	0.09
Dendrelaphis formosus	+	–	LC	1	0.09
Dendrelaphis pictus	–	+	LC	1	0.09
Gonyosoma oxycephalum	–	+	LC	1	0.09
Oligodon bitorquatus	–	+	LC	1	0.09
Rhabdophis chrysargos	+	–	LC	1	0.09
Rhabdophis subminiatus	+	–	LC	1	0.09
Sibynophis geminatus	+	–	LC	1	0.09
Elapoidis fusca	–	+	LC	2	0.18
Tetralepis fruhstorferi	+	+	VU	9	0.80
Elapidae					
Bungarus candidus	–	+	LC	1	0.09
Pareidae					
Aplopeltura boa	+	–	LC	3	0.27
Pareas carinatus	+	+	LC	4	0.36
Pythonidae					
Malayopython reticulatus	+	–	LC	1	0.09
Viperidae					
Craspedocephalus puniceus	+	–	LC	4	0.36
TOTAL				1,125	100

LC: Least Concern; DD: Data Deficient; VU: Vulnerable.

Table 3. Checklist of amphibian and reptile on 20 surveyed sites in Bromo Tengger Semeru National Park. Presence in the surveyed site is indicated by a cross (X).

Taxon/site	Coban Jodo	Bendolawang	Jarak Ijo Sumber	Trisula	Jemplang	Ranu Darungan	Sungai Besuk	Loji	Sudetan	Resort Senduro	Blok Ireng-ireng	Kali Cilik	Kopirejo	Ranu Regulo	Kali Tempuk	Taman Satriyan 1	Coban Pelangi	Coban Siuk	Pronojiwo	Wonokitri
AMPHIBIAN																				
Bufonidae																				
Duttaphrynus melanostictus						X												X	X	
Ingerophrynus biporcatus									X											
Leptophryne borbonica	X	X									X	X						X		
Phrynoidis asper																X				
Dicroglossidae																				
Fejervarya limnocharis									X											
Limnonectes microdiscus	X	X				X	X					X	X		X	X		X	X	
Occidozyga sumatrana						X	X													
Megophrydae																				
Leptobrachium hasseltii	X	X					X			X		X			X	X		X		
Megophrys montana	X	X	X	X			X			X		X			X	X				
Microhylidae																				
Kaloula baleata						X														
Microhyla achatina	X	X				X	X		X									X	X	
Microhyla palmipes						X	X	X				X								
Ranidae																				
Hylarana nicobariensis						X	X	X	X											
Hylarana chalconota						X	X	X			X							X	X	
Odorrana hosii	X	X		X		X	X				X	X			X	X	X	X		
Wijayarana masonii	X	X					X			X	X	X			X	X	X	X		
Rhacophoridae																				
Nyctixalus margaritifer								X		X	X									
Philautus aurifasciatus		X	X	X			X		X	X	X	X			X		X			
Polypedates leucomystax						X	X		X	X					X			X	X	
Rhacophorus reinwardtii		X				X			X	X	X	X			X				X	
REPTILE																				
Agamidae																				
Bronchocela jubata		X		X		X				X					X		X	X	X	
Draco volans						X		X		X									X	
Gonocephalus kuhlii		X				X				X	X	X								
Gekkonidae																				
Cyrtodactylus petani	X	X				X	X	X	X	X					X		X		X	
Scincidae																				
Dasia olivacea						X						X								
Eutropis multifasciata		X				X												X	X	
Eutropis rugifera						X														
Sphenomorphus puncticentralis						X														
S. sanctus tenggeranus								X											X	
Tytthoscincus temmincki	X					X		X									X			
Colubridae																				

(*Continued*)

Table 3. (Continued).

Taxon/site	Coban Jodo	Bendolawang	Jarak Ijo Sumber	Trisula	Jemplang	Ranu Darungan	Sungai Besuk	Loji	Sudetan	Resort Senduro	Blok Ireng-ireng	Kali Cilik	Kopirejo	Ranu Regulo	Kali Tempuk	Taman Satriyan 1	Coban Pelangi	Coban Siuk	Pronojiwo	Wonokitri
Calamaria linnaei						X													X	
Ahaetulla prasina									X										X	
Coelognathus flavolineatus																			X	
Dendrelaphis formosus						X														
Dendrelaphis pictus																			X	
Gonyosoma oxycephalum																			X	
Oligodon bitorquatus																	X			
Rhabdophis chrysargos						X														
Rhabdophis subminiatus													X							
Sibynophis geminatus						X														
Elapoidis fusca																	X			
Tetralepis fruhstorferi					X									X						X
Elapidae																				
Bungarus candidus																			X	
Pareidae																				
Aplopeltura boa		X				X														
Pareas carinatus	X					X													X	
Pythonidae																				
Malayopython reticulatus		X																		
Viperidae																				
Craspedocephalus puniceus						X									X					

and buffer zone sites, 20 species (11 amphibian and nine reptile species) were recorded exclusively in the national park, and six species (six reptile species) were recorded exclusively in the buffer zone (Figure 2(B)). The conservation status (IUCN) of most of the species was Least Concern, with the exception of two species categorised as Vulnerable, and one species as Data Deficient (Table 2). Some of the encountered species were abundant and had wide altitude ranges (750–1500 m), while some species had narrow altitudinal ranges, especially above >1500 m a.s.l. (Figure 3).

Our surveys detected poorly known species endemic to the Bromo Tengger Semeru mountainous landscape (Figure 4), eg (i) *Nyctixalus margaritifer* – we encountered three individuals (two specimens were collected) across three sites, ie Loji, Resort Senduro, and Blok Ireng-ireng, the easternmost record of the species in Java; (ii) *Sphenomorphus sanctus tenggeranus* – we encountered three individuals (three specimens were collected) across two sites, ie Loji and Pronojiwo; and (iii) *Tetralepis fruhstorferi* – we encountered nine individuals (five specimens were collected) across three sites, ie Jemplang, Ranu Regulo, and Wonokitri, thorough examination is needed to confirm the identity of the species from BTSNP.

Species diversity, elevational diversity and important conservation site

The herpetofauna species diversity estimates (based on Hill numbers, 95% credible intervals) showed that the sampling effort was incomplete, as diversity across all sites had not reached asymptotic levels (Chao1 = 47.0, 34.7–59.4; Figure 5(A)). When comparing amphibians and reptiles across all sites, reptiles exhibited higher estimated diversity (Chao1 = 27.0, 17.9–36.1) than amphibians (Chao1 = 20.0, 18.8–21.2); however, only amphibian diversity reached an asymptote, while reptile diversity did not (Figure 5(B)). Measures of diversity of herpetofauna between surveyed sites in national park (16 sites) and buffer zone (four sites) showed that national park sites had higher diversity (Chao 1 = 27.0, 14.6–39.4; Figure 5(C)) than buffer zone sites (Chao 1 = 20.0, 18.8–21.2), although buffer zone sites did not reach asymptotic levels (Figure 5(C)). Survey completeness was estimated at 73.3% for all taxa, 80.5% for amphibians, and 68.4% for reptiles, indicating that additional species – particularly reptiles – are likely to be detected with further surveys.

There was a significant decrease in species diversity index (H') with increasing elevation ($F_{41.89}$, R^2 = 69.9%, R^2(adj) = 68.2%, df = 18, $p \leq .001$) (Figure 6).

Based on the species diversity index (H'), Ranu Darungan had the highest diversity (H' = 2.84, 27 herpetofauna species), followed by Pronojiwo (H' = 2.52, 18 herpetofauna species; Figure 7); it is noteworthy that these two sites were located on the southern part of BTSNP. Other sites with low richness (H' = 0), ie Jemplang, Ranu Regulo, Wonokitri, are also significant because they are home to endemic and rare species.

Discussion

Based on our surveys (Table 2), the amphibian fauna (20 species) comprised 41.7% of the amphibian species found in Java (ie 48 species by Frost 2023) and the reptile fauna (27 species) comprised 17.1% of the reptiles found in Java (ie 158 species by Uetz *et al*. 2023), mostly consisting of species from upper montane forests. When comparing herpetofauna diversity across Java, climate, especially rainfall, plays a crucial role. Western Java, with its higher rainfall, supports more diverse ecosystems and greater species richness (Erawan *et al*. 2021). In contrast, Eastern Java's drier climate limits species diversity, with many species adapted to more specialised, arid conditions. This pattern aligns with our findings, where Eastern Java tends to have lower diversity but remains ecologically significant due to the presence of endemic species.

A previous survey in BTSNP by Arroyyan *et al*. (2020) found 14 species of herpetofauna, which is only 30% of the herpetofauna found during our survey. More recently, a study conducted in January 2025 (Indra *et al*. 2025) recorded only 13 species in BTSNP, which is only 25% of the herpetofauna recorded during our survey. Previous surveys around the buffer zone of BTSNP (Septiadi *et al*. 2018; Indrawati *et al*. 2018; Hidayah *et al*. 2018; Elzain *et al*. 2018; Fathoni *et al*. 2022; Hanifa *et al*. 2022) found records of species that were not found at the time of our survey, ie *Lycodon subcinctus, Hemidactylus frenatus, Gehyra mutilata*, and *Hemiphyllodactylus typus*. Overall, the number of species in BTSNP and its buffer zone that have been surveyed over the past few decades should be more than 50 species, some of which endemic to BTSNP, and this number could increase

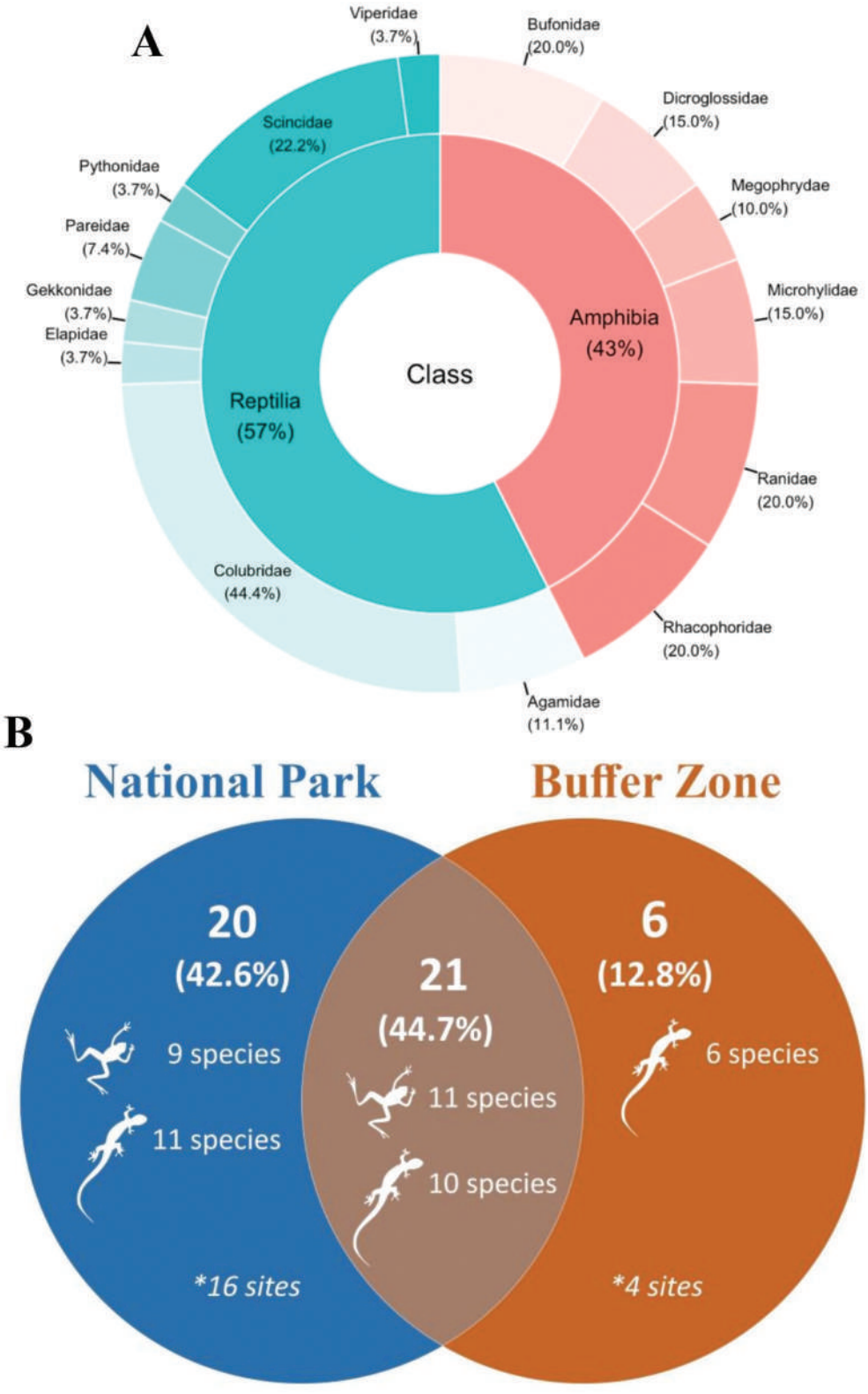

Figure 2. Herpetofauna species richness (A) between amphibians and reptiles (in percentage) and (B) Venn diagram showing the differences in species richness (in percentage) between surveyed sites in Bromo Tengger Semeru National Park and the buffer zone.

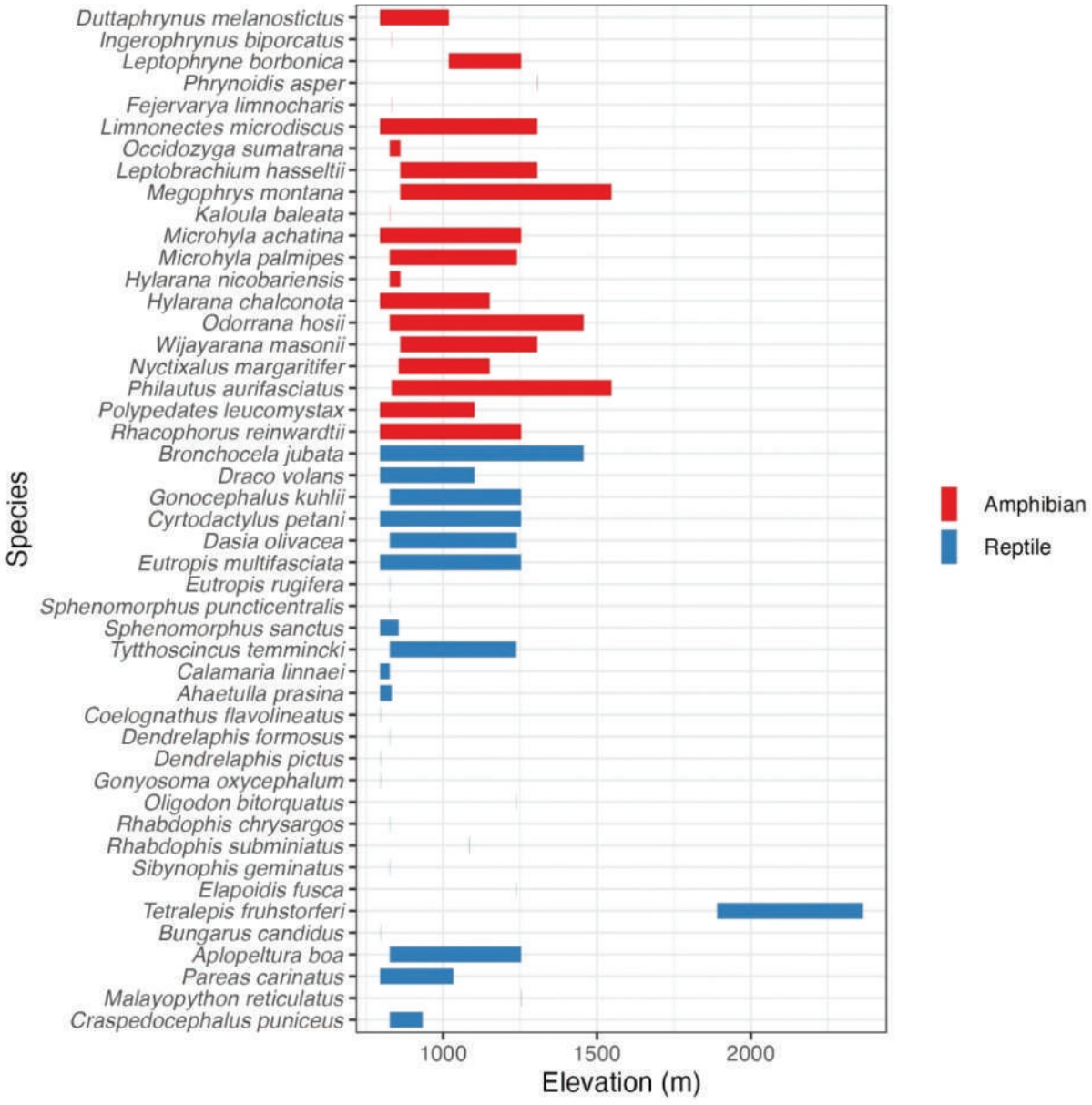

Figure 3. Elevational distribution of the amphibian and reptile species found in Bromo Tengger Semeru National Park and the buffer zone.

if more extensive surveys are conducted. These results suggest that the diversity of herpetofauna in BTSNP is remarkable, especially when compared to nearby areas.

In this report, we highlighted three species of conservation importance in BTSNP due to their endemism and lack of information on their natural history, distribution and population (Figure 4). We reported the easternmost species record for the endemic Javan pearly tree frog, *Nyctixalus margaritifer*, approximately 142 km west of the type locality at Mount Willis, East Java (Priambodo *et al*. 2021). Our morphological analysis indicates that the population in East Java is distinct from the population in West Java, although genetic analysis showed no such difference (Hanifa *et al*. 2023b). We rediscovered the Javan forest skink, *Sphenomorphus sanctus tenggeranus*, a subspecies endemic to Mount Bromo Tengger Semeru (fide Mertens 1957); taxonomic studies are needed as there is potential to elevate this subspecies to a full species. We finally rediscovered the Fruhstorfer mountain snake (also known as 'Ular Bhumi Tengger' by locals), *Tetralepis fruhstorferi*, the only species of the genus and endemic to Mount Bromo Tengger Semeru, after its

Figure 4. Rediscovery of poorly known herpetofauna identified as species of conservation importance in Bromo Tengger Semeru National Park: (A) *Nyctixalus margaritifer* – Javan endemic and easternmost record in Java; (B) *Sphenomorphus sanctus tenggeranus* – subspecies endemic to Bromo Tengger Semeru National Park; and (C) *Tetralepis fruhstorferi* – species endemic to Bromo Tengger Semeru National Park. Photos taken by A. M. S. P. Soeprijadi (A) and M. F. Assiddiqy (B, C).

last sighting in 2019 (Septiadi *et al*. 2023); information regarding its taxonomic identity, natural history, distribution, and biogeographic history is not known, so further research is needed.

Measures of herpetofauna diversity between surveyed sites in the national park (16 sites) and the buffer zone (four sites) showed that the national park exhibited higher estimated diversity (Figure 5). However, this comparison should be interpreted with caution due to the unequal number of surveyed sites between these

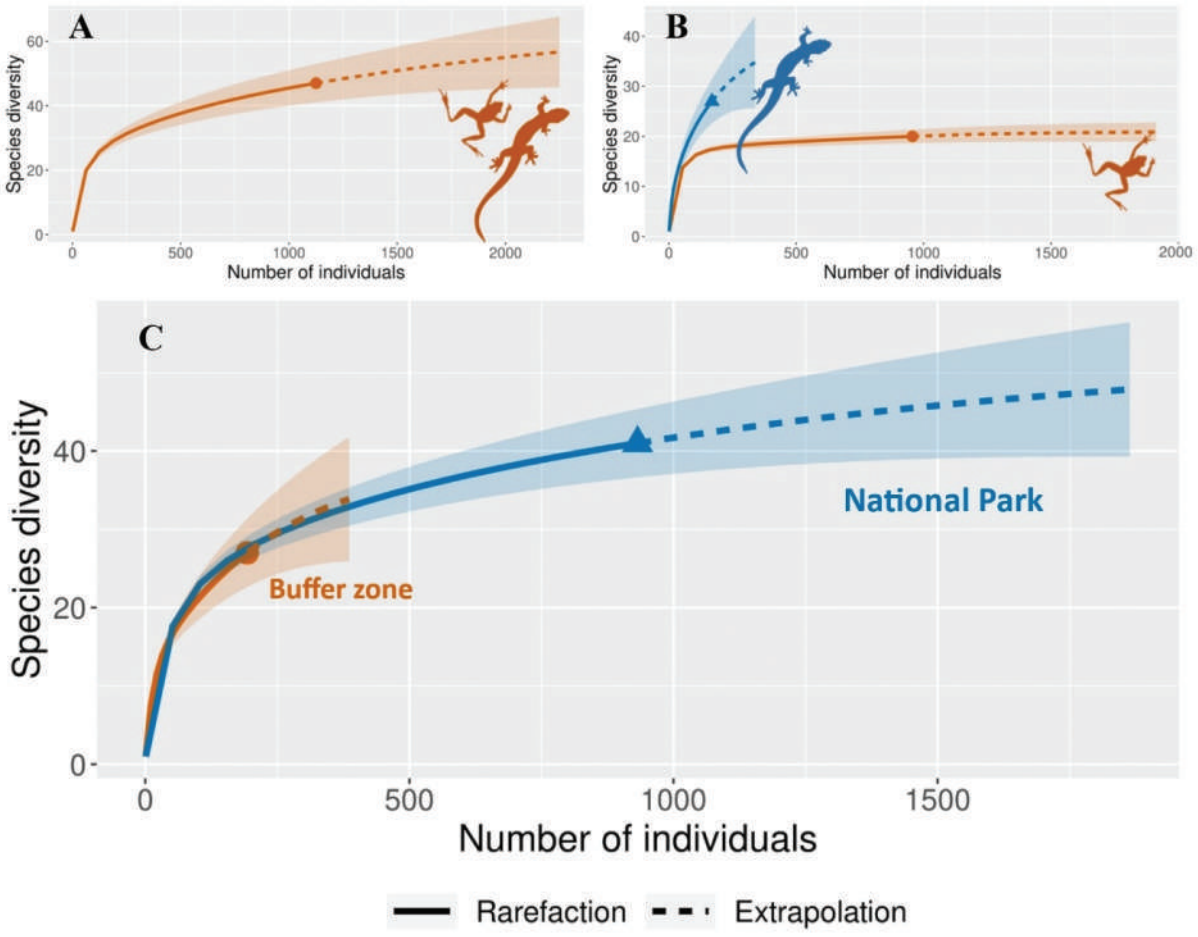

Figure 5. Individual-based rarefaction (solid lines) and extrapolation curves (dashed lines) of herpetofauna richness using the diversity order q = 0 (species richness, Chao1), based on surveyed sites in Bromo Tengger Semeru National Park: (A) herpetofauna in all sites, (B) between amphibians and reptiles in all sites, and (C) herpetofauna between national park and buffer zone sites. Shaded areas indicate the 95% confidence interval.

site categories. Nevertheless, the observed trend may reflect differences in disturbance levels: national park areas benefit from stricter protection and lower anthropogenic pressure, which help maintain more intact ecosystems and support greater herpetofauna diversity compared to the more disturbed buffer zone areas, as demonstrated in several studies (Pringle 2017; Chen *et al*. 2019). Interestingly, Pronojiwo, although categorised as buffer zone, recorded the highest herpetofauna diversity after Ranu Darungan. This likely reflects the relatively intact forest conditions and minimal human disturbance at Pronojiwo, highlighting that certain buffer zone sites can still retain high conservation value when habitat quality is preserved, as reported in several studies (Kintz *et al*. 2006; Silwal *et al*. 2022). Conversely, several sites within the national park, such as Jemplang, Ranu Regulo, and Wonokitri, recorded very low diversity (H′ = 0, with only one species recorded). Although species richness at these sites was minimal during our surveys, they remain ecologically significant because they harbour endemic and rare species with restricted distributions. The low H′ values at these sites likely reflect challenging environmental conditions (eg higher elevation, more open vegetation) and the reduced species richness naturally associated with such habitats (Gangloff and Telemeco 2018), rather than insufficient sampling effort. Therefore, despite the low diversity scores, these sites are important for conservation as they support unique and specialised herpetofauna species.

We found a linear decline in amphibian and reptile diversity with increasing elevation in BTSNP, which one might argue is driven by temperature (Jins *et al*. 2021). This monotonic decline pattern is frequently reported locally and globally for ectothermic taxa including amphibians and reptiles (McCain and Grytnes 2010), eg in West Java (Erawan *et al*. 2021), Sarawak (Das *et al*. 2007), Mindanao-Phillipines (Delima *et al*. 2006), and eastern Nepal Himalaya (Khatiwada and Haugaasen 2015). In West Java, Erawan *et al*. (2021) reported that

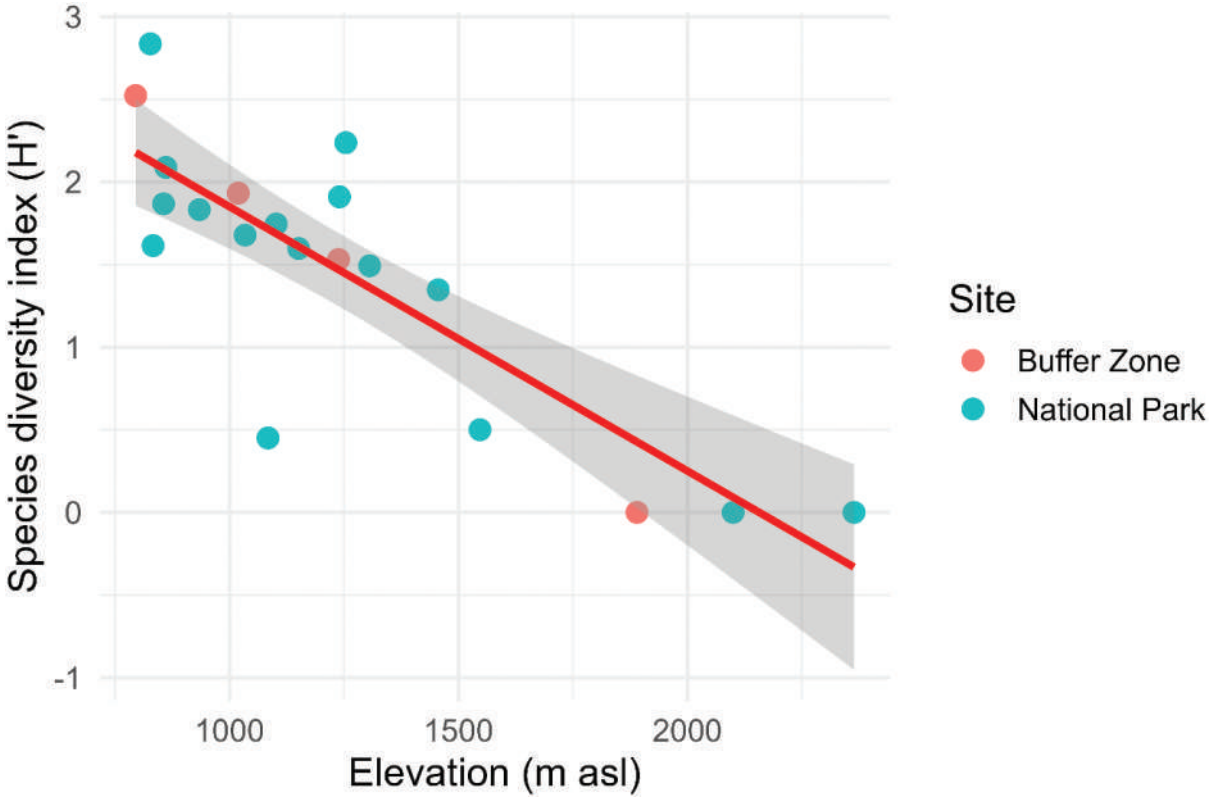

Figure 6. The relationship between species diversity index and elevation shown by linear regression (red line), with each point representing a single surveyed site in Bromo Tengger Semeru National Park. Shaded areas indicate the 95% confidence interval.

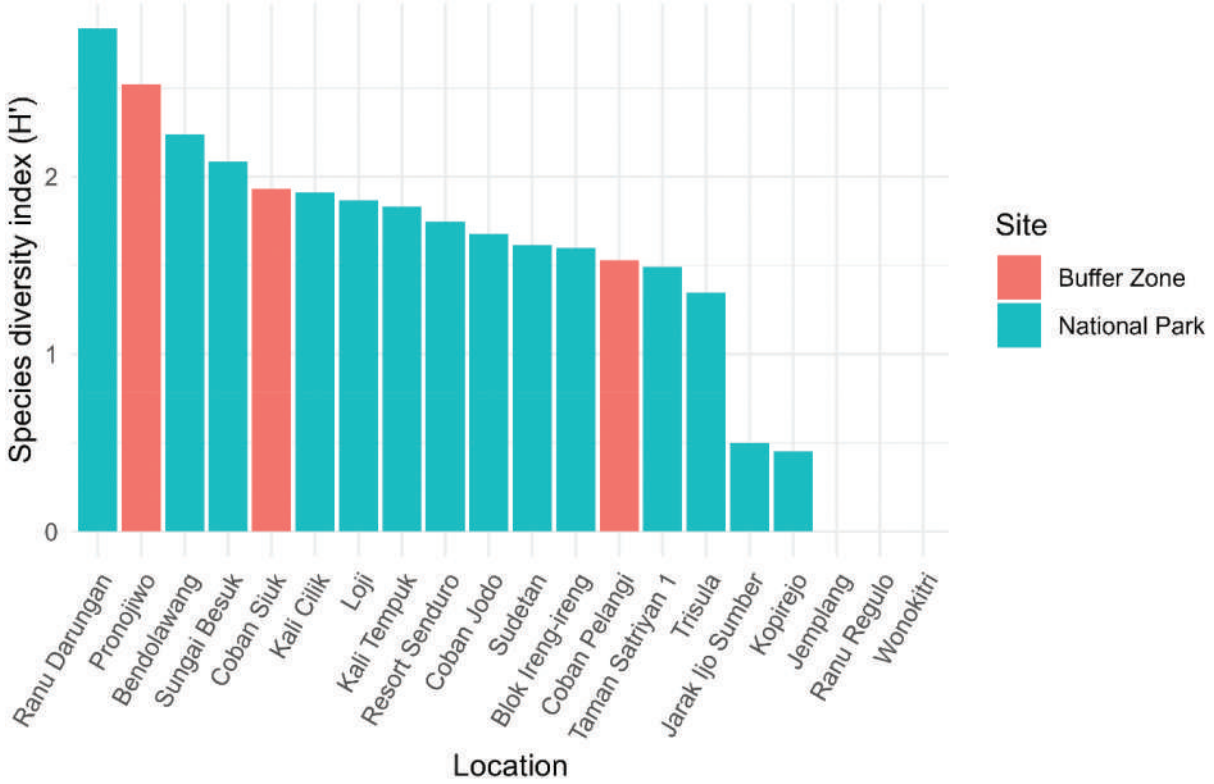

Figure 7. Species diversity index (H') across the surveyed sites in Bromo Tengger Semeru National Park.

herpetofauna are mostly found at elevations below 1000 m asl: amphibians are most diverse at elevations between 400–1200 m asl and 1400–1700 m asl, while reptiles are more diverse at slightly lower elevations, around 400–900 m asl. Our studies in the upper montane forest in East Java showed similar trends, with the highest species diversity being around 750–1400 m asl (Figure 6). Space–area relationships (SAR) suggest that a mountain's base with its large area will support more species than a mountain's top, which has a relatively smaller area (Rahbek 1997; Pitogo *et al*. 2021), which may help to explain the declining pattern in species richness and diversity in our study. While amphibian diversity decreased from lowland to upper montane forest, endemism increased (Pitogo *et al*. 2021). Therefore, surveys of herpetofauna at high altitudes remain crucial, as certain species (especially reptiles) may have evolved specialised adaptations to cope with the challenging conditions at higher elevations, such as low temperatures, hypoxia, and intense ultraviolet radiation. For example, we found *Tetralepis fruhstorferi* at elevations between 1200 and 2600 m asl (Septiadi *et al*. 2023), highlighting the existence of specialised species that thrive in these relatively harsh environments. Generalist species, in contrast, tend to occupy lower elevations with more stable conditions, whereas specialist species such as *Tetralepis fruhstorferi* have adapted to withstand the extreme conditions of higher elevations, highlighting the adaptive flexibility of herpetofauna, as similarly reported in a recent avifauna study (Fjeldså *et al*. 2023).

Our analysis (Figure 5) indicates that there is still potential for additional species detections, especially for reptiles; there are still some reptiles that may be found in the upper montane forests of BTSNP, such as *Liopeltis tricolor* (Kurniawan, unpubl. data). Resort Ranu Darungan had the highest herpetofauna species diversity, indicating a potential area to serve as a refuge or sanctuary, research site, and education centre. However, surveys in the BTSNP's buffer zone also need to be conducted more intensively considering the results of the analysis show the potential for additional species (Figure 5(C)) and sites that have high levels of diversity (Figure 7). Our survey in BTSNP may still have gaps in distribution data (Figure 1) especially in the southeastern part (Resort Ranu Darungan, Resort Candipuro, Resort Pasrujambe) where there are two scenic lakes, ie Ranu Tompe and Ranu Kuning; western part (Resort Patokpicis); and northwestern–northeastern part (Resort Gucialit, Resort Gunung Penanjakan). Then, we highly recommend surveying these areas in the future. Although direct comparisons based on ecological parameters such as disturbance level and habitat types were ideal, logistical constraints in site accessibility limited our ability to stratify survey locations accordingly. Therefore, diversity analyses were used as an alternative approach to compare herpetofauna communities between the core zone and buffer zone.

Continuous surveys in BTSNP will fill an important gap in tracing the underestimated diversity of herpetofauna in the upper montane forests of East Java, revealing biogeographic history, endemicity, and evolutionary links between Sundaland and Wallacea. Although studied since the nineteenth century (Boulenger 1890; Boettger 1892; de Rooij 1917; van Kampen 1923; Kopstein 1930; Mertens 1957; Hodges 1993; Iskandar 1998), East Java's herpetofauna remains poorly understood (Kurniawan *et al*. 2021; Kusrini *et al*. 2021). This reflects a broader global decline in field-based herpetology, which limits evidence-based conservation and hampers responses to the ongoing extinction crisis affecting 41% of amphibians and 21% of reptiles (Soga and Gaston 2025). Revitalising long-term field monitoring in BTSNP and other areas of East Java is therefore crucial to document population changes, uncover hidden diversity, and inform effective conservation strategies.

Emerging global threats to herpetofauna (Luedtke *et al*. 2023) – such as climate change, which will eventually shift the ranges of mountain species to higher altitudes and increase their risk of extinction, as previously observed in Gunung Gede Pangrango, West Java (Kusrini *et al*. 2017); chytridiomycosis, which affects approximately 41% of amphibian species worldwide and has caused severe population declines; and habitat loss due to agricultural expansion – are also becoming a reality in East Java. In BTSNP and its buffer zone, major threats to herpetofauna include habitat loss (Sawitri and Takandjandji 2019; Roedjinandari 2016), agricultural land expansion, intensive tourism activities, volcanic eruptions and forest fires. Despite BTSNP's conservation value, Indonesia lacks an official amphibian and reptile conservation action plan. Thus, we recommend urgent national scientific research to support the development of an action plan, with strategies that incorporate herpetofauna as environmental bioindicators, as demonstrated by Kusrini *et al*. (2017) in their study on mountain amphibians in Gunung Gede Pangrango, West Java.

Future genetic, ecological and climate-related studies are essential to strengthen conservation planning in BTSNP. Genetic analyses can reveal population health and hidden diversity among montane herpetofauna, while ecological research should examine habitat use, reproductive ecology and key environmental factors influencing

species persistence. Climate-related studies, including assessments of elevational shifts, thermal tolerance and adaptability to continuous volcanic activity or ash exposure, will provide critical insights into species resilience and guide long-term management strategies. Furthermore, an integrated management approach involving the Indigenous Tengger community and other stakeholders is crucial to ensure that traditional ecological knowledge is combined with scientific data, thereby fostering a holistic conservation strategy to safeguard the montane forest ecosystems and landscapes of BTSNP.

Conclusions

Our survey documented 47 herpetofauna species in Bromo Tengger Semeru National Park (BTSNP), including three of conservation importance, reaffirming the park's role as a key refuge for East Java's upper montane biodiversity. This study provides one of the most comprehensive assessments of montane herpetofauna in eastern Java and contributes to the broader understanding of diversity patterns across Southeast Asian mountains, showing a consistent decline in species richness and increased endemicity with elevation, shaped by isolation and volcanic dynamics. These findings highlight the ecological distinctiveness of Java's montane assemblages and the need to protect high-elevation habitats that, although species-poor, harbour rare and range-restricted taxa. Future studies are essential to strengthen conservation planning and establish BTSNP as a model system for understanding tropical montane biodiversity and resilience.

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Disclosure statement

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ORCID

Luhur Septiadi http://orcid.org/0000-0001-5195-5550
Muhammad Fathoni http://orcid.org/0000-0001-6500-9995
Berry Fakhry Hanifa http://orcid.org/0000-0003-1847-6261
Muhammad Asmuni Hasyim http://orcid.org/0000-0002-9681-6033
Nia Kurniawan http://orcid.org/0000-0001-7383-8742

Geolocation information

This study took place in the Bromo Tengger Semeru National Park and its buffer zones (5 km), centred around the point 8.024°S, 112.952°E.

References

Amarasinghe AT et al. 2021. Herpetofaunal diversity of West Bali National Park, Indonesia with identification of indicator species for long-term monitoring. Glob Ecol Conserv. 28:e01638. https://doi.org/10.1016/j.gecco.2021.e01638

Arroyyan AN, Idrus MR, Aliffudin MF. 2020. Keanekaragaman Herpetofauna di Kawasan Taman Nasional Bromo Tengger Semeru (TNBTS) Kabupaten Lumajang Jawa Timur. Pros Sem Nas Hayati. 6(1):263–269. https://doi.org/10.24252/psb.v6i1.15862.

Boettger O. 1892. Listen von Kriechtieren und Lurchen aus dem tropischen Asien u. aus Papuasien. Bericht des Offenbacher Vereins für Naturkunde. 29–32:65–164.

Boulenger GA. 1890. The fauna of British India, including Ceylon and Burma, reptilia and Batrachia, secretary of state for India in council. Taylor and Francis.

Burbrink FT et al. 2020. Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. Syst Biol. 69(3):502–520. https://doi.org/10.1093/sysbio/syz062.

Chao A et al. 2023. Rarefaction and extrapolation with beta diversity under a framework of Hill numbers: the iNEXT. Beta3D standardization. Ecol Monogr. 93(4):e1588. https://doi.org/10.1002/ecm.1588.

Chen C et al. 2019. Effects of law enforcement and community outreach on mammal diversity in a biodiversity hotspot. Conserv Biol. 33(3):612–622. https://doi.org/10.1111/cobi.13232.

Das I. 2015. A field guide to the reptiles of South-East Asia. Bloomsbury Natural History Publishing.

Das I, Jankowski A, Makmor MIB, Haas A. 2007. Species diversity, elevational distribution and reproductive modes in an amphibian community at the Matang Range, Sarawak (Borneo). Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut. 104(1):141–174.

de Lang R. 2017. The snakes of Java, Bali and surrounding islands. Edition Chimaira.

Delima EMM, Ates FB, Ibañez JC. 2006. Species composition and microhabitats of frogs within Arakan Valley Conservation Area, Cotabato, Mindanao Island. Philippines Banwa. 3(1 & 2):16–30.

de Rooij N. 1917. The reptiles of the Indo-Australian Archipelago: Ophidia, Vol. 2. E.J. Brill Ltd.

Dorcas ME, Willson JD. 2009. Innovative methods for studies of snake ecology and conservation. In: Mullin SJ, Seigel RA, editors. Snakes: ecology and conservation. Cornell University Press. p. 5–37. https://doi.org/10.7591/9780801459092-005

Elzain LZL, Alwi MZ, Mahali MA, Maghrobi SL, Hanifa BF 2018. Studi Awal Potensi Keanekaragaman Reptil Amfibi di Lokasi Wisata Alam Coban Pelangi Poncokusumo, Malang, Jawa Timur. In: Abdullah M, Mustikaningtyas D, Sasi FA, editors. Seminar Nasional Biologi-Universitas Negeri Semarang. FMIPA Universitas Negeri Semarang. p 136–144.

Erawan TS et al. 2021. Herpetofauna diversity and distribution based on the elevational range in West Java, Indonesia. Biodiversitas. 22(10):4308–4319. https://doi.org/10.13057/biodiv/d221023.

Erfanda MP, Septiadi L, Devi SR, Hanifa BF. 2019. Distribution record of *Leptophryne borbonica* (Tschudi, 1838) (Anura: bufonidae) from Malang, East Java: description, microhabitat, and possible threats. J Trop Biodivers. Biotechnol. 4 (2):82–89. https://doi.org/10.22146/jtbb.45355.

Fathoni M, Hakim L, Kurniawan N. 2022. Anuran diversity and community structure in Lesti upriver across buffer zone habitat in Bromo Tengger Semeru National Park. Biotropika: J Trop Biol. 10(1):78–88. https://doi.org/10.21776/ub.biotropika.2022.010.01.10.

Figueroa A, McKelvy AD, Grismer LL, Bell CD, Lailvaux SP. 2016. A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. PLOS ONE. 11(9):e0161070. https://doi.org/10.1371/journal.pone.0161070.

Fjeldså J, Sonne J, Rahbek C. 2023. The alpine avifauna of tropical mountains. In: Chamberlain D, Lehikoinen A, Martin K, editors. Ecology and conservation of mountain birds. Cambridge University Press. p 336–371. https://doi.org/10.1017/9781108938570.010

Frost DR 2023. Amphibian species of the world: an online reference. Version 6.2; [accessed 2023 Oct 8]. https://amphibiansoftheworld.amnh.org/index.php.

Gangloff EJ, Telemeco RS. 2018. High temperature, oxygen, and performance: insights from reptiles and amphibians. Integr Comp Biol. 58(1):9–24. https://doi.org/10.1093/icb/icy005.

Hakim L, Soemarno M. 2017. Biodiversity conservation, community development and geotourism development in Bromo-Tengger-Semeru-Arjuno Biosphere Reserve, East Java. Geoj Tour Geosites. 2(20):220–230.

Hanifa BF et al. 2023b. New data on and the easternmost record of the Javan endemic pearly tree frog, *Nyctixalus margaritifer* Boulenger, 1882 (Anura, Rhacophoridae). Check List. 19(6):971–982. https://doi.org/10.15560/19.6.971.

Hanifa BF, Aini Q, Hasyim MA, Septiadi L. 2024. Herpetofauna in Ranu Darungan and Blok Ireng-Ireng, Bromo Tengger Semeru National Park: before–after the COVID-19 and eruption. Jurnal Sylva Lestari. 12(1):191–202. 10.23960/jsl.v12i1.819

Hanifa BF, Baihaqi AP, Ahmad M, Kiptiyah K, Hasyim MA. 2023a. Herpetofauna in the Ledok Ombo natural tourism area, Malang district, East Java. Al-Hayat J Biol Appl Biol. 5(2):127–138. https://doi.org/10.21580/ah.v5i2.13566.
Hansen MC et al. 2013. High-resolution global maps of 21st-century forest cover change. Science. 342(6160):850–853. https://doi.org/10.1126/science.1244693.
Hidayah A et al. 2018. Keanekaragaman Herpetofauna di Kawasan Wisata Alam Coban Putri Desa Tlekung Kecamatan Junrejo Kota Batu Jawa Timur. Pros Sem Nas Hayati. 6:79–91. https://doi.org/10.29407/hayati.v6i1.660
Hodges R. 1993. Snakes of Java with special reference to East Java Province. Herpetol Bull. 43:15–32.
Hsieh TC, Ma KH, Chao A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol. 7(12):1451–1456. https://doi.org/10.1111/2041-210X.12613.
Indra RIN, Bahri S, Mohammad AR, Nurmansyah AE. 2025. Identifikasi/Inventarisasi Jenis Herpetofauna Di Kawasan Taman Nasional Bromo Tengger Semeru Kabuparen Lumajang, Jawa Timu.Inovasi Pendidikan Nusantara. 6(1):491–510.
Indrawati Y et al. 2018. Keanekaragaman Jenis Herpetofauna Nokturnal di Area Coban Jahe, Desa Pandansari Lor, Kecamatan Tumpang, Kabupaten Malang, Jawa Timur. Pros Sem Nas Hayati. 6:277–285. https://doi.org/10.29407/hayati.v6i1.635
Iskandar DT. 1998. The amphibians of Java and Bali. Research and Development Centre for Biology–Indonesian Institute of Sciences.
Iskandar DT, Colijn E. 2000. Preliminary Checklist of Southeast Asian and New Guinean Herpetofauna: amphibians I. Research and Development Centre for Biology – Indonesian Institute of Sciences.
IUCN. 2022. The IUCN Red List of Threatened Species. Version 2022-2; [accessed 2023 Oct 8]. https://www.iucnredlist.org.
Jins VJ, Panigrahi M, Jayapal R, Bishop TR. 2021. Elevational gradients of reptile richness in the southern Western Ghats of India: evaluating spatial and bioclimatic drivers. Biotropica. 53(1):317–328. https://doi.org/10.1111/btp.12878.
Kehutanan D. 2009. Profil balai besar Taman Nasional Bromo Tengger Semeru. Departemen Kehutanan Direktorat Jendral Perlindungan Hutan dan Konservasi Alam.
Khatiwada JR, Haugaasen T. 2015. Amphibian species richness and abundance along an elevational gradient in Chitwan. Zoo Ecol. 25(2):110–119. https://doi.org/10.1080/21658005.2015.1016775.
Kintz DB, Young KR, Crews-Meyer KA. 2006. Implications of land use/land cover change in the buffer zone of a national park in the tropical Andes. Environ Manag. 38(2):238–252. https://doi.org/10.1007/s00267-005-0147-9.
Kopstein F. 1930. Die giftschlangen Javas und ihre Bedeutung für den Menschen. Zeitschrift für Morphologie und Ökologie der Tiere. 19(2–3):339–363. https://doi.org/10.1007/BF00439432.
Kurniawan N, Fathoni M, Fatchiyah F, Septiadi L, Smith EN. 2021. Composition, distribution, and habitat type of snakes in Java, with discussion on the impact of human-snake interactions during 2013–2019. Herpetol Note. 14:691–711.
Kurniawan N, Septiadi L, Fathoni M, Kadafi AM, Marhendra APW. 2022. A Checklist of the Herpetofauna of Nusa Kambangan Island, Central Java, Indonesia. Trop Life Sci Res. 33(2):91–131. https://doi.org/10.21315/tlsr2022.33.2.6.
Kusrini MD. 2008. Pedoman penelitian dan survei amfibi di Alam. Fakultas Kehutanan, Institut Pertanian Bogor.
Kusrini MD et al. 2017. Elevation range shift after 40 years: the amphibians of Mount Gede Pangrango National Park revisited. Biol Conserv. 206:75–84. https://doi.org/10.1016/j.biocon.2016.12.018
Kusrini MD et al. 2021. Creation of an amphibian and reptile atlas for the Indonesian islands of Java and Bali reveals gaps in sampling effort. Herpetol Note. 14:1009–1025.
Luedtke JA et al. 2023. Ongoing declines for the world's amphibians in the face of emerging threats. Nature. 622 (7982):308–314. https://doi.org/10.1038/s41586-023-06578-4.
Marthy W, Clough Y, Tscharntke T. 2017. Assessing the potential for avifauna recovery in degraded forests in Indonesia. Raffles Bull Zool. 65:35–48.
McCain CM, Grytnes JA. 2010. Elevational gradients in species richness. eLS. 1–10. https://doi.org/10.1002/9780470015902.a0022548
McKay JL. 2006. A field guide to the amphibians and reptiles of Bali. Krieger Publishing Company.
Mertens R. 1957. Zur Herpetofauna von Ostjava und Bali. Senck Biol. 38:23–31.
Pitogo KME, Saavedra AJL, Aurellado MEB, de Guia APO, Afuang LE. 2021. Functional traits and environment drive montane amphibian distribution in the southern Philippines. Biodivers Conserv. 30(14):4177–4197. https://doi.org/10.1007/s10531-021-02299-0.
Priambodo B et al. 2021. Rediscovery of pearly tree frog, *Nyctixalus margaritifer* Boulenger, 1882 (Amphibia: rhacophoridae) from Mt. Wilis after 135 years. Turk J Zool. 45(4):329–334. https://doi.org/10.3906/zoo-2104-22.
Pringle RM. 2017. Upgrading protected areas to conserve wild biodiversity. Nature. 546(7656):91–99. https://doi.org/10.1038/nature22902.
Rachmawati E, Faizah NK, Eksh M. 2007. Potensi bahaya di kawasan wisata Gunung Bromo, Resort Tengger Laut Pasir, Taman Nasional Bromo Tengger Semeru, Jawa Timur. Media Konservasi. 12(3):140–144.
Rahbek C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. Am Nat. 149 (5):875–902. https://doi.org/10.1086/286028.
R Core Team. 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing.
Roedjinandari N 2016. Pengembangan Potensi Wisata Minat Khusus Desa Ranu Pani di Kawasan Taman Nasional Bromo Tengger [Master thesis]. Sekolah Pascasarjana Universitas Gadjahmada.
Sawitri R, Takandjandji M. 2019. Konservasi Danau Ranu Pane dan Ranu Regulo di Taman Nasional Bromo Tengger Semeru. Jurnal Penelitian Hutan dan Konservasi Alam. 16(1):35–50. https://doi.org/10.59465/jphka.16.1.35-50.

Septiadi L et al. 2018. Study of reptile and amphibian diversity at Ledok Amprong Poncokusumo, Malang East Java. Biotropika - J Trop Biol. 6(2):45–53. https://doi.org/10.21776/ub.biotropika.2018.006.02.02.
Septiadi L et al. 2023. Found but forgotten: on the records, misidentification, and potential rediscovery of the rare Bromo Tengger Semeru Mountain endemic snake (Serpentes: Colubridae: *Tetralepis fruhstorferi*). Russ J Herpetol. 30(4):249–254. https://doi.org/10.30906/1026-2296-2023-30-4-249-254.
Shannon CE, Weaver W. 1949. A mathematical model of communication. University of Illinois Press.
Silwal T, Devkota BP, Poudel P, Morgan M. 2022. Do buffer zone programs improve local livelihoods and support biodiversity conservation? The case of Sagarmatha National Park, Nepal. Trop Conserv Sci. 15:19400829221106670. https://doi.org/10.1177/19400829221106670.
Smiet AC. 1990. Forest ecology on Java: conversion and usage in a historical perspective. J Trop For Sci. 2(4):286–302.
Soga M, Gaston KJ. 2025. Extinction of experience among ecologists. Trends Ecol Evol. 40(3):212–215. https://doi.org/10.1016/j.tree.2024.12.010.
Streicher JW, Ruane S. 2018. Phylogenomics of snakes. eLS. 1–8. https://doi.org/10.1002/9780470015902.a0027476
Supriatna J, Margules C. 2025. Java and Bali. In: Supriatna J, Margules C, editors. The national parks of Indonesia. Springer Nature Switzerland. p 87–177. https://doi.org/10.1007/978-3-031-76638-1_2
Uetz P, Freed P, Aguilar R, Reyes F, Hošek J 2023. The reptile database. [accessed 2023 October 8] http://www.reptile-database.org.
van Kampen PN. 1923. The amphibia of the Indo-Australian archipelago. EJ Brill Ltd.
Whitten T, Soeriaatmadja RE, Afiff SA. 1996. Ecology of Java & Bali, Vol. 2. Periplus Editions.