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Biodiversity dynamics of terrestrial gastropods in the tropical montane rainforests of Nuwara Eliya, Sri Lanka

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Abstract: Sri Lanka is home to 253 terrestrial gastropod species, most of which are endemic. However, limited research has explored the diversity, distribution, and influencing variables of these gastropods. This study sampled gastropods in tropical montane rainforests by establishing 10-50 1m^2 sampling plots across 60 randomly selected sites. Among the 46 recorded species, 79% were native, and 17% were exotic. Representative species of the five endemic genera to the island and two endemic semi-slug species were recorded from these forests. Native gastropod species were primarily found in forest interiors, while exotic species inhabited forest buffer regions. The distribution of most native species is influenced by elevation, air temperature, relative humidity, rainfall, and soil pH, while elevation and rainfall play a significant role in the distribution of most exotics. Exotics display broader environmental tolerance compared to natives, enabling exotics to invade the forests. The restricted habitat of many native species within deep canopy forests makes them highly vulnerable to habitat change, whereas exotics thrive under altered conditions.

Keywords: species distribution, biodiversity, terrestrial gastropods, tropical montane rainforest

Abbreviations: invasive alien species (IAS); lower montane forests (LMF); upper montane forests (UMF); intermediate zone evergreen forest (IZF), global positioning system (GPS); analysis of variance (ANOVA); canonical correspondence analysis (CCA); generalized linear model (GLM); generalized linear mixed model (GLMM); Akaike information criterion (AIC); inverse distance weighted (IDW); above sea level (a.s.l.); endemic species (E); exotic species (EX); national conservation status (NCS); data deficient (DD); not evaluated (NE); least concern (LC); near threatened (NT); vulnerable (VU); endangered (EN); critically endangered (CR)

INTRODUCTION

Sri Lanka has a high terrestrial gastropod diversity comprising 253 species, including 244 snail, 6 slug, and 3 semi-slug species [1]. Significantly, 81% of these terrestrial gastropods are endemic. The majority of these are pulmonates, which are represented by 28 families, while prosobranchs are represented by four families. Among the pulmonates, the family Ariophantidae, primarily featuring the genera *Cryptozona* and *Euplecta*, stands out with 50 species, alongside the family Glessulidae, which has 22 species. Among the prosobranchs, the Cyclophoridae family takes the lead with 54 species [1-4]. The island hosts five terrestrial gastropod genera considered endemic, including four pulmonate genera (*Ravana, Ratnadvipia, Acavus,* and *Oligospira*) and one prosobranch genus (*Aulopoma*) [1]. Furthermore, 13 terrestrial gastropod genera (*Ruthvenia, Thysanota, Cryptozona, Euplecta, Mariaella, Eurychlamys, Corilla, Beddomea, Trachia, Leptopomodes, Micraulax, Tortulosa,* and *Nicida*) are restricted to Sri Lanka and the Western Ghats [1]. The majority of these endemic terrestrial gastropods are concentrated in the southwestern wet zone of the country [4], and many of these species thrive specifically in montane zone rainforests [5,6].

Apart from the native terrestrial gastropod assemblage, Sri Lanka has experienced the introduction of several terrestrial gastropod species in recent times

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[7]. However, only a handful of studies have examined the environmental impact of these exotic species. Research indicates that, similar to global findings, some of these introduced gastropods can cause serious harm to native biodiversity, as well as harm Sri Lanka's agriculture and economy [8,9]. The country now hosts 20 exotic terrestrial gastropod species, with one, *Lissachatina fulica*, (Férussac, 1821) earning a spot among the world's 100 worst invasive alien species (IAS) [1]. Most of these exotic species are recorded in association with agricultural land, particularly in the central highlands, where climatic conditions favor their survival and reproduction. Although a few exotic species occur along forest buffers, none have been recorded in the core zones of Sri Lanka's natural forests [4,8,10].

The diversity and distribution patterns of most terrestrial gastropods are shaped by the combined influence of abiotic and biotic factors and their intricate interactions [11,12]. Biotic factors such as disease, inter- and intraspecific interactions, and competition for limited resources influence species distribution [11]. Abiotic factors include physical conditions and non-living resources that impact living organisms regarding distribution, growth, maintenance, and reproduction [12]. While some of these abiotic factors affect larger-scale species distribution, some affect smaller-scale local species distributions. Climatic conditions, altitude, latitude, longitude, litter cover, forest canopy cover, undergrowth, and soil properties are among the abiotic factors that contribute to regional and local terrestrial gastropod distribution patterns [12,13].

The tropical rainforests in Sri Lanka harbor high species diversity due to favorable environmental conditions [14,15]. However, most of the existing forests are small, fragmented forest patches, as exemplified by the Nuwara Eliya district in the central highland. This district, characterized by scattered montane rainforest patches, is used extensively for agriculture and horticulture. Notably, most of the exotic pest gastropods introduced to the country have found suitable habitats in agricultural lands in the Nuwara Eliya district [7]. For example, the introduced European garden slugs *Deroceras reticulatum* (Müller, 1774) and *Deroceras laeve* (O. F. Müller, 1774) pose significant threats to vegetable cultivation [9]. The introduction of exotic gastropods may have profound consequences for the native gastropods of the island. However, only a handful of studies have explored the diversity, distribution, and invasive potential of these exotic species within natural forest systems. The biodiversity dynamics of terrestrial gastropods in the tropical rainforests of Sri Lanka are influenced by various factors, including elevation, canopy cover, and pH [4,10]. Elevation is a key environmental factor affecting the distribution of pest gastropods in the Nuwara Eliya region, with certain species causing significant damage to agricultural crops [9]. Similarly, elevation, as well as the type of forest, determines species composition in Mo'orea, French Polynesia [16]. Some studies have highlighted the role of habitat disturbance and human activity in influencing the diversity and abundance of terrestrial gastropods on the slopes of Mount Arjuna-Welirang, East Java, Indonesia [17]. These studies underscore the complex interplay of environmental factors in shaping the biodiversity of terrestrial gastropods in tropical rainforests.

The present study was conducted to elucidate terrestrial gastropod diversity, distribution, and the environmental factors influencing distribution, including the potential invasiveness of exotic species in the tropical montane rainforests.

MATERIALS AND METHODS

Ethics statement

Ethical clearance is not required for surveys based on terrestrial gastropods.

Study site

The study was carried out in tropical montane rainforest fragments in the Nuwara Eliya district, located in the central highlands of Sri Lanka, between 80° 24' 5" and 80° 57' 8" east longitudes and 7° 16' 5" and 6° 45' 02" north latitudes. Nuwara Eliya has a subtropical highland climate with an average annual temperature between 11-20°C, average annual rainfall of about 1,900 mm, and an average annual relative humidity between 65%-87% during the daytime and 69%-93% during the night. Even though Nuwara Eliya is a relatively small district, it has several main vegetation types, including lower and upper montane forests (LMF and UMF, respectively), wet and dry patana, and intermediate zone evergreen forests (IZF). The present study was conducted in LMF, UMF, and IZF throughout the district, including Piduruthalagala Restricted Nature Reserve, Horton Plains National Park, Galway's Land National Park, Sri Pada (Adam's Peak) Restricted Nature Reserve, Victoria-Randenigala-Rantembe Sanctuary, and other forests under the purview of the Forest Department and the Department of Wildlife Conservation of Sri Lanka. A total of 60 rainforest locations were sampled for a one-year period from July 2018 to July 2019 (Supplementary Fig. S1).

Data collection

A timed direct sampling approach was implemented to gather data on terrestrial gastropods [8,13]. Depending on the size of the forest fragment, line transects of either 20 m or 100 m were established from the forest edge to its center. Along these transects, 10 to 50 plots (each measuring 1 m^2) were established for the terrestrial gastropod survey. Each plot was sampled for a maximum of 15 min. Leaf litter samples were collected from each plot and sifted through a Winkler's sifter with 0.5 cm mesh size to separate micro snails. Both live specimens and empty shells were utilized to record terrestrial gastropod species, their abundance, and microhabitats. Species identification was done using available guides and published literature [5,18]. Simultaneously, key environmental parameters were documented at each sampling location, including geocoordinates, air temperature, elevation, soil pH, relative humidity, daily rainfall, canopy cover, and microhabitat. A portable Magellan Global Positioning System (GPS) receiver was employed to record geographical coordinates and elevation. Atmospheric temperature and relative humidity were measured using a mobile weather tracker. Rainfall data from the nearest weather stations were collected from the Department of Meteorology, Colombo, Sri Lanka. Soil pH was measured for five soil samples from each location. These soil samples were air-dried, and 10 g of air-dried soil was mixed with distilled water and the soil pH was measured using a HANA soil pH meter. Canopy cover was visually assessed, and each site was categorized as having open canopy (<20% canopy cover), moderate canopy (20% to 40% canopy cover), or dense canopy (>40% canopy cover).

Data analysis

The analyses for all locations were based on the total number of terrestrial gastropods (live snails and shells) encountered over one year. Species-based rarefaction curves, Chaos 2, and Jackknife 2 estimators were calculated for each location using EstimateS (version 9.1.0) [19,20]. The statistical significance of the comparisons was assessed through one-way ANOVA at a 95% confidence level, employing Tukey's comparison.

The relationship between species composition and environmental variables was examined using canonical correspondence analysis (CCA) via CANOCO software (version 5.0; [21]). Pearson's correlation and generalized linear regression models (GLM) were also applied using the vegan package in R, maintaining a 95% significant level [22]. The relative importance of the various environmental variables in explaining variations in species composition was determined through forwarding selection and sequential global permutation tests ($P<0.05$ for inclusions; 499 permutations) for CCA. GLM analysis incorporated measures of local and estimated species richness and abundance with environmental variables to account for spatial correlation. Three main models, the environmental, geometric constraint, and abundance, and a combined model with all factors were constructed to assess spatial correlation. The environmental model exclusively considered site characteristics related to the environment as predictors, while the terrestrial gastropod abundance model treated the abundance of terrestrial gastropods as a predictor for species richness. These models were then compared with the best-fit model, combining predictors from all three models selected based on the variance explained (R^2) and fit (utilizing the Akaike information criterion (AIC)). This comparison aimed to elucidate the two measures of species richness.

The study employed the generalized linear mixed-effect model (GLMM) with the vegan package to investigate the impact of environmental factors on the composition of terrestrial gastropod communities at the site level. In this model, fixed factors included atmospheric temperature, elevation, soil pH, relative humidity, daily rainfall, canopy cover, and microhabitats, and sampling locations were treated as random factors.

For GLMM

$$y = \beta_O + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n + \Upsilon_2 z_2 + \ldots + \Upsilon_n z_n + \varepsilon$$

where y = species abundance or species richness, β_O = intercept, β_n = coefficient for different random factors, x = random factors (sampling location), γ = coefficient for different fixed factors, z = fixed factors (environmental variables) and ε = error factor.

Preparation of distribution maps

Distribution maps for the terrestrial gastropods in tropical montane rainforest habitats were prepared using the inverse distance weighted (IDW) interpolation method in ARC MAP 10.4.

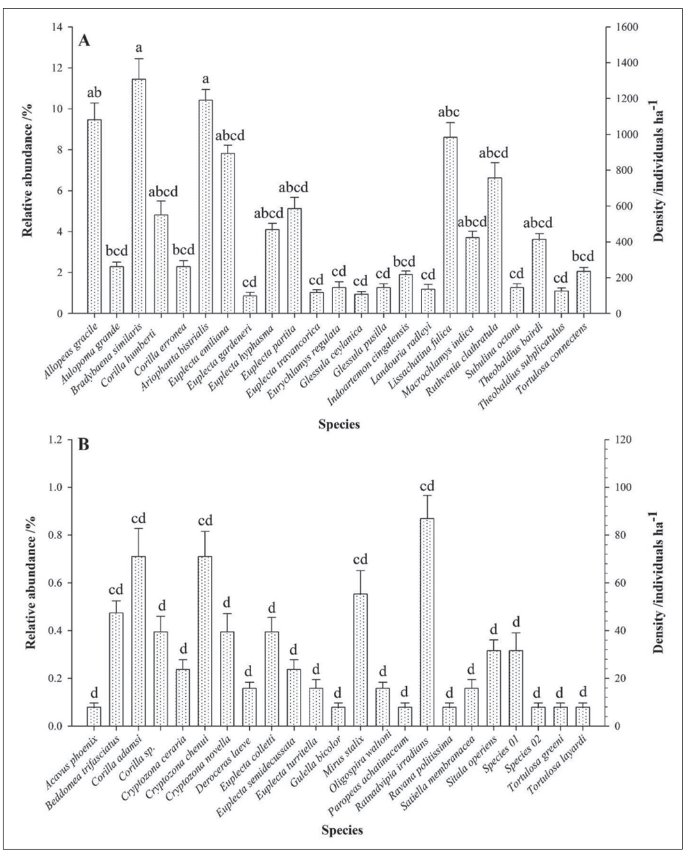

Fig. 1. Species occurrence in the tropical montane rainforest patches. Relative abundance of terrestrial gastropods (N=1267) and the density of terrestrial gastropods for a one-year period from July 2018 to July 2019. **A** – highly abundant species; **B** – least abundant species. a, b, c, and d denote the significant differences among species; F=4.81, P<0.05.

RESULTS

Diversity of terrestrial gastropods in montane rainforest fragments

Over the one-year sampling period in the Nuwara Eliya district, a total of 1,267 terrestrial gastropods (including live and dead specimens) representing 27 genera and 46 species (Supplementary Table S1, Supplementary Figs. S2 and S3) were recorded. Among these 46 species, two micro snail species were not identified due to a lack of published literature and a limited number of individuals. Within the recorded species, 70% were endemic, 9% were non-endemic native species, and 17% were exotics. Notably, the exotic species comprised one slug species (*Deroceras laeve*) and five snail species (*Allopeas gracile*, *Bradybaena similaris*, *Lissachatina fulica*, *Paropeas achatinaceum,* and *Subulina octona*), all known agricultural pests, along with two unconfirmed pest snails (*Glessula pusilla* and *Gulella bicolor*). The study identified five endemic genera in Sri Lanka: *Acavus*, *Aulopoma*, *Oligospira*, *Ratnadvipia,* and *Ravana* in these tropical montane rainforests. Two semi-slug species endemic to Sri Lanka (*Ratnadvipia irradians* and *Satiella membranacea*) were also recorded (Supplementary Table S1). As per the National Red List 2012 of Sri Lanka [1], 61% of the recorded mollusks fell under threatened categories (EN, VU, and CR). These gastropods, belonging to 15 families, represented the highest species richness in the Ariophantidae family, representing 37% of the 46 sampled species (Supplementary Table S1).

The rarefaction curve for sampled terrestrial gastropods in forests and forest fragments did not reach asymptote (Supplementary Fig. S4). Non-parametric estimators, Chao 2 and Jackknife 2, suggested the presence of 51 and 58 mollusk species, respectively. In this study, only *Ariophanta bistrialis* in the forest center and *Bradybaena similaris* in the forest edge had an abundance exceeding 10%. All other species, with a few exceptions, were relatively less abundant (<10%). The relative abundance of species encountered in tropical rainforests was significantly different (F=4.81, P<0.05) (Fig. 1).

Spatially, exotics, endemics, and non-endemic natives exhibited variation, with most endemics and non-endemic native species in the center and exotics at the

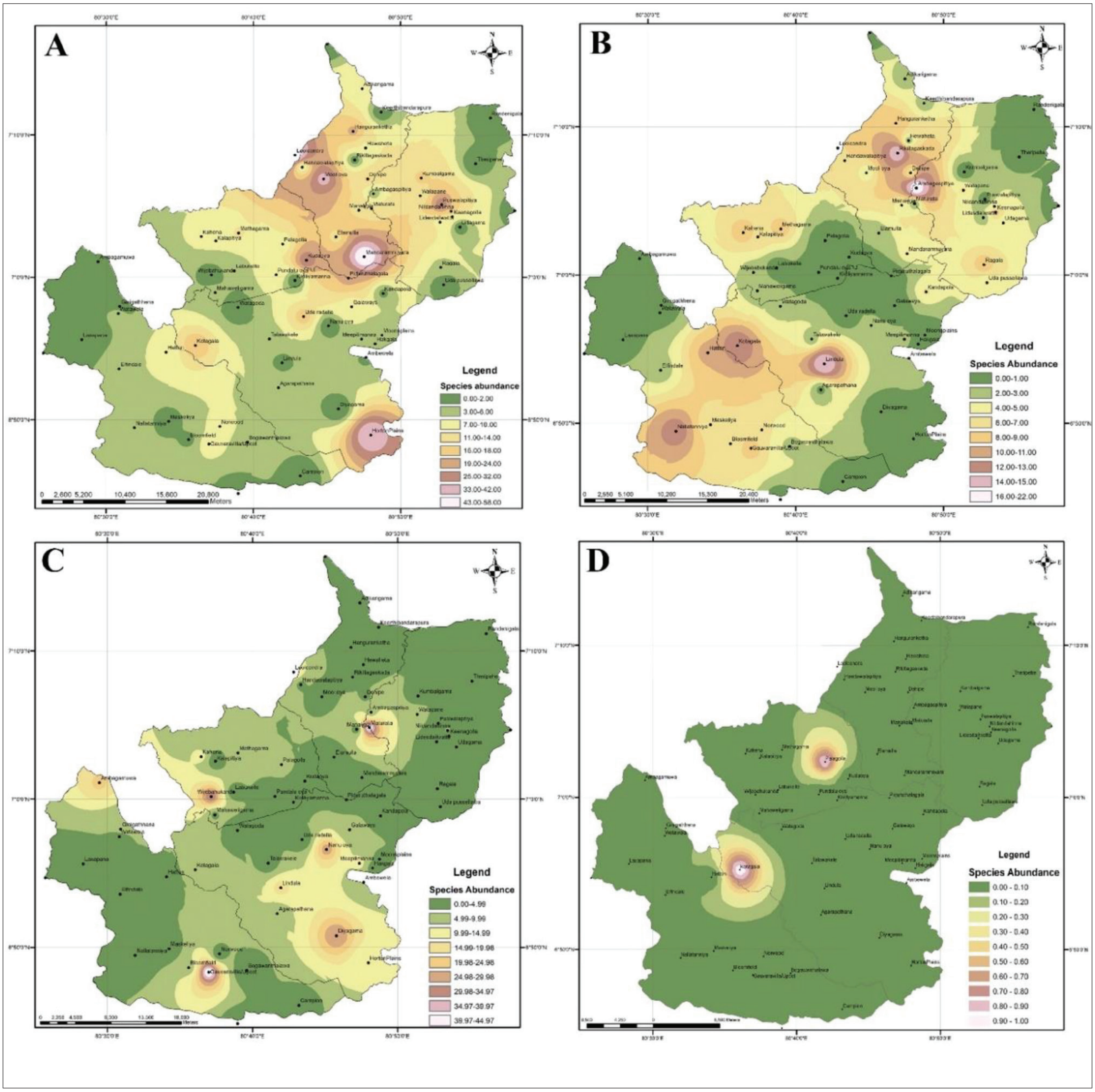

Fig. 2. Distribution of sampled terrestrial gastropods in tropical montane rainforests of Sri Lanka. **A** – distribution of endemic snails; **B** – distribution of non-endemic native snails; **C** – distribution of exotic snails; **D** – distribution of exotic slugs.

forest edge and marginal vegetation between the forest and agricultural lands. Endemics were notably abundant in national parks and restricted nature reserves in the Nuwara Eliya district (Fig. 2). However, most natives displayed clumped, narrow-range distributions in the forest fragments, with exceptions like *Ariophanta bistrialis*, *Euplecta emiliana,* and *Macrochlamys indica* showing broader distribution patterns.

Correlation between species distribution and environmental variables in tropical montane rainforests

Environmental parameters play a crucial role in species distribution and diversity. Among the measured environmental factors, elevation and daily rainfall exhibited broad ranges, and relative humidity, atmospheric

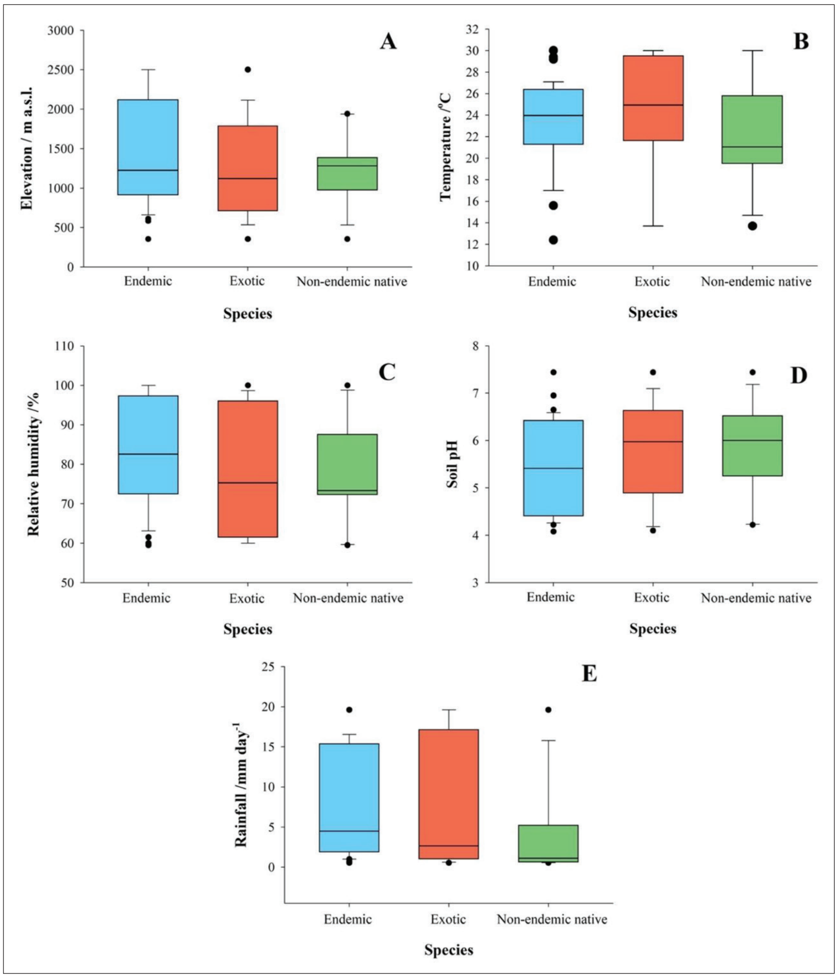

Fig. 3. Environmental factor range for endemic, exotic, and non-endemic native terrestrial gastropods in tropical montane rainforests. **A** – elevation; **B** – atmospheric temperature; **C** – relative humidity; **D** – soil pH; **E** – daily rainfall.

Table 1. Analysis of interactive-forward-selection in constrained canonical correspondence analysis (CCA).

Environmental factor	Explained %	Contribution (%)	F value	P value
Elevation	1.80	25.70	2.90	<0.05*
Daily rainfall	1.50	21.10	2.40	<0.05*
Relative humidity	1.20	16.80	1.90	<0.05*
Temperature	1.20	16.40	1.90	<0.05*
Soil pH	0.50	7.00	0.80	0.72

temperature, and soil pH showed narrow ranges. Each species in the study demonstrated distinct tolerance ranges for these environmental factors (Fig. 3 and Supplementary Fig. S5). Most endemics were recorded between 1,000 m and 2,000 m a.s.l., non-endemic natives at 1,000 m and 1,500 m a.s.l., and exotics between 700 m and 1,700 m a.s.l. (Fig. 3A). Regarding air temperature, endemics, non-endemic natives, and exotics were recorded between 21-26°C, 19-25°C and 21-30°C, respectively (Fig. 3B). The preferred relative humidity range for endemic, non-endemic natives, and exotics were 72-98%, 70-88%, and 60-97%, respectively (Fig. 3C). Endemics thrived in soils with a pH ranging from 4.5 to 6.5, non-endemic natives in soils from 5.5 to 6.7, while exotics were recorded in soils with a pH between 5.0 to 6.7 (Fig. 3D). In addition, many endemics favored a daily rainfall of 3-15 mm, non-endemic natives a 2-5 mm day^{-1}, and exotics preferred a 2-17 mm day^{-1} (Fig. 3E).

According to the constrained CCA, the distribution of recorded gastropods in the montane rainforest patches was influenced by elevation, atmospheric temperature, relative humidity, daily rainfall, soil pH, canopy cover, and microhabitat type. The eigenvalues for the first two CCA axes were 0.46 and 0.43, respectively ($P<0.05$), explaining 53.33% of the total variation in the montane rainforest gastropod community. The results suggest that elevation, atmospheric temperature, relative humidity, and daily rainfall significantly ($P<0.05$) account for the variation in species assemblage (Table 1). Along the first axis, species were primarily ordered by elevation (eigenvalue=0.90) and secondarily by soil pH (eigenvalue=-0.52). Along the second axis, species were arranged by daily rainfall (eigenvalue=-0.77) and relative humidity (eigenvalue=-0.64) (Fig. 4A). Elevation and rainfall emerged as major governing factors in the distributions of most exotic species in the natural forest system, while all five measured environmental factors influenced the distribution of most native species (Fig. 4A).

The gastropod microhabitats were classified into five main categories based on their location: in soil, on soil, in leaf litter, on stems and bark, and on leaves. In addition, the forest canopy was divided into three main categories based on the percentage of forest canopy

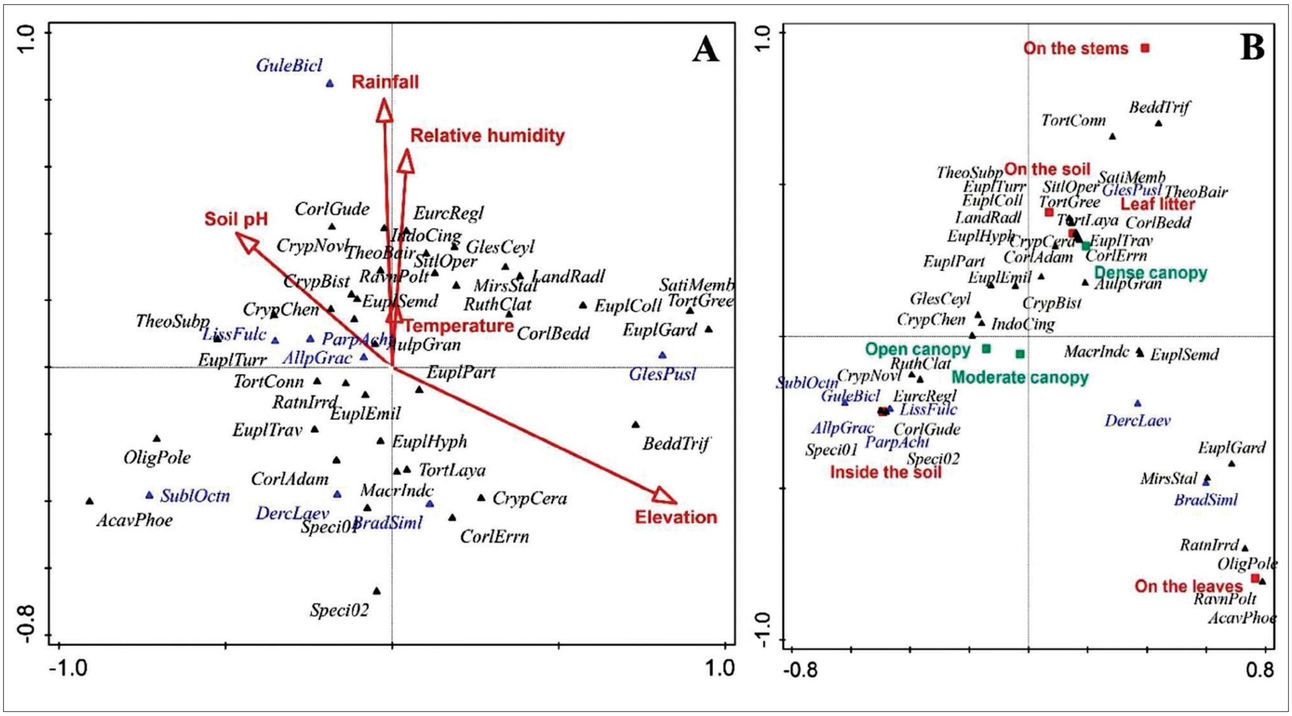

Fig. 4. Constrained canonical correspondence analysis (CCA) biplots. **A** – Species-environmental biplot; **B** – Species-habitat characteristics biplot in the tropical montane rainforests. (Note: All the abbreviations are explained in Supplementary Table S1; Blue color indicates exotic species while all others are native species).

Table 2. Regression analyses of local species richness and abundance with environmental factors.

Factor	Species richness		Species abundance	
	R^2	P value	R^2	P value
Elevation	0.02	<0.05*	0.002	0.54
Temperature	0.001	0.67	0.001	0.66
Relative humidity	0.04	<0.05*	0.005	0.36
Daily rainfall	0.01	0.20	0.01	0.15
Soil pH	0.0001	0.74	0.004	0.42
Micro habitat	0.11	<0.05*	0.06	0.06
Canopy cover	0.003	0.76	0.02	0.19
Species abundance	0.32	<0.05*	-	-

cover: open canopy (<20% cover), moderate canopy (20% to 40% cover), and dense canopy (>40% cover). The species habitat character biplot identified four main groups: in soil, on leaves, on stems, and litter dwelling/on soil. Exotic species predominantly occupied in-soil and leaf microhabitats, especially in areas with open to moderate canopy cover. Conversely, most endemic and non-endemic native species were associated with soil and leaf litter microhabitats, especially in habitats with dense canopy cover (Fig. 4B).

Regression analyses, accounting for spatial autocorrelations, revealed that species richness positively correlated with elevation (R^2=0.02, P<0.05), relative humidity (R^2=0.04, P<0.05), and microhabitat (R^2=0.11, P<0.05) (Table 2). Among the three alternative models, the abundance model explained a greater proportion of the total variation (R^2=0.32) in local species richness compared to the environmental and geometric constraint models, which explained only 9% and 11%, respectively. The best-fit model, encompassing elevation (F=6.60, P<0.05), relative humidity (F=10.55, P<0.05), microhabitat (F=8.73, P<0.05), and abundance (F=58.29, P<0.05), demonstrated the highest explanatory power (R^2=0.43) for the tropical montane rainforest terrestrial gastropod community.

Environmental models, incorporating both fixed and random effects to account for sampling locations, indicated negligible impact of location on species richness (AIC=477.88). However, species abundance was affected by the combination of elevation, soil pH, rainfall, microhabitat, canopy cover, and the sampling location (AIC=1363.0) (Table 3).

Table 3. Comparison of the generalized linear mixed models (GLMM) based on the combined effects of fixed factors (environmental variables) and random factors (sampling locations) on species abundance and richness.

Model	AIC value	P value
Richness ~ Elevation + Rainfall + Relative humidity + Temperature + soil pH + [Site]	483.70	0.99
**Richness ~ Elevation + Relative humidity + Rainfall + Micro-habitat	477.88	
Abundance ~ Elevation + Rainfall + Relative humidity + Temperature + soil pH + [Site]	1364.50	0.28
Abundance ~ Elevation + Rainfall + Soil pH + Canopy cover + Micro-habitat + [Site]	1363.00	

*Best fitted model was selected using maximum likelihood method (AIC values), **Site effect is zero

DISCUSSION

Terrestrial gastropods in tropical montane rainforests are predominantly comprised of endemic and non-endemic native species, with exotic species being rare in natural forest environments. Conversely, semi-natural forest habitats and cultivated areas such as home gardens and agricultural fields, where human activities have modified the floral and faunal composition, host a relatively small number of native gastropods while exhibiting greater diversity and abundance of exotic species [9,23]. Despite growing interest in the ecological aspects of terrestrial gastropods in Sri Lanka, their spatial and temporal distribution patterns and population dynamics remain poorly understood [5,8,23].

The present survey identified species primarily belonging to the families Ariophantidae (represented by five genera), Corillidae (represented by one genus), and Cyclophoridae (represented by two genera). Similar studies conducted in tropical rainforests, including the Knuckles Forest Reserve, Gannoruwa forest, and Sinharaja forest in Sri Lanka, also highlight the dominance of Ariophantidae members, although species abundance and composition vary across different sites [4,8,23]. Notably, the dominance of the families Ariophantidae and Cyclophoridae characterizes most rainforests in the tropics. In the subtropics, the dominant families shift to Vertiginidae in the Northern Hemisphere and Streptaxidae and Subulinidae in the Southern Hemisphere [24].

Similar to other tropical rainforests in Sri Lanka, we observed the coexistence of both exotic (*Allopeas gracile*, *Lissachatina fulica,* and *Bradybaena similaris*) and non-endemic native species assemblages (*Ariophanta bistrialis* and *Macrochlamys indica*) along the borders of agricultural lands and the edges of the tropical montane rainforests [4,10]. Most exotic species utilize marginal vegetation around cultivated lands for daytime resting. The exotic pest snails recorded in this study are found on the edges of national parks and restricted nature reserves. Forest buffer encroachment of exotic gastropods like *Lissachatina fulica, Allopeas gracile,* and *Subulina octona* poses a threat to native species in these forests [4]. These exotics can endanger native fauna and flora due to their voracious feeding behavior, especially on seedlings of native plants, algae, and decaying plant matter. Independent studies in other geographic regions have also recorded the presence of pest gastropods such as *Lissachatina fulica*, *Arion* sp., *Deroceras reticulatum*, *Deroceras laeve*, *Milax gagates,* and *Laevicaulis* sp. inside natural forests systems that pose threats to native species [25-31].

In this study, species richness did not exhibit signs of stabilization, and the non-parametric estimator yielded higher values for terrestrial gastropod richness, pointing to the need for more sampling. However, many estimators for invertebrate taxa in the tropics, including this study, often do not reach the asymptote [4,8,32-34]. It is evident that with a larger sample size, the predicted richness is slightly higher than the observed values, while under a smaller sample size, the estimator may perform poorly, yielding high values that are not correct. This can explain why the species-based rarefaction curve does not reach a plateau for the tropical montane rainforest terrestrial gastropod community in Nuwara Eliya.

Species density and abundance serve as reliable indicators of limited resource distribution. The center of a limiting resource exhibits high species accumulation, with species becoming increasingly rare towards the edges, potentially reducing the fitness of individuals at the periphery [32,33]. This is attributed to the suboptimal conditions at the resource edge, impacting dispersal, habitat selection, and reproductive ability [34]. Exotic species and a few native species like *Cryptozona* sp., *Euplecta* sp., and *Corilla* sp. [4,8,23], demonstrate a broader range of tolerance for different environmental factors. These species are thus better adapted to compete for limited resources at the edges of tropical montane rainforests and agricultural lands for growth and reproduction.

Elevation, relative humidity, and microhabitats play pivotal roles in the distribution of terrestrial gastropods in tropical rainforests [4,10]. In contrast, several other studies suggest that longitude, latitude, canopy density, and canopy height also significantly influence terrestrial gastropod distribution and diversity in Sri Lanka's tropical rainforests [4,8,10]. There is a weak correlation between soil pH and species composition in tropical montane rainforests. Other studies have stated that soil pH is a crucial factor affecting terrestrial gastropod communities in both tropical and temperate regions [35]. Soil pH is an ultimate indicator of soil calcium levels, with basic pH indicating calcium-rich soil essential for snail shell construction and growth. Despite its traditional consideration as a limiting factor for terrestrial gastropod diversity and distribution [35,36], some scientists question this relationship, either not finding a direct correlation or identifying other factors as more significant [25,37].

According to the present study, microhabitat type significantly affects the distribution of terrestrial gastropods in montane rainforests. While a few studies indicate that the type of habitat, whether forest or home garden, can explain significant variations in terrestrial gastropod composition [4,10], the present study found that in montane rainforests, factors such as leaf litter, the number of dead trees, fern and grass cover, essentially the type of microhabitat contribute to species distribution. Most exotics were found primarily in the soil and on leaves or on ground vegetation, especially in areas with an open to moderate canopy cover. In contrast, most endemic and non-endemic native species were on soil and leaf litter microhabitats, showing a preference for habitats with a dense canopy cover. Overall, terrestrial gastropods thrive best in habitats with a permanent vegetation cover and consistently moist soil to prevent desiccation. Hawkins et al. [38] demonstrated that almost 90% of snails occur within 5 cm of the soil surface. Further, other studies indicate that terrestrial gastropods' abundance, diversity, and composition often positively correlate with litter depth [39,40]. The architecture of soil litter and the underlying soil can strongly impact terrestrial gastropod community structure [41]. Similar studies in the tropics and temperate regions also highlight the significance of herbaceous layer coverage, dead wood, and canopy cover in affecting terrestrial gastropod distribution [42-46].

The combined influence of environmental and biotic factors on species richness and composition is crucial for predicting terrestrial gastropod composition and distribution. While some researchers argue that species distribution models based solely on statistical analysis are insufficient, incorporating ecological models and theories enhances predictive accuracy. Probability-based models, conveying the likelihood of species presence in each area, are preferred over simple presence-absence conclusions. These models offer confidence estimates and facilitate the creation of spatial maps, revealing the likelihood of species occurrence. Comparing similar areas based on these maps establishes a relationship between habitat suitability and species presence [46].

Tropical montane rainforests covering just 25%-30% of the Nuwara Eliya district are vital in preserving endemic and native gastropod species. The abundance of recorded endemic and non-endemic native gastropods underscores the need to protect the remaining forests with long-term conservation. Deforestation for tea and vegetable cultivation, forest fragmentation, and the invasion of exotic pest gastropods pose serious threats to the native gastropod community. The present study indicates that endemic and non-endemic native species have narrower tolerance ranges for various environmental variables and are more sensitive to changes [46]. As in other tropical regions, forest cover loss in Sri Lanka has been substantial [4]. Given that many endemic and native species are restricted to smaller areas within natural forests, particularly under dense canopy cover, any habitat alterations will negatively impact these species, while exotic species thrive in changed environments. Therefore, preserving natural forest cover and proactive monitoring and conservation measures are essential for safeguarding terrestrial gastropod diversity in these forest habitats.

CONCLUSIONS

Deforestation, climate change, and invasive species threaten native terrestrial gastropod diversity in Sri Lanka. The Nuwara Eliya district, harboring a substantial portion of the island's dense tropical montane rainforest cover and rich in biodiversity, is particularly vulnerable. Native gastropods, with narrower environmental tolerances, inhabit specific areas within these forests. Extensive agricultural use, mainly for upcountry vegetable cultivation, exposes natural forests to invasion by exotic gastropod pests. This study identifies species like *Lissachatina fulica* and *Bradybaena similaris*, common in agricultural lands, encroaching on forest edges due to their broader environmental tolerance. Climate shifts, deforestation, and forest fragmentation may further facilitate the intrusion of these pests into forest habitats. If established in natural environments, these exotic species could pose additional threats to native terrestrial gastropods and plant species. Thus, effective management strategies focusing on landscape planning and habitat preservation are required for conserving native gastropod diversity in tropical montane rainforests.

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Conflict of interest disclosure: The authors declare that they do not have any conflict of interest.

Data availability: Voucher specimens are available at the Department of Zoology, Faculty of Science, University of Peradeniya, Sri Lanka. Data underlying the reported findings have been provided as a raw dataset, which is available here: https://www.serbiosoc.org.rs/NewUploads/Uploads/Thilakarathne%20et%20al_Dataset.xlsx

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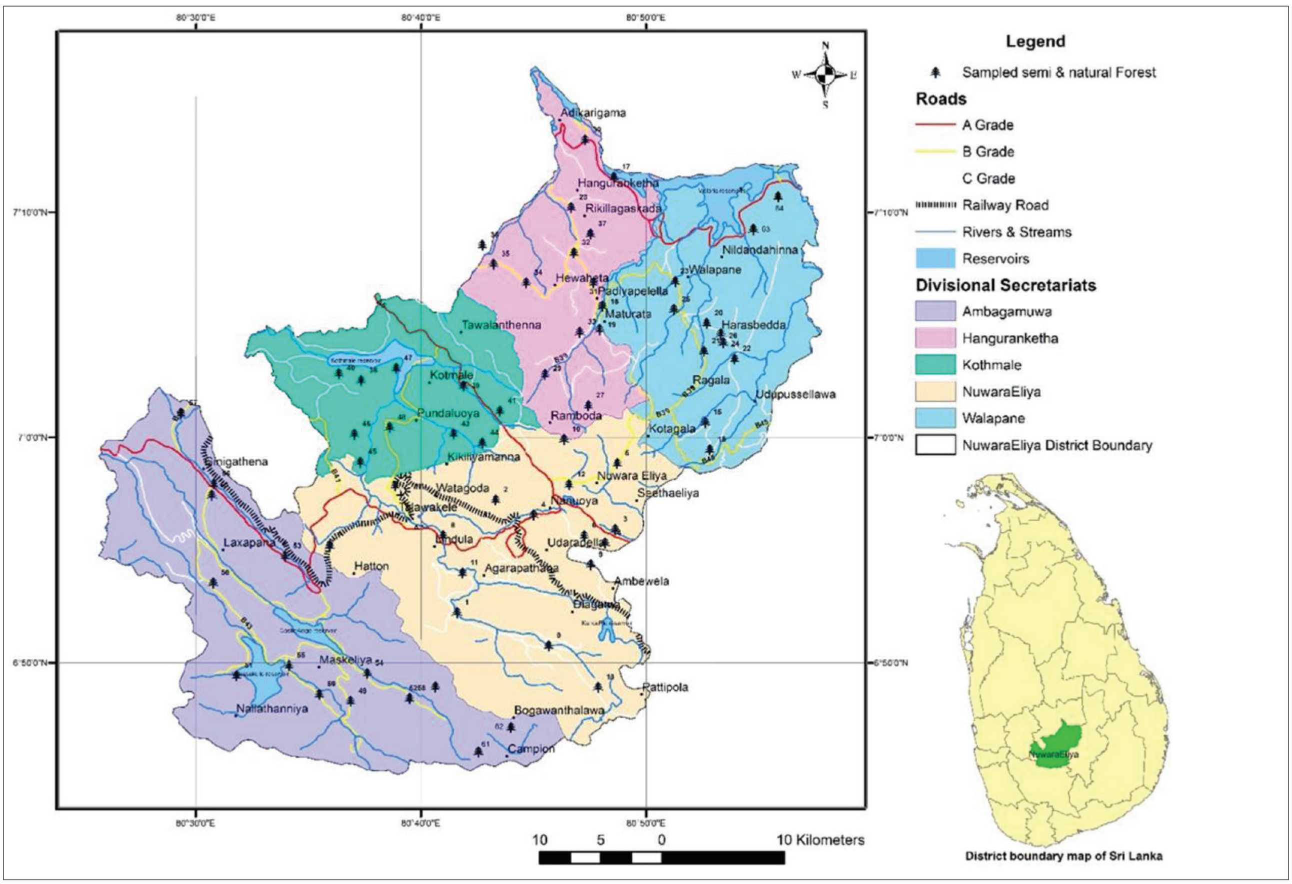
SUPPLEMENTARY MATERIAL

Supplementary Table S1. Terrestrial gastropod species recorded from tropical montane rainforests in the Nuwara Eliya district during the survey from July 2018 to July 2019.

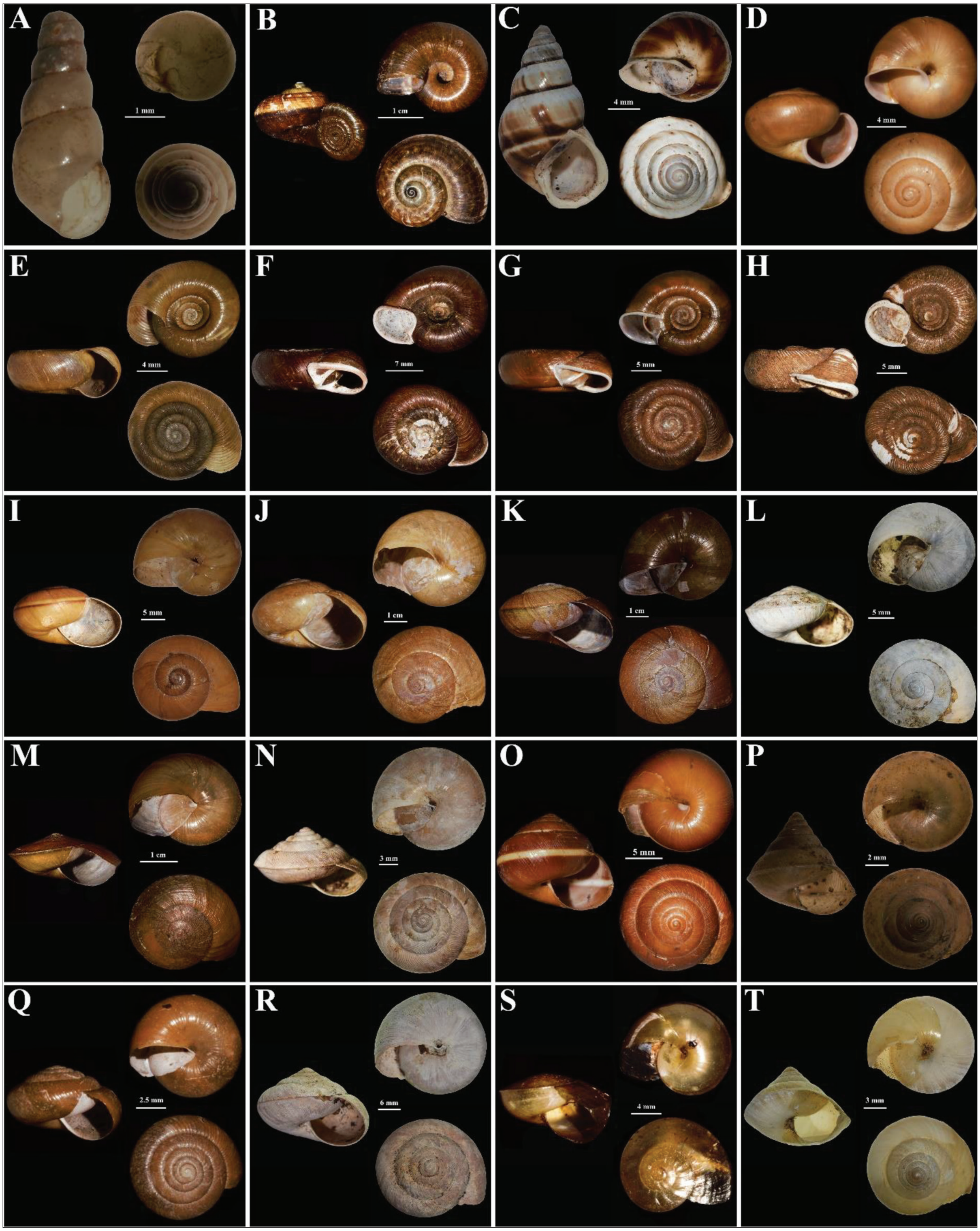
Family	Species	Species code	NCS	Forest type		
				IZF	LMF	UMF
Acavidae	*Acavus phoenix*[E]	AcavPhoe	NT	+	-	-
Acavidae	*Oligospira waltoni*[E]	OligPole	EN	+	+	-
Achatinidae	*Lissachatina fulica*[EX]	LissFulc	NE	+	+	+
Agriolimacidae	*Deroceras laeve*[EX]	DeroLaev	NE	-	+	-
Ariophantidae	*Ariophanta bistrialis*	CrypBist	LC	+	+	+
Ariophantidae	*Cryptozona ceraria*[E]	CrypCera	VU	-	+	+
Ariophantidae	*Cryptozona chenui*[E]	CrypChen	VU	-	+	-
Ariophantidae	*Cryptozona novella*[E]	CrptNovl	EN	+	+	-
Ariophantidae	*Euplecta colletti*[E]	EuplColl	EN	-	+	+
Ariophantidae	*Euplecta emiliana*[E]	EuplEmil	EN	+	+	+
Ariophantidae	*Euplecta gardeneri*[E]	EuplGard	VU	-	-	+
Ariophantidae	*Euplecta hyphasma*[E]	EuplHyph	VU	+	+	+
Ariophantidae	*Euplecta partita*[E]	EuplPart	NT	+	+	+
Ariophantidae	*Euplecta semidecussata*[E]	EuplSemd	VU	-	+	-
Ariophantidae	*Euplecta travancorica*	EuplTrav	NT	-	+	-
Ariophantidae	*Euplecta turritella*	EuplTurr	DD	-	+	-
Ariophantidae	*Macrochlamys indica*	MacrIndc	DD	+	+	+
Ariophantidae	*Ratnadvipia irradians*[E]	RatnIrrd	VU	-	+	+
Ariophantidae	*Ravana politissima*[E]	RavaPolt	EN	-	+	-
Ariophantidae	*Satiella membranacea*[E]	SatiMemb	CR	-	-	+
Ariophantidae	*Sitala operiens*[E]	SitlOper	DD	-	+	-
Bradybaenidae	*Bradybaena similaris*[EX]	BradSiml	NE	-	+	+
Buliminidae	*Mirus stalix*[E]	MiruStal	EN	-	+	+
Camaenidae	*Landouria radleyi*[E]	LandRadl	EN	-	+	+
Camaenidae	*Beddomea trifasciatus*[E]	BeddTrif	VU	-	-	+
Charopidae	*Ruthvenia clathratula*[E]	RuthClat	EN	+	+	+
Corillidae	*Corilla adamsi*[E]	CorlAdam	EN	-	+	-
Corillidae	*Corilla humberti*[E]	CorlBedd	EN	-	+	+
Corillidae	*Corilla erronea*[E]	CorlErrn	EN	-	+	+
Corillidae	*Corilla sp.*[E]	CorlGude	CR	-	+	-
Cyclophoroidae	*Aulopoma grande*[E]	AulpGran	VU	+	+	+
Cyclophoroidae	*Theobaldius bairdi*[E]	TheoBair	VU	+	+	+
Cyclophoroidae	*Theobaldius subplicatulus*[E]	TheoSubp	VU	+	+	-
Euconulidae	*Eurychlamys regulata*[E]	EurcRegl	EN	-	+	-
Glessulidae	*Glessula ceylanica*[E]	GlesCeyl	EN	-	+	-
Glessulidae	*Glessula pusilla*[EX]	GlesPusl	NE	-	+	+

Pupinidae	*Tortulosa layardi*[E]	TortLaya	EN	-	-	+
Pupinidae	*Tortulosa connectens*[E]	TortConn	DD	+	+	+
Pupinidae	*Tortulosa greeni*[E]	TortGree	EN	-	-	+
Streptaxidae	*Gulella bicolor*[EX]	GuleBicl	NE	+	-	-
Streptaxidae	*Indoartemon cingalensis*[E]	IndoCing	CR	+	+	+
Subulinidae	*Allopeas gracile*[EX]	AllpGrac	NE	+	+	+
Subulinidae	*Paropeas achatinaceum*[EX]	ParpAcht	NE	+	-	-
Subulinidae	*Subulina octona*[EX]	SublOctn	NE	+	+	-
Unknown	*Species 01*	Speci01	-	-	+	-
Unknown	*Species 02*	Speci02	-	-	+	-
	Species richness			19	38	27
	Family richness			8	16	13
	Species abundance			211	819	237
	Density/individuals ha^{-1}			2110	8190	2370

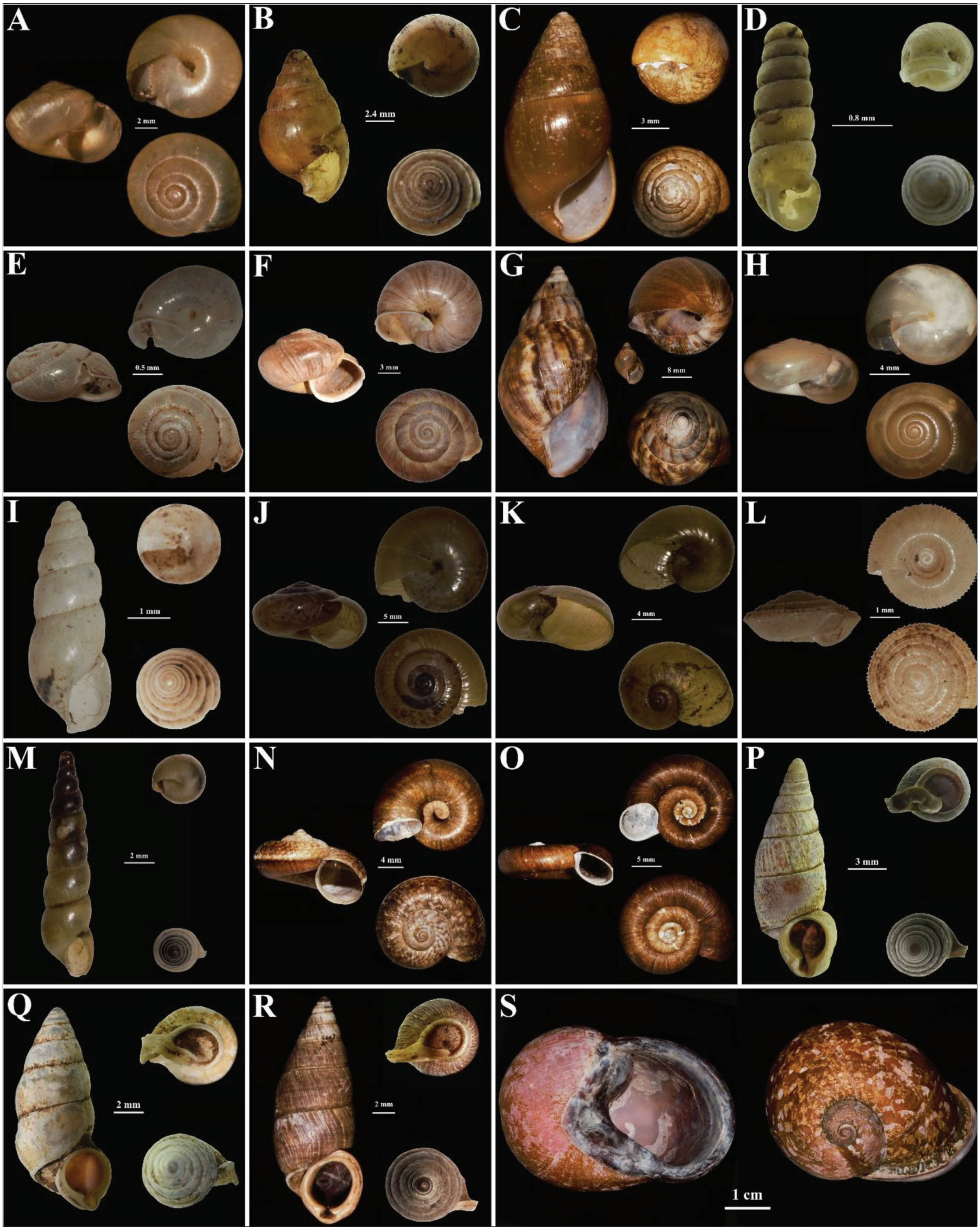
[E] Endemic species, [EX] exotic species, and others shown are non–endemic native species; NCS – national conservation status (based on the National Red List of 2012 of Sri Lanka, MOE (2012); DD – data deficient, NE – not evaluated, LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered, CR – critically endangered; [+] present, [-]absent; IZF – intermediate zone forests, LMF – lower montane rainforests, UMF – upper montane rainforests.



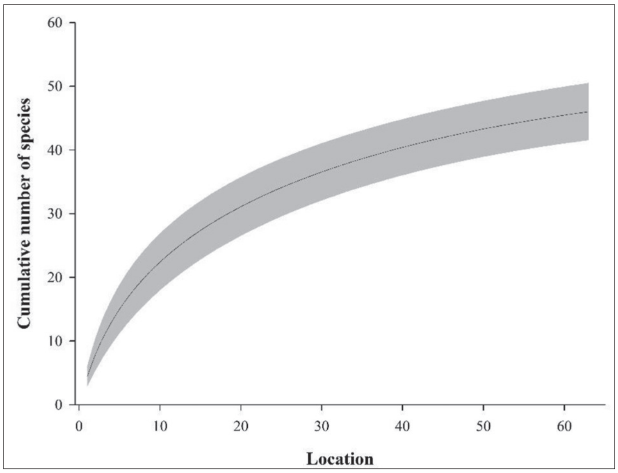
Supplementary Fig. S1. Terrestrial gastropods surveyed sites in tropical montane rainforest fragments in the Nuwara Eliya district, Sri Lanka.



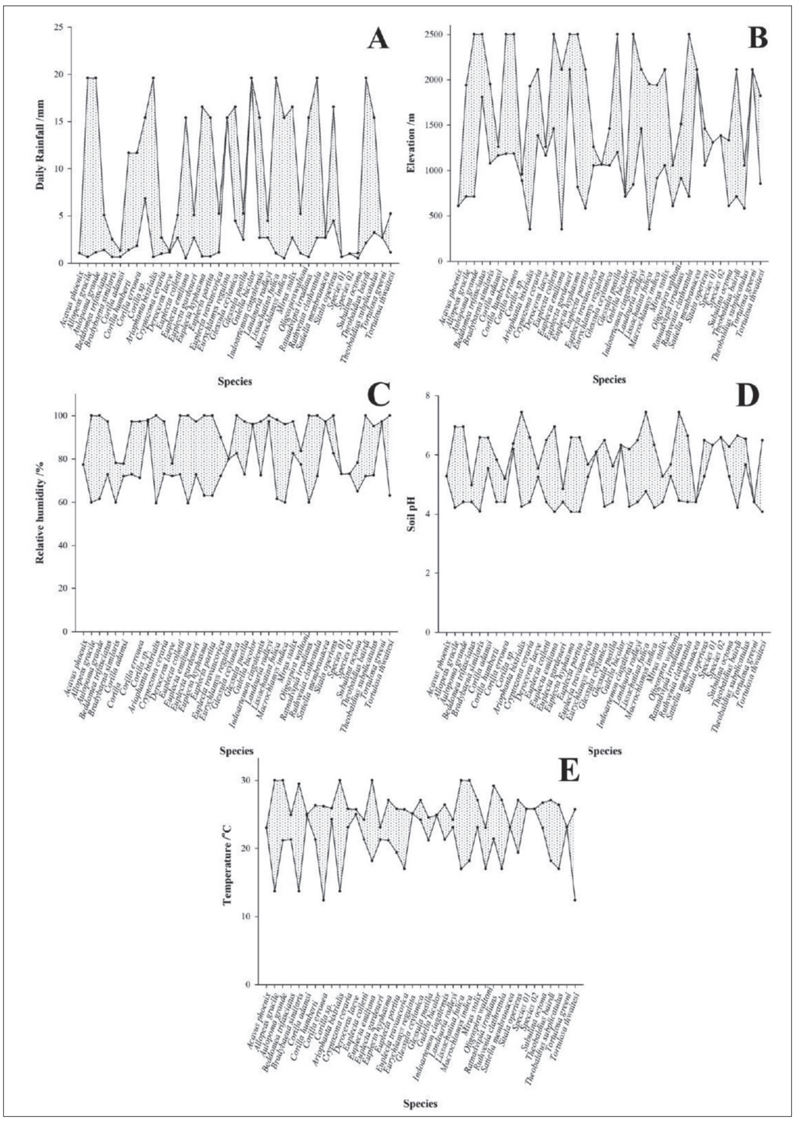
Supplementary Fig. S2. Terrestrial gastropods encountered from tropical montane rainforests during the study period from 2018 to 2019. **A** – *Allopeas gracile*, **B** – *Aulopoma grande*, **C** – *Beddomea trifasciatus*, **D** – *Bradybaena similaris*, **E** – *Corilla adamsi*, **F** – *Corilla humberti*, **G** – *Corilla erronea*, **H** – *Corilla sp.*, **I** – *Ariophanta bistrialis*, **J** – *Cryptozona ceraria*, **K** – *Cryptozona chenui*, **L** – *Cryptozona novella*, **M** – *Euplecta colletti*, **N** – *Euplecta emiliana*, **O** – *Euplecta gardeneri*, **P** – *Euplecta hyphasma*, **Q** – *Euplecta partita*, **R** – *Euplecta semidecussata*, **S** – *Euplecta travancorica*, **T** – *Euplecta turritella*.



Supplementary Fig. S3. Terrestrial gastropods encountered from tropical montane rainforests during the study period from 2018 to 2019. **A** – *Eurychlamys regulata*, **B** – *Glessula ceylanica*, **C** – *Glessula pusilla*, **D** – *Gulella bicolor*, **E** – *Indoartemon cingalensis*, **F** – *L andouria radleyi*, **G** – *Lissachatina fulica*, **H** – *Macrochlamys* indica, **I** – *Paropeas achatinaceum*, **J** – *Ratnadvipia irradians*, **K** – *Ravana politissima*, **L** – *Ruthvenia clathratula*, **M** – *Subulina octona*, **N** – *Theobaldius bairdi*, **O** – *Theobaldius subplicatulus*, **P** – *Tortulosa connectens*, **Q** – *Tortulosa greeni*, **R** – *Tortulosa layardi*, **S** – *Oligospira waltoni*.



Supplementary Fig. S4. Species accumulation curves for tropical montane rainforests, Sri Lanka. Cumulative species richness (solid lines) was calculated from a total of 60 forest patches.



Supplementary Fig. S5. Environmental factor tolerance of encountered terrestrial gastropods from tropical montane rainforests, Sri Lanka. **A** – daily rainfall; **B** – elevation; **C** – relative humidity; **D** – soil pH; **E** – temperature.